Dissociable Neural Systems Supporting Knowledge about Human Character and Appearance in Ourselves and Others

Joseph M. Moran, Su Mei Lee, and John D. E. Gabrieli

Abstract

■ Functional neuroimaging has identified a neural system comprising posterior cingulate (pCC) and medial prefrontal (mPFC) cortices that appears to mediate self-referential thought. It is unclear whether the two components of this system mediate similar or different psychological processes, and how specific this system is for self relative to others. In an fMRI study, we compared brain responses for evaluation of character (e.g., *honest*) versus appearance (e.g., *svelte*) for oneself, one's mother (a close other), and President Bush (a distant other). There was a double dissociation between dorsal mPFC, which was more engaged for character than appearance judgments, and pCC, which was more engaged for appearance than character judgments. A ventral region of mPFC was engaged for judgments involving one's own character and appearance, and one's mother's character, but not her appearance. A follow-up behavioral study indicated that participants rate their own character and appearance, and their mother's character, but not her appearance, as important in their self-concept. This suggests that ventral mPFC activation reflects its role in processing information relevant to the self, but not limited to the self. Thus, specific neural systems mediate specific aspects of thinking about character and appearance in oneself and in others. ■

INTRODUCTION

"Who am I?" is a fundamental question in our inner mental lives. Given the broad philosophical nature of such inquiry, it is perhaps surprising that there is a well-identified neural system that is engaged when people decide who they are by judging to what extent trait adjectives (e.g., *kind*, *bold*, *clever*) describe their characters. When people judge their own characters during functional neuroimaging, they engage medial prefrontal (mPFC) and posterior cingulate/precuneal (pCC) cortices (collectively referred to as cortical midline structures [CMS], Northoff & Bermpohl, 2004; Moran, Heatherton, & Kelley, 2009; Pfeifer, Lieberman, & Dapretto, 2007; Heatherton et al., 2006; Johnson et al., 2006; Moran, Macrae, Heatherton, Wyland, & Kelley, 2006; Saxe, Moran, Scholz, & Gabrieli, 2006; Ochsner et al., 2005; Macrae, Moran, Heatherton, Banfield, & Kelley, 2004; Kelley et al., 2002; Craik et al., 1999). Although there is variability across studies, typically mPFC and pCC activate in common and appear to comprise two major components of an interactive network. Northoff and Bermpohl (2004) further subdivide mPFC into dorsal and ventral aspects, suggesting that dorsal mPFC is involved in evaluation of stimuli during self-reflection, and that ventral mPFC is involved in representation of stimuli as self-relevant. Here, we asked how this neural system engaged by self-reflection upon one's character is differentially engaged by (1) reflection about character traits versus appearance traits, and (2) reflection about oneself versus either a close, personally known other person (one's mother) or a distant, personally unknown other person (President Bush).

Multiple neuroimaging studies have examined the neural correlates of self-reflection by asking people to judge whether a trait adjective (e.g., *polite*) describes their character. It is uncertain whether activations of mPFC and pCC reflect self-reflection in general, or self-reflection about character traits in particular. Here we compared responses during self-reflection about character (psychological traits) versus physical appearance (physical traits). If activations in mPFC and pCC are similar for both judgments, then those activations may reflect a broad kind of self-reflection. If activations in mPFC and pCC are greater for character than appearance judgments, then those activations may primarily reflect evaluation of psychological character traits. Alternatively, mPFC and pCC could exhibit dissociable activations, such that one region is more involved in self-reflection about character, and another region is more involved in self-reflection about appearance. Any of these findings would clarify the brain organization of self-knowledge and make a suggestion about the mental organization of self-knowledge.

Prior neuroimaging findings support a hypothesis that dorsal mPFC may be more engaged in reflection about a person's character and pCC may be more engaged in reflection about a person's appearance. Activation in dorsal mPFC has been observed when people attend to

Massachusetts Institute of Technology

current internal feelings (e.g., Gusnard, Akbudak, Shulman, & Raichle, 2001; Lane, Fink, Chau, & Dolan, 1997), which, like character, are not perceptually apparent. Conversely, activation in pCC has been observed when people attend to appearances of objects, people, or themselves, such as imagery of previously perceived objects (Kensinger & Schacter, 2006), viewing perceptually familiar faces (Gobbini & Haxby, 2006) and self-centered mental imagery (Cavanna & Trimble, 2006). Further, a dissociation between mPFC and pCC activation was found such that there was greater mPFC activation when people considered their own hopes and aspirations, and greater pCC/precuneus activation when people considered their duties and obligations (Johnson et al., 2006). This dissociation may reflect a greater emphasis on self-perception of character in relation to desires versus a greater emphasis on self-perception of external or environmental factors in relation to duties and obligations.

Other brain regions might also be dissociable in regards to analysis of character versus appearance. Areas of the ventral (e.g., fusiform gyrus) and dorsal (e.g., superior parietal lobule) visual stream are involved in mental imagery of previously presented visual objects (ventral: Wheeler, Petersen, & Buckner, 2000; Miyashita, 1993), recall of learned visual objects (dorsal: Roland & Gulyas, 1995), and may be more involved when people reflect on their own and others' appearances.

Some neuroimaging studies have examined participants thinking about both psychological and physical characteristics of people (e.g., Lombardo et al., 2010; Kjaer, Nowak, & Lou, 2002). In one study, participants reflected on their own and an unfamiliar other person's psychological and physical characteristics (Kjaer et al., 2002). Crucially, no comparison was made between psychological and physical characteristics, but rather only between the self and an unfamiliar other person. In another study, physical characteristics were used as a control condition to investigate differences in judgments about traits in oneself versus a highly familiar (close) other person, but analyses focused only on trait judgments (Lombardo et al., 2010). The critical advance here is to pit character and appearance information against one another factorially so as to determine whether there might exist differentiable contributions of the anterior and posterior CMS to differing aspects of self-knowledge for character and appearance.

Another goal of this study was to investigate the relation between self-knowledge and knowledge about other people. There is behavioral evidence that self-concept also may include close others (Aron, Aron, Tudor, & Nelson, 1991); for example, there are more source confusions between oneself and a relationship partner than between oneself and a familiar, but less well known other (Mashek, Aron, & Boncimino, 2003). Although there is a neuroimaging consensus on engagement of mPFC and pCC during self-reflection about character, there has been conflicting evidence as to the specificity of this engagement in regards to reflection about oneself. Some have found that mPFC and pCC are engaged during self-reflection relative to reflection about other people in regards to traits (e.g., Pfeifer et al., 2007; Heatherton et al., 2006; Lou et al., 2004; Kelley et al., 2002; Kjaer et al., 2002). Others have found that mPFC and pCC are similarly engaged during self-reflection and reflection about other people with regard to traits (e.g., Lombardo et al., 2010; Jenkins, Macrae, & Mitchell, 2008; Mitchell, Macrae, & Banaji, 2006; Ochsner et al., 2005; Schmitz, Kawahara-Baccus, & Johnson, 2004). Further, ventral mPFC activation for judgments about other people may be related to how similar the other people are to oneself, whereas dorsal mPFC activation may be insensitive to similarity of another person (Jenkins et al., 2008; Mitchell et al., 2006). The behavioral and imaging findings converge to support the hypothesis that ventral mPFC is engaged when reflecting upon oneself and a close other (one's mother), but not a personally unknown other (President Bush). However, there is no evidence about whether these differences about self and other interact with differences about knowledge of character and appearance.

We performed two experiments to answer these questions. Participants in Experiment 1 (neuroimaging) made judgments about both character and appearance traits of themselves (self-reflection), their mother (a close other), and President Bush (a distant other). Participants in Experiment 2 (behavioral) rated the importance of the character and appearance of themselves, their mother, and President Bush to their own conception of themselves.

METHODS

Experiment 1

Participants

Twenty-one participants between the ages of 19 and 41 years (8 men, mean age = 24.3 years) were recruited from the local MIT community. Participants reported no significant abnormal neurological history, had normal or corrected-to-normal vision, and were strongly right-handed as measured by the Edinburgh Handedness Inventory (Oldfield, 1971). Participants were paid for their participation and gave informed consent in accordance with the guidelines set by the Committee on the Use of Humans as Experimental Participants at MIT.

Functional Imaging

Anatomical and functional whole-brain imaging was performed on a Siemens 3-T Tim Trio Scanner (Siemens Medical, Erlangen, Germany). An Apple Macbook Pro running the Psychophysics Toolbox extensions in Matlab (Pelli, 1997; The Mathworks, Natick, MA) was used to present stimuli to the participants. Anatomical images were acquired by using a high-resolution MP-RAGE sequence (128 sagittal slices, TE = 6 msec, TR = 25 msec, flip angle = 25°, $1 \times 1 \times 1$ mm voxels). Functional images were collected in three functional runs of 90 time points each, using a gradient spin-echo, echo-planar sequence sensitive to BOLD contrast (T2*) (33 axial slices per whole-brain volume, 3 mm in-plane resolution, 3 mm thickness, 0.6 mm skip, TR = 2000 msec, TE = 35 msec, flip angle = 90°).

Behavioral Task

In a pilot study, participants (n = 20) viewed trait adjectives taken from a list previously normed for valence (Anderson, 1968) and a list of physical characteristics drawn up by the experimenters. Participants' task was to determine how "externally observable" they thought the trait or characteristic described by each word was, and to indicate their response via a button press (9-point scale, 1 = "not at all observable"). From this pilot study, we identified two sets of words [appearance: mean observability (*SEM*) = 7.89 (0.06); character: mean observability (*SEM*) = 4.29 (0.07)] for use in the main experiment. Words that were most observable included "beard" (mean observability rating = 8.85), "clean-shaven" (8.7), and "bald" (8.65). Words judged as least observable by the pilot participants included "lucky" (3.05), "ethical" (3.15), and "subtle" (3.2). Importantly, no words included in either set overlapped in terms of observability rating: appearance least observable word—"frumpy" (6.7), character most observable word—"kind" (5.3).

In the main experiment, participants (n = 21) judged whether 180 words (90 appearance/90 character) were descriptive (yes/no) of themselves, their mother, or then–U.S. President George Bush in an event-related design. Words were presented for 1500 msec in white print on a black background beneath a fixation cross. Above the fixation cross was a prompt (SELF, MOM, or BUSH), indicating to which person the participant should refer. Following each word, a fixation cross was presented for 500 msec, prior to the beginning of the next trial. Null events consisting of a fixation cross for 2000 msec were pseudorandomly interspersed to introduce jitter into the fMRI time series. We did not draw participants' attention to the fact that words from differing categories (character and appearance) were being used.

Data Analysis

A whole-brain repeated measures ANOVA [2 (trait: character/appearance) × 3 (person: self/mother/Bush)] was performed to identify brain regions differentially involved in either the two kinds of judgments or for the three kinds of targets. ANOVA maps were thresholded by using a false discovery rate (FDR) ($p < .05$, Genovese, Lazar, & Nichols, 2002; F thresholds are listed in Table 2). Then, ROIs identified by the ANOVA were examined to identify the nature of any main effects or interactions defined by the ANOVA. For the three brain regions consistently engaged by self-reflection, namely, ventral mPFC, dorsal mPFC, and pCC (Northoff et al., 2006 meta-analysis), we created 8-mm spheres around the peak voxels based on the main effects in our whole-brain ANOVA so that our findings would target these specific brain regions. These regions were ventral mPFC (MNI coordinates: [−6 60 9]), dorsal mPFC [9 51 21], and pCC [0 −33 45]. We examined significant effects in these regions to determine the nature of differences revealed by the ANOVA. In addition, we performed exploratory analyses of those regions at a less stringent threshold in Trait × Person ANOVA. For other significant activations derived from the whole-brain ANOVA, the activation clusters were similarly analyzed to characterize the nature of any significant main effects.

fMRI data were analyzed with SPM2 (Wellcome Department of Cognitive Neurology, London, UK) and in-house code to implement a 2 (trait: character/appearance) × 3 (person: self/mother/Bush) repeated measures voxelwise ANOVA across the whole brain. Prior to statistical analysis, data were preprocessed to remove sources of noise and artifact. Functional data were realigned within and across runs to correct for head movement, were unwarped to correct for geometric distortions, and were transformed into a standard anatomical space (3 mm isotropic voxels) based on the ICBM-152 brain template (Montreal Neurological Institute). Normalized data were then spatially smoothed (8 mm full width at half maximum) using a Gaussian kernel. Finally, using in-house artifact detection software, individual runs were analyzed (on a participant-by-participant basis) to find outlier time points. We excluded from further analysis volumes during which participant head motion exceeded 0.5 mm or 1°, and volumes in which the overall signal for that time point fell more than two standard deviations outside the mean global signal for the entire run. Outlier time points were excluded from the GLM analysis via the use of participant-specific regressors of no interest. The number of outliers excluded across person (self, mother, Bush) and trait type (character, appearance) did not differ (2 × 3 ANOVA, all Fs < 1), and moreover, the mean (*SEM*) number of outliers excluded across subjects and conditions was 1.43 (0.12).

In the first-level analysis, a GLM incorporating task effects for the six conditions of interest (self-character, self-appearance, mother-character, mother-appearance, Bush-character, Bush-appearance) and covariates of no interest (a session mean, a linear trend, six movement parameters derived from realignment corrections, and regressors to exclude outlier volumes) computed parameter estimates (β) and contrast images (containing weighted parameter estimates) for each comparison at each voxel and for each participant. Contrast images comparing each condition to the control (fixation) were then used to compute a voxelwise whole-brain ANOVA that yielded F-statistical maps for both main effects (trait and person) and the interaction. For the whole-brain analysis, we determined the direction of effects by computing second-level t-contrast images for the main effects of interest (e.g., character > appearance).

Experiment 2

Participants

Forty participants between the ages of 18 and 45 years were recruited from the local MIT community. Participants gave informed consent in accordance with the guidelines set by the Committee on the Use of Humans as Experimental Participants at MIT.

Task

Participants answered a brief paper-and-pencil questionnaire, in which they were asked a series of six questions, probing how important they thought the character and appearance of themselves, their mother, and President Bush were to their own conceptions of themselves. Participants indicated on a 5-point scale (1 = "not at all important") how important they thought each person's character and appearance were in their conception of themselves.

RESULTS

Experiment 1: Neuroimaging

Behavioral Results

A 2 (trait: character/appearance) × 3 (person: self/mother/Bush) repeated measures ANOVA revealed main effects of Trait [$F(1, 20) = 60.54, p < .0001$] and person [$F(2, 40) = 50.50, p < .001$] on reaction times, and a Trait × Person interaction [$F(2, 40) = 10.63, p < .001$] (Table 1). Reaction times were significantly longer for character versus appearance traits (main effect of Trait: character $M = 1350 \pm 34$ msec; appearance $M = 1285 \pm 37$ msec) and for Bush versus self and mother [Bush > mother: $F(1, 20) = 88.38, p < .001$; Bush > self: $F(1, 20) = 84.68, p < .001$], but did not differ reliably for self versus mother ($F < 1$) (Table 1). The interaction reflected a greater difference in reaction times for character versus appearance conditions for Bush ($M = 115$ msec) than for self ($M = 38$ msec) and mother ($M = 40$ msec) [planned comparison: $F(1, 20) = 20.22, p < .001$].

fMRI Results

Whole-brain analyses. An ANOVA of Trait (character/appearance) × Person (self/mother/Bush) revealed differential activation for dmPFC, pCC, bilateral insular cortex, and multiple parietal, frontal, and temporal regions as a function of trait. There was differential activation due to the person factor in ventral mPFC, anterior cingulate cortex, and the cuneus [Figure 1 (thresholded at $p < .001$ for display purposes) and Table 2].

Table 1. Reaction Times for All Trial Types: Mean (*SEM*)

	Self	*Mother*	*Bush*
Character	1305.15 (32)	1299.51 (39)	1444.12 (34)
Appearance	1267.24 (38)	1259.01 (37)	1329.20 (39)

ROI analyses. DORSAL MPFC: CHARACTER > APPEARANCE. This region was defined on the main effect of trait. This region showed greater activation for character than for appearance trials [planned comparison; character vs. appearance: $F(1, 20) = 15.06, p < .001$; Figure 2A]. There was no main effect of Person [$F(2, 40) = 1.30$, *ns*] and no interaction between Trait and Person ($F < 1$, *ns*).

PCC: APPEARANCE > CHARACTER; SELF > OTHERS. This region was defined on the main effect of Trait. We investigated simple effects for this factor, and found that this region showed greater activation during appearance than character trials [planned comparison; character vs. appearance: $F(1, 20) = 31.22, p < .0001$; Figure 2B]. This region also showed more activation for traits about oneself than one's mother or President Bush [main effect of person: $F(2, 40) = 6.58, p < .005$; planned comparison, self > mother and Bush: $F(1, 20) = 10.53, p < .005$]. There was no interaction between Trait and Person [$F(1, 20) < 1$, *ns*].

VENTRAL MPFC: SELF AND MOTHER > BUSH FOR CHARACTER; SELF > MOTHER AND BUSH FOR APPEARANCE. This region was defined on the main effect of person. This region showed greater activation during self than other trials [main effect of person: $F(2, 40) = 10.12, p < .001$; planned comparison, self > mother and Bush: $F(1, 20) = 24.35, p < .0001$; Figure 2C]. There was no main effect of trait [$F(1, 20) = 3.89, p > .05$]. There was a significant interaction between trait and person [$F(2, 40) = 3.29, p < .05$] such that, within appearance traits, there was greater activation for self versus others [planned comparison within appearance, self > mother and Bush: $F(1, 20) = 16.97, p < .001$]. Within character traits, there was more activation for both self and mother relative to Bush [planned comparison within character, self and mother > Bush: $F(1, 20) = 11.73, p < .002$].

Experiment 2: Behavioral

A 2 (trait: character/appearance) × 3 (person: self/mother/Bush) repeated measures ANOVA revealed that character was more important than appearance across people for one's self-concept [main effect of trait: $F(1, 39) = 47.4, p < .0001$]. Participants considered their own traits as more important for their self-concept than their mother's [main effect of person: $F(2, 78) = 81.04, p < .0001$; planned comparison, self > mother: $F(1, 39) = 48.7, p < .0001$], and their mother's traits as more important for their self-concept than President Bush's [planned comparison, mother > Bush: $F(1, 39) = 45.6, p < .0001$].

The interaction between Trait and Person [$F(2, 78) = 5.24, p < .007$] revealed that for one's mother, character was disproportionately more important for the self-concept

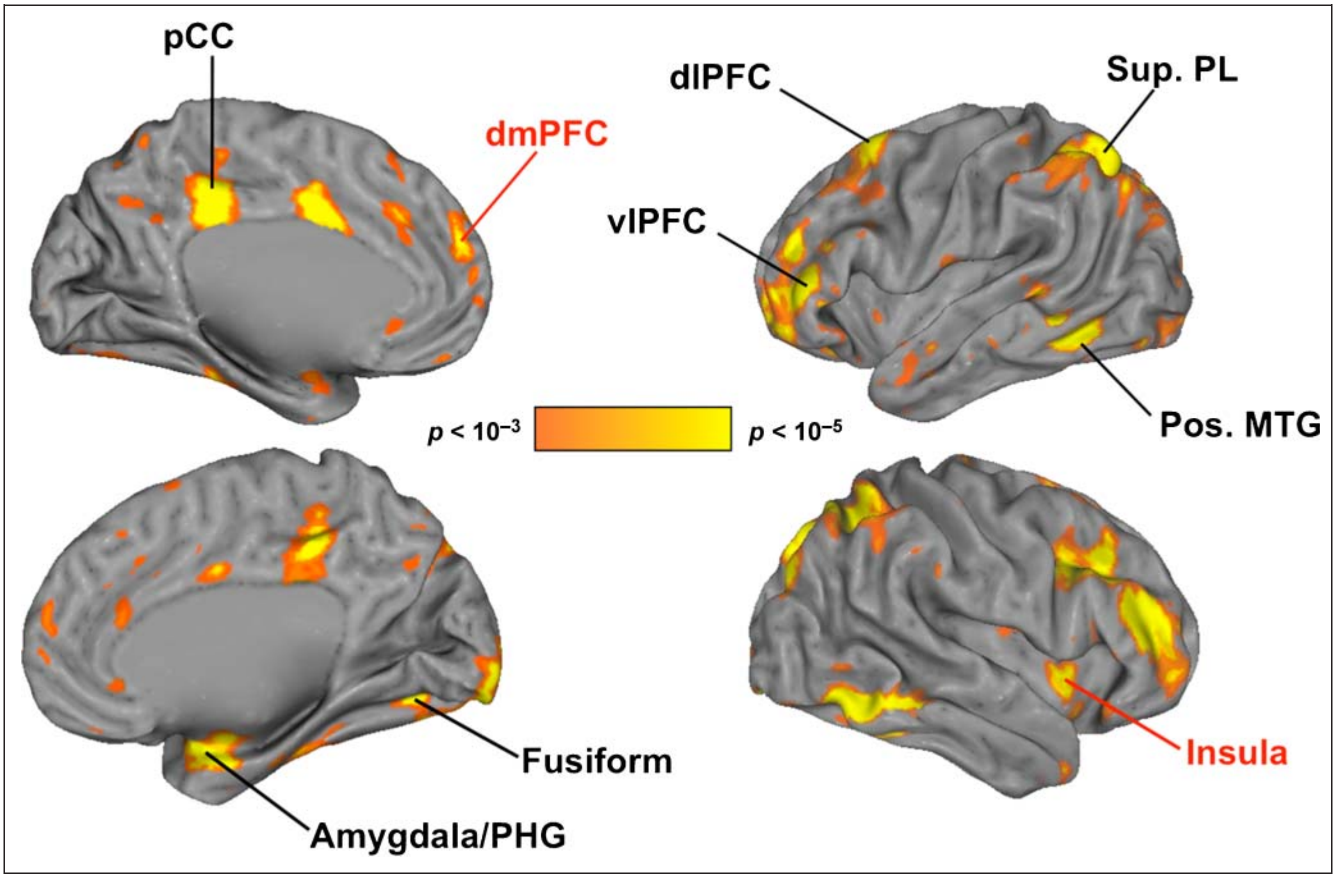

Figure 1. Regions showing a main effect of trait (character/appearance) in the omnibus ANOVA at $p < .05$ (FDR-corrected). Labels in red are for character > appearance, labels in black are for appearance > character. Coordinates are in Table 2.

than appearance (mean difference = 1.35) relative to that difference for self [mean difference for self = 0.85, *t* test on the differences: $t(39) = 2.431$, $p < .01$], and relative to that difference for Bush [mean difference for Bush = 0.78, *t* test on the differences: $t(39) = 3.219$, $p < .0015$]. Further, this difference was not significant for Self and Bush [$t(39) = 0.386$, $p < .36$]. These findings demonstrate relatively greater importance for mother's character than appearance for one's self-concept (Figure 3).

DISCUSSION

We found differential involvement of multiple and distinct brain regions in reflecting on people dependent on the kind of trait being judged (appearance vs. character) and the kind of person being judged, that is, oneself, a close other (one's mother), or a distant other (President Bush). The pCC and ventral and dorsal visual regions were most engaged for judgments based on knowledge of a person's appearance, whereas the dorsal mPFC and insula were most engaged by judgments about a person's character. Thus, there was a double dissociation between two regions (pCC and dorsal mPFC) previously considered as a single midline system in self-reflection. For these regions, the dissociation held irrespective of whether one was thinking about oneself, one's mother, or President Bush. In ventral mPFC, activation was greatest for thinking about one's own and one's mother's character, and one's own appearance. This pattern of activation was similar to the behavioral ratings in Experiment 2, in which people rated both their own character and appearance as important when thinking about themselves, but only rated their mother's character (and not appearance) as important when thinking about themselves. Therefore, activation in ventral mPFC appears to reflect *self-relevance* per se across traits and people.

Neural System Engaged in Reflection about a Person's Character

The engagement of dorsal mPFC in reflection upon character is consistent with identification of this brain region for inference about mental states (e.g., Fletcher et al., 1995), including activations when thinking about the psychological states of people and dogs versus thinking about body parts of those targets (Mitchell, Banaji, & Macrae, 2005). Importantly, this region did not differentiate among self, mother, and President Bush, providing evidence for a role in character judgment about all social targets. Also activated for judgments about character relative to appearance were bilateral insular cortices. These regions are held to play a role both in interoception

Table 2.

Region	BA	Coordinates	F	Effect
(A) Main Effect of Trait (Character vs. Appearance) (FDR .05 = 11.20)				
Frontal				
R mPFC	10	9 51 21	15.06	Character
L dlPFC	46	−45 33 18	57.71	Appearance
R dlPFC	46	48 −42 9	67.15	Appearance
L dlPFC	9	−45 6 21	23.48	Appearance
L vlPFC	47	−27 30 −12	27.41	Appearance
R vlPFC	47	30 39 −12	28.94	Appearance
R MFG	8	48 15 51	15.20	Appearance
Parietal				
L SPL	7	−30 −60 45	66.41	Appearance
R SPL	7	39 −63 54	37.07	Appearance
pCC	31	0 −33 45	31.22	Appearance
pCC	31	3 −36 33	26.36	Appearance
Temporal				
R MTG	21	48 −42 3	15.50	Character
L FG	37	−48 −45 −21	38.81	Appearance
R FG	37	48 −45 −21	27.28	Appearance
R FG	37	48 −51 −18	22.92	Appearance
L pMTG	37	−57 −51 −12	73.28	Appearance
R pMTG	37	54 −51 −6	28.09	Appearance
Other				
L Insula	13	−39 9 3	12.81	Character
L Amygdala	–	−18 −3 −21	12.82	Appearance
(B) Main Effect of Person (Self/Mother/Bush) (FDR .05 = 8.87)				
Cuneus	17	3 −90 3	36.24	Bush > Other
mPFC	10	−6 60 9	10.12	Self > Other
aCC	32	3 45 0	18.28	Self > Other
mCC	30	6 −24 39	13.01	Self > Other

and in the representation of the embodied self during first-person autobiographical memory retrieval (Eich, Nelson, Leghari, & Handy, 2009). Because the insula is activated when people think about their own heart rate (Critchley, Wiens, Rosthstein, Ohman, & Dolan, 2004), this activation could reflect a sort of embodied cognition that builds upon interoception of bodily states to interpret internal, unobservable aspects of character in themselves and others. The character traits examined in this study, however, included adjectives that were more (e.g., "shy") to less (e.g., "lucky") related to internal states, so a more controlled set of trait adjectives would be needed to directly relate trait judgments to interoception in the insula.

Neural System Engaged in Reflection about a Person's Appearance

For judgments about both character and appearance, stimuli were perceptually similar (i.e., visual words), such that regions more active for judgments about appearance were more active due to the kind of knowledge being considered than any perceptual property of the stimulus. pCC was preferentially engaged when considering appearance rather than character. This is consistent with evidence for involvement of this area in tasks that demand mental imagery and reactivating visual memories of a person's physical appearance (Cavanna & Trimble, 2006). Also activated preferentially for judgments about the visual appearance of people were widespread visual pathways also implicated in reactivation of pictorial memories (Wheeler et al., 2000). Presumably, participants had to utilize visual memories about themselves, their mother, and President Bush when thinking about their appearances. Some of these regions (i.e., fusiform gyrus and pCC) have been associated with activation to concrete versus abstract words (Binder, Desai, Graves, & Conant, 2009), which may contribute to their activation here.

Neural System Engaged Preferentially for Reflection about Oneself

Both pCC and ventral mPFC exhibited overall greater activation when reflecting upon oneself than others, but the patterns of activation differed in the two midline regions. Greater activation of pCC and ventral mPFC is consistent with other evidence that these brain regions have a specific role in reflection about oneself relative to either close or distant others (Northoff & Bermpohl, 2004). In pCC, there was greater and additive activation, both for reflection about oneself and reflection about appearance, and there was no interaction between the kind of knowledge and the person being considered. This pattern of activation was strongly dissociable from that seen in dorsal mPFC, which was greater for character than appearance, and similar for reflecting upon oneself, a close other, or a distant other.

An unexpected pattern of activation emerged for ventral mPFC, with greatest activation for character in oneself and in one's mother and for appearance in oneself. Thus, ventral mPFC exhibited activation for one's own appearance, but not that of others. This neuroimaging finding motivated Experiment 2, in which we asked people what factors were important in thinking about their own self-concept, and the three strongest factors were their own character, their own appearance, and their mother's character—precisely those factors that engaged mPFC. The inclusion of their mother's character as important for

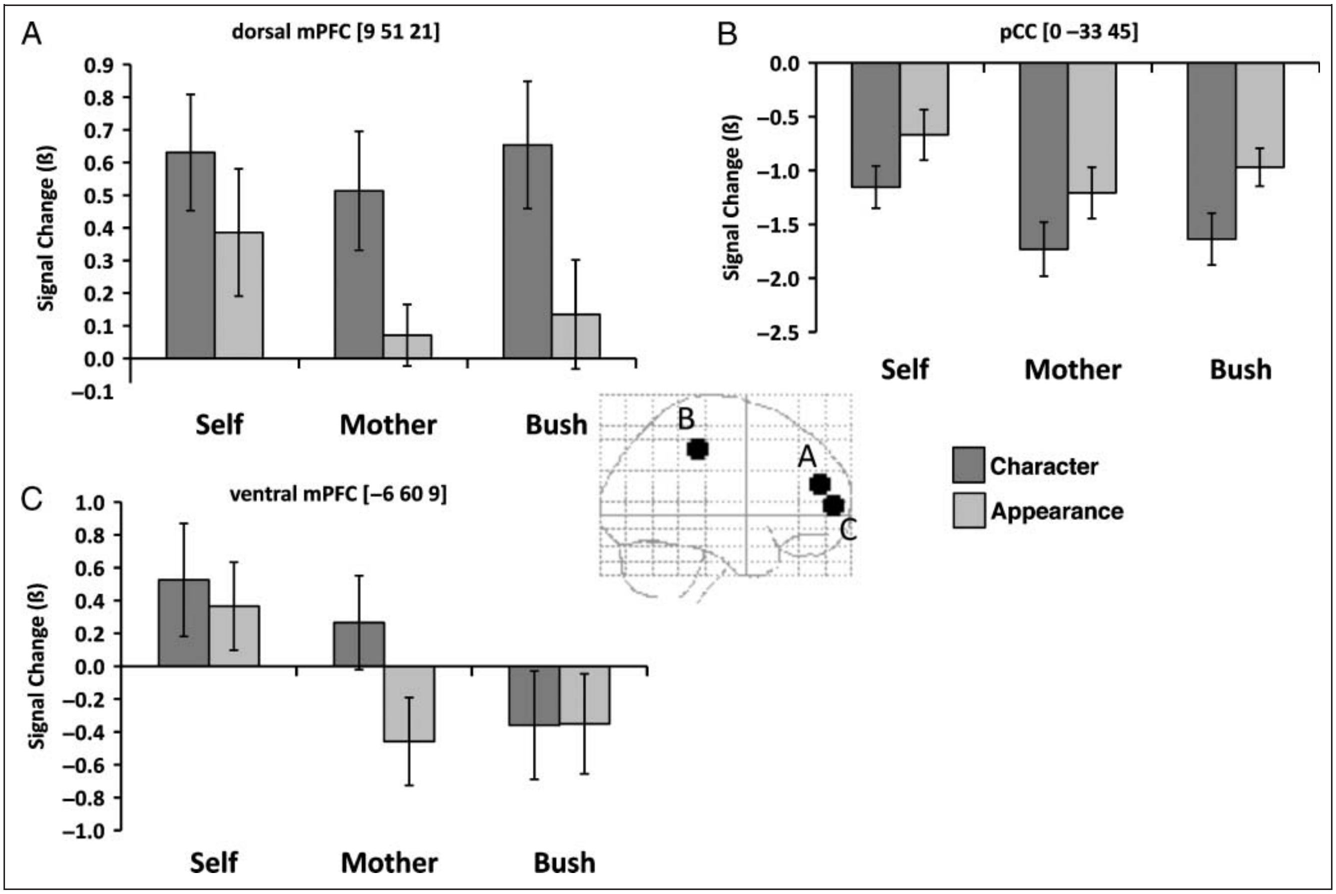

Figure 2. Different patterns of activation when people thought about character or appearance in regards to themselves, their mothers, or President Bush. (A) Greater activation for character than appearance in dorsal mPFC. (B) Greater activation for appearance than character in pCC. (C) Greater activation for appearance in oneself and for character in oneself and one's mother. Error bars represent standard error of mean.

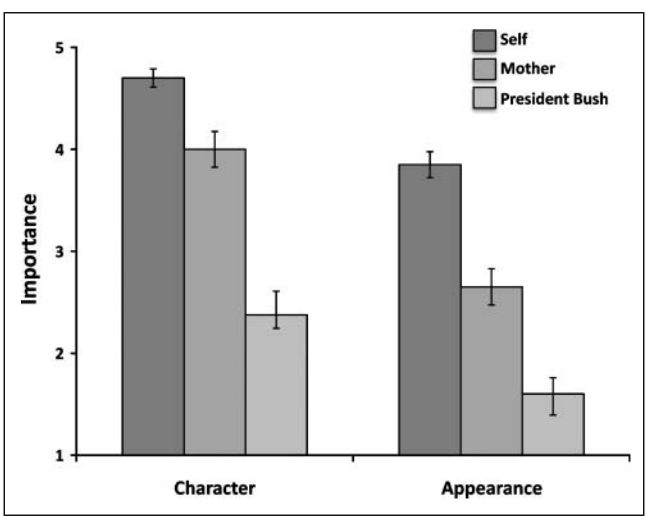

Figure 3. Experiment 2 rating of importance to oneself for character and appearance of oneself, one's mother, or President Bush. Interaction reveals greater importance for self and mother's character than President Bush's (left bars), and greater importance for oneself's appearance than mother's and President Bush's (right bars). Error bars represent standard error of the mean.

self-concept is consistent with behavioral findings that close others' character traits are included in one's self-concept. Interestingly, one's own appearance was rated as important for self-concept, but not the appearance of one's mother. Thus, ventral mPFC appears to represent or process knowledge that is self-relevant (Moran et al., 2006), including information about self-relevant aspects of other people.

Limitations

A limitation of this study concerns the stimuli used in the different experimental conditions. Although care was taken to ensure that items did not overlap on observability, and that mean observability was kept constant across self and other conditions, there are other factors that we were unable to control for. Firstly, although differences in valence have been shown to produce differential brain activations (Nielen et al., 2009), the CMS does not respond differentially to trait adjectives of differing valence (Moran et al., 2006). This suggests that word valences did not influence the results.

Secondly, we were not able equate the two lists for word length [character mean: 9.05 letters; appearance mean: 7.33 letters; $t(178) = 3.69$, $p < .001$]. However, previous research has shown monotonic increases in fusiform and lingual gyrus activation with increasing word length (Mechelli, Humphreys, Mayall, Olson, & Price, 2000). Results from our study revealed greater activation in both structures during trials on which participants read shorter words (appearance > character), suggesting that, in this instance, their increased activation was more likely due to differences in judgment type than in word length.

Thirdly, our word lists differed in frequency [Kucera–Francis character mean: 21.2; appearance mean: 72.9; $t(178) = 2.45$, $p < .02$]. Lower word frequency has been related to greater left inferior prefrontal activation during semantic judgments (Chee, Hon, Caplan, Lee, & Goh, 2002). In our experiment, greater left inferior prefrontal activation was associated with words of higher frequency (appearance words), suggesting that this factor did not drive activation in this region.

Fourth, words used for appearance judgments are inherently more concrete than those used for character judgments, and this raises the possibility that activation differences reflected these word properties rather than the kind of judgment. A meta-analysis found, across studies, greater activations for concrete relative to abstract words in posterior cingulate cortex and fusiform gyrus (Binder et al., 2009). The posterior cingulate activations for concrete relative to abstract words occurred in a region lateral, posterior, and ventral to those identified for appearance versus character in this report ([~−10 to −18; ~−50 to −60; ~+10 to +20] vs. [0 −33 45]). The fusiform gyrus appears to be more medial ($x = -38$ to -22) than those observed here ($x = -48$). In the reverse contrast, the meta-analysis found, across studies, greater activation in left inferior prefrontal cortex for abstract relative to concrete words, the opposite pattern to that obtained here. This divergence in findings further suggests that activations in the present report were not driven by simple differences in concreteness. Thus, although concreteness is evidently a factor differentiating words in the conditions used here, the typical activations associated with this difference in semantic processing tasks are not in evidence in our data. Further work attempting to equate for concreteness in the context of thinking about different aspects of person knowledge would serve to strengthen conclusions from this investigation.

Most importantly, our experiment was designed to find differences in brain responses to different kinds of trait judgments or different kinds of people being judged, but is not well designed to identify brain responses that were similar for kinds of trait judgments or different kinds of people being judged. All judgment trials could be contrasted with fixation periods, but such activations could reflect many broad differences between task performance and rest, such as visual processing of stimuli, language processing of words, as well as decision and response processes related to making judgments. Future studies could include perceptual or semantic judgments about words as a baseline so as to better identify brain regions involved similarly in both kinds of judgments and for all kinds of people being judged.

A concern raised about social cognitive neuroscience (and often about human cognitive neuroscience in general) is that neuroimaging and other methods may localize particular aspects of social cognition to particular brain regions (such as the present dissociation between knowledge about a person's character or appearance), but that they do not offer new insights into social cognition. Here, the unexpected pattern of activation in ventral mPFC inspired a behavioral survey that revealed how knowledge about appearance selectively influences self-concept. Thus, ventral mPFC may mediate both how close others come to be neurally incorporated into our self-concept (e.g., one's mother), and also which aspects of close others are incorporated into our self-concept (e.g., one's mother's character, but not her appearance).

These findings support the idea that midline brain regions that are typically activated in concert during tasks that demand judgments about one's own character traits are actually distinct in their contributions to thinking about oneself and other people. Such social knowledge is focused on appearance in pCC, on character in dorsal mPFC, and on self-relevance in ventral mPFC.

Acknowledgments

This work was supported by a Simons Foundation Grant to J. D. E. G. We thank A. Weinberg, T. Meagher, S. Shannon, C. Triantafyllou, S. Arnold, and S. Whitfield-Gabrieli for their technical assistance.

Reprint requests should be sent to Joseph M. Moran, MIT 46-5081, 77 Massachusetts Ave., Cambridge, MA 02139, or via e-mail: jmmoran@mit.edu.

REFERENCES

Anderson, N. H. (1968). Likableness ratings of 555 personality-trait words. *Journal of Personality and Social Psychology, 9,* 272–279.

Aron, A., Aron, E. N., Tudor, M., & Nelson, G. (1991). Close relationships as including other in the self. *Journal of Personality and Social Psychology, 60,* 241–253.

Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex, 19,* 2767–2796.

Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: A review of its functional anatomy and behavioral correlates. *Brain, 129,* 564–583.

Chee, M. W. L., Hon, N. H. H., Caplan, D., Lee, H. L., & Goh, J. (2002). Frequency of concrete words modulates prefrontal activation during semantic judgments. *Neuroimage, 16,* 259–268.

Craik, F. I. M., Moroz, T. M., Moscovitch, M., Stuss, D. T., Winocur, G., Tulving, E., et al. (1999). In search of the

self: A positron emission tomography study. *Psychological Science, 10,* 26–34.
Critchley, H. D., Wiens, S., Rosthstein, P., Ohman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature Neuroscience, 7,* 189–195.
Eich, E., Nelson, A. E., Leghari, M. A., & Handy, T. C. (2009). Neural systems mediating field and observer memories. *Neuropsychologia, 47,* 2239–2251.
Fletcher, P. C., Happe, F., Frith, U., Baker, S. C., Dolan, R. J., Frackowiak, R. S. J., et al. (1995). Other minds in the brain: A functional imaging study of theory of mind in story comprehension. *Cognition, 57,* 109–128.
Genovese, C. R., Lazar, N. A., & Nichols, T. A. (2002). Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *Neuroimage, 15,* 870–878.
Gobbini, M. I., & Haxby, J. V. (2006). Neural response to the visual familiarity of faces. *Brain Research Bulletin, 71,* 76–82.
Gusnard, D. A., Akbudak, E., Shulman, G. L., & Raichle, M. E. (2001). Medial prefrontal cortex and self-referential mental activity: Relation to a default mode of brain function. *Proceedings of the National Academy of Sciences, U.S.A., 98,* 4259–4264.
Heatherton, T. F., Wyland, C. L., Macrae, C. N., Demos, K. E., Denny, B. T., & Kelley, W. M. (2006). Medial prefrontal activity differentiates self from close others. *Social Cognitive and Affective Neuroscience, 1,* 18.
Jenkins, A., Macrae, C. N., & Mitchell, J. P. (2008). Repetition suppression of ventromedial prefrontal activity during judgments of self and others. *Proceedings of the National Academy of Sciences, U.S.A., 105,* 4507–4512.
Johnson, M. K., Raye, C. L., Mitchell, K. J., Touryan, S. R., Greene, E. J., & Nolen-Hoeksema, S. (2006). Dissociating medial frontal and posterior cingulate activity during self-reflection. *Social Cognitive and Affective Neuroscience, 1,* 56.
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.
Kensinger, E. A., & Schacter, D. L. (2006). Neural processes underlying memory attribution on a reality-monitoring task. *Cerebral Cortex, 16,* 1126–1133.
Kjaer, T., Nowak, M., & Lou, H. (2002). Reflective self-awareness and conscious states: PET evidence for a common midline parietofrontal core. *Neuroimage, 17,* 1080–1086.
Lane, R. D., Fink, G. R., Chau, P. M.-L., & Dolan, R. J. (1997). Neural activation during selective attention to participative emotional responses. *NeuroReport, 8,* 3969–3972.
Lombardo, M. V., Chakrabarti, B., Bullmore, E. T., Wheelwright, S. J., Sadek, S. A., Suckling, J., et al. (2010). Shared neural circuits for mentalizing about the self and others. *Journal of Cognitive Neuroscience, 22,* 1623–1635.
Lou, H. C., Luber, B., Crupain, M., Keenan, J. P., Nowka, M., Kjaer, T. W., et al. (2004). Parietal cortex and representation of the mental self. *Proceedings of the National Academy of Sciences, U.S.A., 101,* 6827–6832.
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.
Mashek, D. J., Aron, A., & Boncimino, M. (2003). Confusion of self with close others. *Personality and Social Psychology Bulletin, 29,* 382–392.
Mechelli, A., Humphreys, G. W., Mayall, K., Olson, A., & Price, C. J. (2000). Differential effects of word length and visual contrast in the fusiform and lingual gyri during reading. *Proceedings: Biological Sciences, 267,* 1909–1913.
Mitchell, J. P., Banaji, M. R., & Macrae, C. N. (2005). The link between social cognition and self-referential thought in the medial prefrontal cortex. *Journal of Cognitive Neuroscience, 17,* 1306–1315.
Mitchell, J. P., Macrae, C. N., & Banaji, M. R. (2006). Dissociable medial prefrontal contributions to judgments of similar and dissimilar others. *Neuron, 50,* 655–663.
Miyashita, Y. (1993). Inferior temporal cortex: Where visual perception meets memory. *Annual Review of Neuroscience, 16,* 245–263.
Moran, J. M., Heatherton, T. F., & Kelley, W. M. (2009). Modulation of cortical midline structures by implicit and explicit self-relevance evaluation. *Social Neuroscience, 4,* 197–211.
Moran, J. M., Macrae, C. N., Heatherton, T. F., Wyland, C. L., & Kelley, W. M. (2006). Neuroanatomical evidence for distinct cognitive and affective components of self. *Journal of Cognitive Neuroscience, 18,* 1586–1594.
Nielen, M. M., Heslenfeld, D. J., Heinen, K., van Strien, J. W., Witter, M. P., Jonker, C., et al. (2009). Distinct brain system underlie the processing and valence of affective pictures. *Brain and Cognition, 71,* 387–396.
Northoff, G., & Bermpohl, F. (2004). Cortical midline structures and the self. *Trends in Cognitive Sciences, 8,* 102–107.
Northoff, G., Heinzel, A., de Greck, M., Bermpohl, F., Dobrowolny, H., & Panksepp, J. (2006). Self-referential processing in our brain: A meta-analysis of imaging studies on the self. *Neuroimage, 31,* 440–457.
Ochsner, K. N., Beer, J. S., Robertson, E. R., Cooper, J. C., Gabrieli, J. D., Kihsltrom, J. F., et al. (2005). The neural correlates of direct and reflected self-knowledge. *Neuroimage, 28,* 797–814.
Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia, 9,* 97–113.
Pelli, D. B. (1997). The Video Toolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10,* 437–442.
Pfeifer, J. H., Lieberman, M. D., & Dapretto, M. (2007). "I know you are but what am I?!": Neural bases of self- and social knowledge retrieval in children and adults. *Journal of Cognitive Neuroscience, 19,* 1323–1337.
Roland, P. E., & Gulyas, B. (1995). Visual memory, visual imagery and visual recognition of large field patterns by the human brain: Functional anatomy by positron emission tomography. *Cerebral Cortex, 5,* 79–93.
Saxe, R., Moran, J. M., Scholz, J. K., & Gabrieli, J. D. E. (2006). Overlapping and non-overlapping brain regions for theory of mind and self. *Social Cognitive and Affective Neuroscience, 1,* 229–234.
Schmitz, T. W., Kawahara-Baccus, T. N., & Johnson, S. C. (2004). Metacognitive evaluation, self-relevance, and the right prefrontal cortex. *Neuroimage, 22,* 941–947.
Wheeler, M. E., Petersen, S. E., & Buckner, R. L. (2000). Memory's echo: Vivid remembering reactivates sensory-specific cortex. *Proceedings of the National Academy of Sciences, U.S.A., 97,* 11125–11129.