

Finding the Self? An Event-Related fMRI Study

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Abstract

■ Researchers have long debated whether knowledge about the self is unique in terms of its functional anatomic representation within the human brain. In the context of memory function, knowledge about the self is typically remembered better than other types of semantic information. But why does this memorial effect emerge? Extending previous research on this topic (see Craik et al., 1999), the present study used event-related functional magnetic resonance imaging to investigate potential neural substrates of self-referential processing. Participants were imaged while making judgments

about trait adjectives under three experimental conditions (self-relevance, other-relevance, or case judgment). Relevance judgments, when compared to case judgments, were accompanied by activation of the left inferior frontal cortex and the anterior cingulate. A separate region of the medial prefrontal cortex was selectively engaged during self-referential processing. Collectively, these findings suggest that self-referential processing is functionally dissociable from other forms of semantic processing within the human brain. ■

INTRODUCTION

An impressive human talent is the ability to reflect on past experiences and to project the self into imagined futures. Indeed, it is this introspective ability that has prompted a host of noted thinkers to raise some vexing questions about the nature and status of the self (James, 1890). In experimental psychology, the debate has centered on two main issues. Is the self a unique cognitive structure? Does self-referential processing have some privileged status in the brain, or is it functionally equivalent to semantic processing about other classes of stimuli, such as cars, politicians, and Caribbean islands (Klein & Kihlstrom, 1986; Klein & Loftus, 1988; Maki & McCaul, 1985; Bower & Gilligan, 1979; Markus, 1977; Rogers, Kuiper, & Kirker, 1977)? Put simply, is self-referential processing special in any way?

Early research on this topic was revealing as it demonstrated a memorial advantage for information that was processed in a self-referential manner. Rogers et al. (1977), for instance, showed that trait adjectives that were processed with reference to the self (e.g., “Does the word ‘honest’ describe you?”) were better recalled than comparable items that were processed only for their general meaning (e.g., “Does the word ‘honest’ mean the same as ‘trustworthy?’”). This finding was important as it extended the seminal work of Craik and Tulving (1975) on depth of processing, which had previously shown that words processed for their semantic meaning were remembered better on a subsequent

memory test than words processed for their structural features (e.g., “Is the word ‘dependable’ in lowercase letters?”). The message that has emerged from subsequent studies that have investigated the relationship between self and memory function is a consistent one—self-reference permits superior memory relative to other semantic encoding tasks (see Symons & Johnson, 1997). But why exactly does this self-reference effect occur?

Two putative explanations have been offered for the self-reference effect in memory. One account suggests that the self is a unique cognitive structure that possesses extraordinary or additional mnemonic abilities, hence the enhanced memorability of material that is processed in a self-referential manner (e.g., Maki & McCaul, 1985; Rogers et al., 1977). As Rogers et al. have suggested, the self functions as a “superordinate schema” (p. 686) that serves to facilitate the encoding and retrieval of information. However, other researchers take a different view. The basis of their argument is that there is nothing special about the self per se (i.e., no distinct structure or neural process devoted to self-referential processing). Rather, the memory enhancement afforded to self-reference can be interpreted as an extension of the basic depth-of-processing effect (e.g., Greenwald & Banaji, 1989; Klein & Kihlstrom, 1986). That is, the wealth of knowledge we have about ourselves in memory simply encourages more elaborative encoding (and representation) of material that is processed in relation to the self (Klein & Loftus, 1988). In turn, this elaborative processing supports the enhanced memorability of self-relevant information.

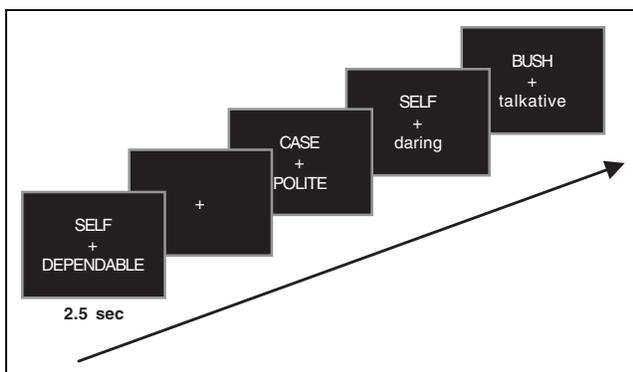


Figure 1. Examples of the self, other, case, and fixation trial types. Trials were randomly intermixed, and one trial was presented every 2.5 sec. For each of the three judgment trial types, the “cue” (presented above the central fixation) indicated which type of judgment to make for the trait adjective (presented below the fixation).

Despite the clarity of these competing viewpoints, how self-referential processing boosts memory performance remains open to debate. A problematic feature of these candidate theoretical accounts is that they are difficult to evaluate competitively using purely behavioral measures. As such, researchers have recently turned to neuroimaging techniques in an attempt to inform current understanding of self-referential processing and its impact on memory function (e.g., Craik et al., 1999). Building on this work, the present investigation used event-related functional magnetic resonance imaging (fMRI) to investigate whether there is indeed anything special about self-referential processing. To address this question, participants were imaged while making various judgments about trait adjectives (see also Craik et al., 1999). Each trait word was presented concurrently with a “cue” that instructed participants as to which type of judgment they were required to make (Figure 1). Participants judged each trait adjective in one of three ways: self (“Does the adjective describe you?”), other (“Does the adjective describe current U.S. President George Bush?”)¹; and case (“Is the adjective presented in uppercase letters?”).

These judgments were expected to produce varying levels of subsequent memory performance (self > other > case). Critically, however, they also permitted a direct test of the competing explanations for the self-reference effect. Functional imaging studies have previously identified multiple regions within the left frontal cortex that show greater activation for elaborative semantic encoding of words than for nonsemantic, surface-based encoding of words (Wagner et al., 1998; Gabrieli et al., 1996; Demb et al., 1995; Kapur et al., 1994; for review, see Buckner, Kelley, & Petersen, 1999). If the self-reference effect results from an extension of ordinary memory processes, then one might expect to observe greater activation for self-relevant judgments than for other- and case-based judgments in those same left frontal regions known

to be sensitive to semantic encoding. Alternatively, if the self-reference effect results from properties of a unique cognitive self, then one might expect self-referential processing to selectively engage brain regions that are distinct from those involved in general semantic processing. We investigated these possibilities in the following experiment.

RESULTS

Behavioral Results

Table 1 shows behavioral performance measures for each trial type. An analysis of variance (ANOVA) showed that response latencies for encoding trials were slowest for other judgments ($M = 1881$ msec) and fastest for case judgments ($M = 1607$ msec) [$F(2,40) = 44.03, p < .0001$]. Post hoc statistical tests revealed that response latencies were significantly faster for case judgments than for self judgments [$F(1,20) = 80.10, p < .0001$] and other judgments [$F(1,20) = 47.61, p < .0001$]. The difference in response latencies between other and self judgments was also significant [$F(1,20) = 7.12, p < .05$].

Accurate performance on the yes/no recognition memory test was used as an indication that successful encoding had occurred. Recognition memory performance was determined by calculating corrected recognition scores (proportion of hits–false alarms). An ANOVA revealed a significant main effect of trial type [$F(1,40) = 80.88, p < .0001$]. Post hoc statistical tests revealed significant differences in subsequent memory between self and other adjectives [$F(1,20) = 45.75, p < .0001$], self and case adjectives [$F(1,20) = 145.44, p < .0001$], and other and case adjectives [$F(1,40) = 42.77, p < .0001$]. Response latencies during the recognition memory test did not differ across trial types [$F(3,60) = 1.66, ns$].

fMRI Results

Figure 2 shows statistical activation maps for all encoding trials relative to baseline. A network of brain regions was commonly activated, including bilateral regions of the striate and extrastriate visual cortex, the parietal cortex, the dorsal frontal cortex, the inferior frontal cortex, the

Table 1. Behavioral Performance during Encoding and Recognition Tasks

Task	Encoding Reaction Time (msec)	Hits–False Alarms	Recognition Reaction Time (msec)
Self	1812 (27)	0.49 (0.02)	1137 (31)
Other	1881 (24)	0.36 (0.03)	1188 (23)
Case	1607 (34)	0.17 (0.03)	1152 (24)

Standard errors are given in parentheses.

Figure 2. Whole-brain statistical activation maps show general task-related activity in relation to baseline averaged across all 21 participants. Images are axial sections in the Talairach & Tournoux (1988) atlas space. Sections from left to right correspond to $z = -4$, $z = 24$, and $z = 44$. Colored pixels exceeded the statistical threshold and are superimposed on corresponding anatomy images. The left side of the image corresponds to the left side of the brain. Increases in activation (red color scale; areas labeled in yellow letters) were observed in (A) the posterior visual cortex extending into (B) the extrastriate visual cortex, (C) the inferior frontal cortex, (D) the dorsal frontal cortex, (E) the lateral parietal cortex, and (F) the anterior cingulate. Decreases in activation (blue color scale, areas labeled in blue letters) were noted in (G) the medial temporal cortex, (H) the medial prefrontal cortex, and (I) the posterior cingulate.

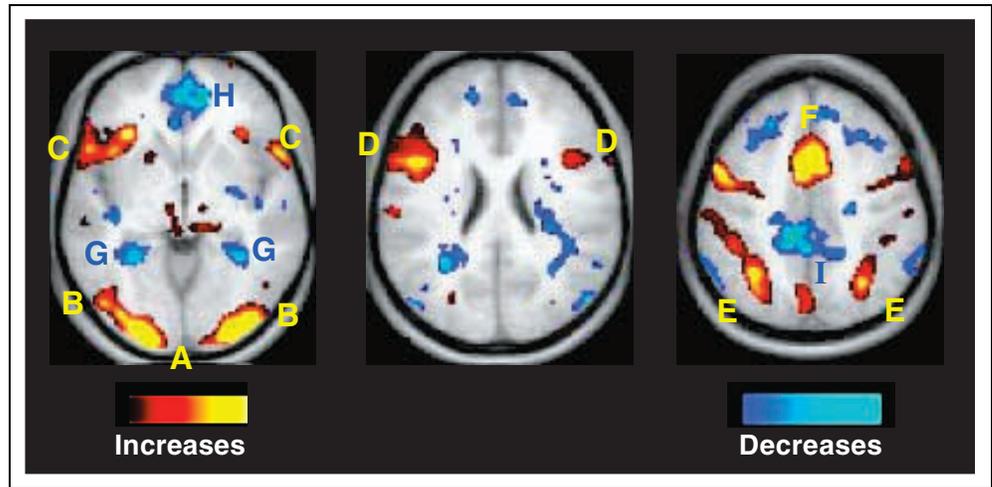


Figure 3. Statistical activation maps comparing self and other trials to case trials demonstrate greater activity during semantic encoding trials (self and other) than nonsemantic encoding trials (case) in (A) the left inferior frontal cortex ($-42, 16, -4$) and (B) the anterior cingulate ($0, 14, 42$). Displayed at the left are axial sections through the activation foci averaged across participants. The left side of the image corresponds to the left side of the brain. Time courses (right panel) were computed for each condition within a 3-D region surrounding the peak voxel identified from the combined statistical map (shown in Figure 2). Regions were defined using an automated algorithm that identified all contiguous voxels within 10 mm of the peak that reached the significance level ($p < .0001$). Bars indicate standard error of the mean (SEM).

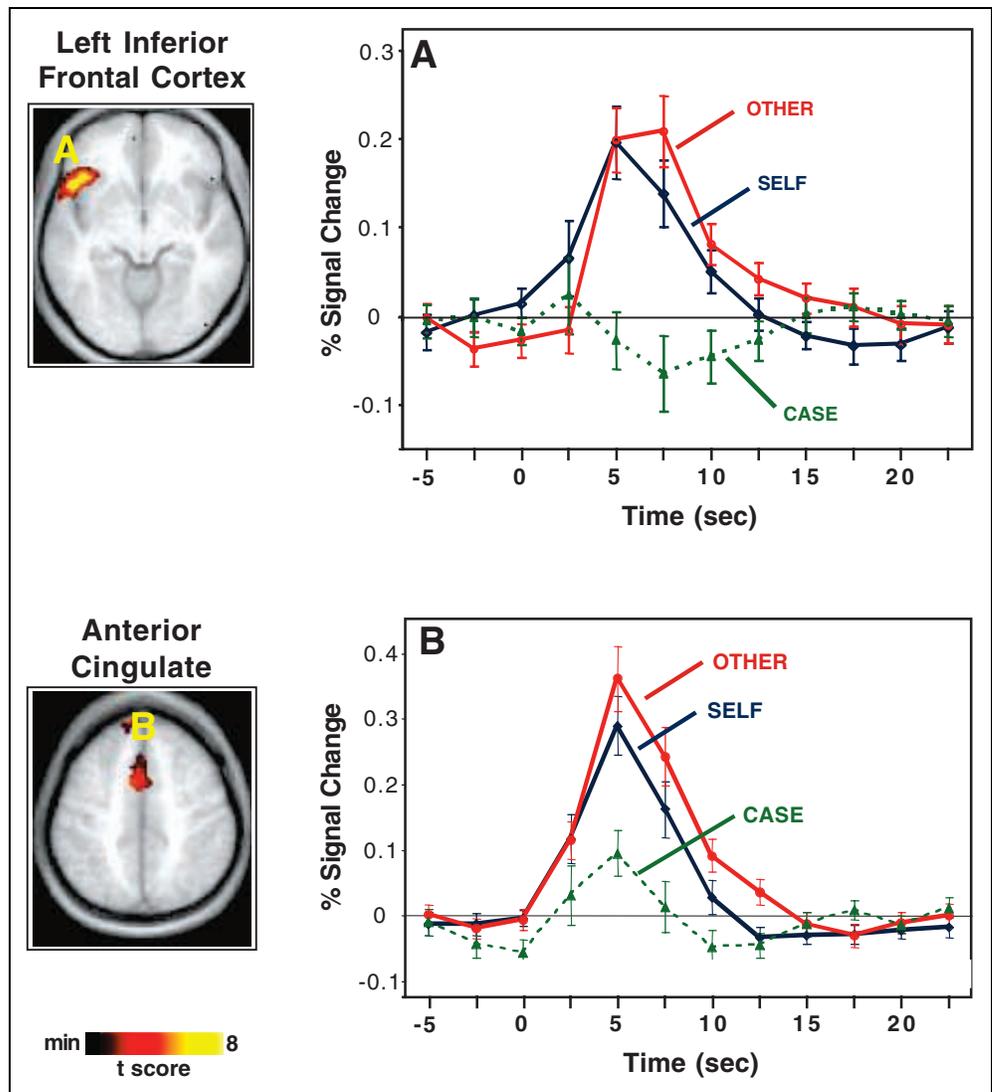


Table 2. Identification of BOLD Signal Increases and Decreases for All Encoding Trials Relative to Baseline

<i>Brain Region</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>Z score</i>
<i>Increases relative to baseline</i>				
Occipital cortex				
Left BA 17/18	-24	-94	-12	6.68
Right BA 18	32	-92	-4	6.14
Medial BA 18	0	-70	-12	4.42
Medial BA 18	-4	-46	4	4.35
Medial BA 19	-2	-78	40	4.24
Parietal cortex				
Left BA 7	-32	-66	54	5.86
Right BA 7	30	-64	50	5.46
Dorsal frontal cortex				
Left BA 44	-48	12	22	5.31
Right BA 44	48	8	32	4.07
Inferior frontal cortex				
Left BA 47	-42	16	-4	4.98
Left BA 47	-32	26	-8	4.92
Right BA 47	54	16	-6	5.13
Motor cortex				
Right BA 4	42	0	58	5.47
Anterior cingulate				
BA 32	0	14	42	6.57
Subcortical				
Left thalamus	-6	-20	8	5.42
Left caudate nucleus	-10	4	6	4.71
Cerebellum				
Right cerebellum	34	-62	-32	6.07
Left cerebellum	-28	-60	-32	5.17
<i>Decreases relative to baseline</i>				
Prefrontal cortex				
BA 10	10	52	2	6.35
BA 10	-8	54	2	5.92
BA 8	6	40	44	4.37
BA 25	-4	4	-10	4.26
Right BA 8	18	34	52	5.20
Right BA 8	34	26	46	5.02
Right BA 9	14	58	28	4.37
Left BA 9	-14	50	26	4.36
Left BA 11	-24	36	-10	4.77

Table 2. (continued)

<i>Brain Region</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>Z score</i>
Parietal cortex				
BA 7	12	-48	50	6.18
Left BA 40	-56	-58	38	5.16
Occipital cortex				
Left BA 37	-34	-40	-12	6.10
Left BA 31	-16	-84	18	4.23
Temporal cortex				
Left BA 39	-44	-76	30	4.46
Right hippocampus	24	-8	-18	5.45
Right BA 20	56	-24	-14	5.16

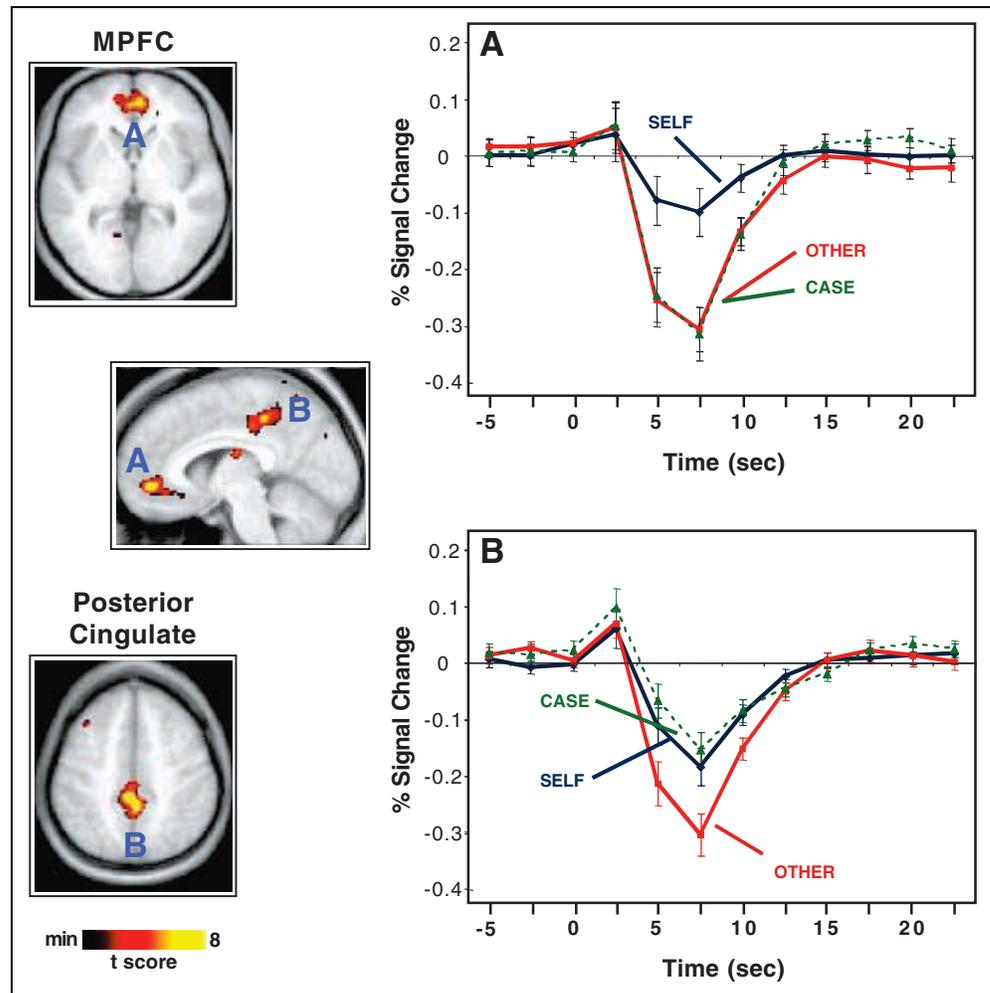
Activations determined to be significant ($p < .0001$) are listed along with the best estimate of their location. BA = approximate Brodmann's area location. Coordinates are from the Talairach & Tournoux (1988) atlas. Locations of the activations are determined based on the functional responses superimposed on averaged anatomical MRI images and are referenced to the Talairach atlas.

motor cortex, and the cerebellum. Activations were also observed medially in the anterior cingulate gyrus, the left thalamus, and the left caudate nucleus. Peak locations for activated regions are listed in Table 2 (both positive and negative differences are reported). While a number of brain regions revealed significant increases in activation for encoding trials relative to baseline, other brain regions exhibited decreases in activation. Brain regions that exhibited significant decreased activity included the medial prefrontal cortex (MPFC), the posterior cingulate (near precuneus), and bilateral regions in the lateral frontal, parietal, and medial temporal cortex.

Figure 3 shows significant activations that were observed when relevance trials (self and other) were directly compared to case judgment trials. This contrast can be conceptualized as a traditional levels-of-processing contrast that compares deep, or semantic-based processing, to shallow, or surface-based processing. Areas showing greater activity for relevance judgments than for case judgments include the left inferior frontal cortex and the anterior cingulate. The time courses for each region are shown in Figure 3 (right panel). In both brain regions, the temporal profile of activity reveals clear differences between semantic judgments (self and other trials), which yielded robust positive hemodynamic responses, and nonsemantic judgments (case trials), which produced a much weaker response. The time courses for self and other trial types did not differ from each other in these two regions.

To identify brain regions that showed different patterns of activation across the two types of semantic judgments, self judgment trials were directly compared to other judgment trials. Figure 4 shows significant

Figure 4. Statistical activation maps directly comparing self and other trials demonstrate greater activity during self encoding trials in (A) the MPFC (10, 52, 2) and (B) the posterior cingulate (12, -48, 50). Displayed at the left are axial and sagittal sections through the activation foci averaged across participants. The left side of the image corresponds to the left side of the brain. Time courses (right panel) were computed for each condition within a 3-D region surrounding the peak voxel identified from the combined statistical map (shown in Figure 2). Regions were defined using an automated algorithm that identified all contiguous voxels within 10 mm of the peak that reached the significance level ($p < .0001$). Bars indicate standard error of the mean (SEM). Activity in the MPFC (A) was uniquely sensitive to self encoding trials, whereas activity in the posterior cingulate (B) was comparable across self and case encoding trials.



activations that were observed in this direct comparison. Self judgments, when compared directly to other judgments, revealed greater activation in the MPFC and the posterior cingulate.

It should be noted that both of these regions exhibited decreased activity when all encoding trials were contrasted with baseline (see Figure 2). The “apparent” positive activation of these regions in the direct comparison results from the difference between two decreases relative to baseline (with other trials exhibiting a greater decrease from baseline relative to self trials). This can be seen clearly by examining the time courses for each region (Figure 4, right panel).

It is also important to note that the pattern of activation across the three trial types differs between the two brain regions. The hemodynamic response observed in the MPFC exhibits selectivity for self judgments. In this region, both other and case judgments produced robust decreases in activity relative to baseline that did not differ from each other. Self judgments yielded a much weaker decrease in the MPFC. By contrast, the activation pattern observed in the posterior cingulate was not uniquely sensitive to self-referential processing. In this region, other judgments elicited the

greatest decrease; self and case judgments produced weaker decreases of comparable magnitudes.

DISCUSSION

Consistent with levels-of-processing predictions (Craik & Tulving, 1975), trait adjectives judged in a semantic fashion (self and other) were later remembered better than adjectives judged only for surface-based features (case). More importantly, however, adjectives judged for self-relevance were remembered better than adjectives judged for relevance to a familiar other (President Bush). This finding is consistent with a number of behavioral studies that have demonstrated a self-reference superiority effect in memory (see Symons & Johnson, 1997).

Behavioral differences in subsequent memory for the three different trial types were accompanied by differences in neural activation during encoding judgments as indexed by blood oxygen level-dependent (BOLD) contrast fMRI. The activation pattern suggests a hierarchy of neural involvement. A number of brain regions were commonly activated across all three trial types, including activations in the occipital and parietal lobes, the motor

cortex, the thalamus, and the cerebellum. These activations likely reflect brain regions involved in general aspects of task performance that were common to all three trial types (e.g., viewing words and generating a motor response).

Other brain regions exhibited greater specificity. The left inferior frontal cortex and the anterior cingulate were selectively active during semantic judgments. The greater activation of the left inferior frontal cortex is consistent with a number of previous imaging studies that report left inferior frontal activation during tasks that encourage meaning-based encoding of verbal materials (for review, see Buckner et al., 1999). One interpretation of these findings is that left frontal activation may subserve the levels-of-processing effect observed by psychologists. To the degree that a task encourages elaborative semantic encoding, left frontal regions are activated, and those items are later remembered well. In the present study, both self-relevant and other-relevant judgments encouraged semantic-based processing of trait adjectives and, as a result, produced greater left frontal activation and better subsequent memory than did case judgments. However, self judgments produced even greater subsequent memory than did other judgments. If the self-reference effect is to be thought of as an ordinary extension of the levels-of-processing effect, left frontal activity might be expected to mediate the effect. In the present study, however, self judgments did not result in any additional activation of left frontal regions. If left frontal activity is viewed as a surrogate for ordinary semantic processing, then these results argue against the notion that the self-reference effect is driven by ordinary memory processes.

It should be noted that behavioral studies suggest that subsequent memory performance for words judged in reference to another person may depend on how well known the other is to the participant. For instance, when judgments are made with reference to intimate others (e.g., a parent, spouse, or best friend), the self-reference effect is reduced (Keenan & Baillet, 1980; Bower & Gilligan, 1979). When the other is a familiar public figure, as was the case in the current study, the self-reference effect is noticeably stronger (Conway & Dewhurst, 1995; Keenan & Baillet, 1980; Bower & Gilligan, 1979). Future research is needed to examine the role that familiarity may play in the neural effects reported herein.

So, is there anything special about the self? The current results suggest that a region of the MPFC is selectively engaged during self-referential judgments. This finding is consistent with previous imaging studies of self-referential mental activity. Most relevant to the current investigation, Craik et al. (1999) used positron emission tomography (PET) to investigate the neural basis for the self-reference effect in memory and observed a number of activations within prefrontal cortex that were selectively engaged during self-referential processing. These activations included the MPFC activa-

tion observed here as well as additional right prefrontal activations (near BA 10) that were not observed in the current study. Unfortunately, PET imaging constraints made it difficult to implement the behavioral paradigms necessary to elicit the self-reference memory effect in an optimal manner. As a result, it is difficult to interpret the PET imaging data in the absence of a significant self-reference effect. Alternatively, the absence of the fronto-polar activation in the present study may reflect procedural differences between the two imaging techniques (PET vs. fMRI). There is some speculation that fMRI may be less likely to detect fronto-polar activation than PET (Mottaghy et al., 2000).

More recently, Gusnard, Akbudak, Shulman, & Raichle (2001) used a blocked-design fMRI paradigm to examine judgments about affectively normed pictures and observed MPFC activity that was preferentially associated with introspective judgments. The view that the MPFC plays a prominent role in self-referential processing is also supported by neuropsychological evidence (Wheeler, Stuss, & Tulving, 1997; Stuss & Benson, 1986). A lack of self-reflection, introspection, and daydreaming have long been associated with damage to areas of the PFC (Ackerly & Benton, 1947). Indeed, Wheeler et al. (1997) have argued that persons with damage to specific areas of the PFC are unable to reflect on personal knowledge. It is possible that the self-reference superiority effect depends on an intact ability to be self-reflective, and that neural activations in the MPFC reflect such a process.

It is important to emphasize that the response observed in the MPFC both in the current investigation and in the study by Gusnard et al. (2001) differs from that which is typically referred to as an activation by researchers (defined as an increase in regional brain activation relative to baseline). Responses in the MPFC are almost always observed as decreases in activation relative to baseline (Gusnard & Raichle, 2001). In fact, the MPFC appears to be part of a network of brain regions that consistently exhibit task-related decreases in activity (Shulman et al., 1997). Decreases in these regions appear to be largely task-independent, occurring across a wide variety of goal-directed tasks. The consistency of this pattern of deactivations prompted Raichle et al. (2001, pp. 676) to suggest the existence of "an organized, baseline default mode of brain function that is suspended during specific goal-directed behaviors." This description fits nicely with the finding that baseline metabolic activity in the MPFC is high at rest (Raichle et al., 2001; Ingvar, 1979) and provides a context in which to consider the self-reference effect observed in the present study. Self-referential mental activity may be the by-product of "stimulus independent thoughts" (Teasdale et al., 1995; Antrobus, Singer, Goldstein, & Fortgang, 1970). In other words, it is what people spontaneously do when they are not actively engaged in the processing of externally generated information. In this regard, self-relevant mental activity

may be categorized not by its unique difference from resting brain activity, but by its “similarity” to spontaneous human brain activity. Importantly, self-referential thought seems to be mediated by a specific, anatomically distinct brain region. To the degree that participants engage in directed self-referential decisions, MPFC activity mirrors that of the MPFC at rest. When decisions are externally directed, activity in this region attenuates.

The present results suggest that self-referential activity in MPFC is transient, or item-specific, and can be directly wedded to individual trials in which participants make directed self-relevant decisions. Previous linkages between self-referential thought and MPFC activity have been made indirectly using blocked-design paradigms (where a number of like trial types are presented in succession—see Craik et al., 1999). Blocked procedures are problematic, however, as they potentially confound task specificity with stimulus specificity; activations (or deactivations) observed in blocked-design studies may reflect item-related processes, processes associated with a more global cognitive state, or both (for an elegant demonstration of how state and item effects can be dissociated, see Donaldson, Petersen, Ollinger, & Buckner, 2001). Because trial types were randomly intermixed in the current study, item-related activity was examined in isolation. As such, our results tie activity in the MPFC directly to the type of decision that was made.

In summary, the present results contribute to a debate that has interested cognitive and social psychologists for decades—is their something special about self-referential processing? If the self-reference effect in memory is accomplished by the additional engagement of “ordinary” brain regions involved in semantic processing, then self judgments would be expected to produce greater left inferior frontal activity than other judgments. However, left inferior frontal involvement did “not” differ during self and other judgments. Instead, the difference between self and other judgments was the additional recruitment of the MPFC, presumably reflecting access to knowledge unique to one’s self. Accordingly, the current results are consistent with the idea that self-referential processing is unique in terms of its functional representation in the human brain, a notion that has received emerging support from recent functional imaging studies (Gusnard et al., 2001; Craik et al., 1999). Finally, the present results offer a potential neural substrate (MPFC) for the self-reference effect in memory, a possibility that awaits further empirical investigation.

METHODS

Participants

Twenty-four participants between the ages of 18 and 30 (13 men, 11 women, mean age = 20 years) were recruited from the local Dartmouth community. All

participants were strongly right-handed as measured by the Edinburgh handedness inventory (Raczkowski, Kalat, & Nebes, 1974). Participants reported no significant abnormal neurological history and all had normal or corrected-to-normal visual acuity. Participants were either paid for their participation or received course credit. All participants gave informed consent in accordance with the guidelines set by the Committee for the Protection of Human Subjects at Dartmouth College. Of the 24 participants, 2 were removed from subsequent analysis due to technical difficulties with fMRI data reconstruction. A third participant was removed as a result of excessive movement during imaging (>1 mm between successive image acquisitions). Results reported here reflect data analyzed from the remaining 21 participants (12 men, 9 women, mean age = 20 years).

Apparatus

Imaging was performed on a 1.5-T whole body scanner (General Electric Medical Systems Signa, Milwaukee, WI) with a standard head coil. Visual stimuli were generated using an Apple G3 Laptop computer running PsyScope software (Cohen, MacWhinney, Flatt, & Provost, 1993). Stimuli were projected to participants with an Epson (model ELP-7000) LCD projector onto a screen positioned at the head end of the bore. Participants viewed the screen through a mirror. A fiber-optic, light-sensitive key press interfaced with the PsyScope Button Box (New Micros, Dallas, TX) was used to record participants’ behavioral performance. Cushions were used to minimize head movement.

Imaging

Anatomical images were acquired using a high-resolution 3-D spoiled gradient recovery sequence (SPGR; 124 sagittal slices, TE = 6 msec, TR = 25 msec, flip angle = 25°, voxel size = 1 × 1 × 1.2 mm). Functional images were collected in runs using a gradient spin-echo, echo-planar sequence sensitive to BOLD contrast (T2*) (TR = 2500 msec, T2* evolution time = 35 msec, flip angle = 90°, 3.75 × 3.75 mm in-plane resolution). During each functional run, 75 sets of axial images (33 slices; 4.5-mm slice thickness, 1 mm skip between slices) were acquired allowing complete brain coverage.

Behavioral Tasks

Participants were imaged during two functional runs while making judgments about trait adjectives. Judgments were one of three types: self (“Does this adjective describe you?”), other (“Does this adjective describe current U.S. President George Bush?”), and case (“Is this adjective printed in uppercase letters?”). Participants

indicated their responses via a left- or right-handed key press. Each trial lasted 2500 msec and consisted of a four-letter “cue” word (either self, Bush, or case) presented for 2000 msec above a central fixation and a unique trait adjective (e.g., “POLITE”) presented for 2000 msec below a central fixation (Figure 1). The central fixation remained on the screen throughout the duration of each trial. All text was presented in Geneva font (white letters on a black background; letters subtended $\sim 0.5^\circ$ of visual angle). Prior to the first functional run, participants were given practice trials to familiarize them with the tasks. Practice continued until participants indicated they were comfortable with the tasks.

A total of 270 unique adjectives were selected from a pool of normalized personality trait adjectives (Anderson, 1968). Lists were counterbalanced for word length, number of syllables, and valence (half of the words in each list were positive traits, the remaining half were negative traits). Across participants, lists were rotated through conditions such that trait adjectives that appeared in the self judgment trials for one participant appeared in a different condition (other or case) for other participants. During each of the two functional runs, 15 self trials, 15 other trials, 15 case trials, and 30 fixation trials were pseudorandomly intermixed such that each trial type followed every other trial type equally often. Fixation trials consisted of a central fixation point presented on the screen for 2500 msec. These trials were included to introduce “jitter” into the time series so that unique estimates of the hemodynamic responses for the trial types of interest could be computed (Ollinger, Shulman, & Corbetta, 2001) (see Data Analysis below).

Following the two encoding runs, participants were given a “surprise” recognition memory test. Participants viewed the 90 trait adjectives that were previously presented during the encoding scans along with 90 novel trait adjectives that had not been presented during the encoding scans. Words were presented sequentially in the center of the computer screen for 2000 msec. A fixation point (500 msec) preceded each word. For each word, participants indicated (via left- and right-handed key presses) whether the word was old or new.

Data Analysis

fMRI data were analyzed using Statistical Parametric Mapping software (SPM99, Wellcome Department of Cognitive Neurology, London, UK) (Friston et al., 1995). For each functional run, data were preprocessed to remove sources of noise and artifact. Functional data were corrected for differences in acquisition time between slices for each whole-brain volume, realigned within and across runs to correct for head movement, and coregistered with each participant’s anatomical

data. Functional data were then transformed into a standard anatomical space (2-mm isotropic voxels) based on the ICBM 152 brain template (Montreal Neurological Institute) which approximates Talairach & Tournoux’s (1988) atlas space. Normalized data were then spatially smoothed (6 mm full width half maximum [FWHM]) using a Gaussian kernel. Analyses took place at two levels: formation of statistical images and regional analysis of hemodynamic responses.

Statistical Images

First, for each participant, a general linear model, incorporating task effects (modeled with a canonical set of three functions: the hemodynamic response function, its temporal derivative, and its dispersion derivative; Friston et al., 1998), a mean, and a linear trend were used to compute parameter estimates (β) and *t*-contrast images (containing weighted parameter estimates) for each comparison at each voxel. These individual contrast images were then submitted to a second-level, random-effects analysis to create mean *t*-images (thresholded at $p = .0001$, uncorrected; minimal cluster size = 20 mm³). An automated peak-search algorithm identified the location of peak activations and deactivations based on *z* value and cluster size. This analysis allowed several comparisons to be made. First, individual trial types could be collectively compared to baseline (self + other + case > baseline) to identify general task-related activations and deactivations that were common to one or more trial types. In addition, individual trial types could be directly compared to each other (e.g., self > other) to identify activations that differed between trial types.

Hemodynamic Responses

To obtain time courses for the three trial types in an unbiased manner, regions-of-interest (ROIs) were defined based on peaks identified in the mean *t*-image comparing all three trial types to baseline. In this way, each trial type contributed equally to the generation of ROIs. All significant voxels ($p < .0001$) within 10 mm of a peak location were included in each region. For each participant, hemodynamic response functions (10 frames long) for each trial type were then estimated across each ROI using a finite impulse response formulation of the general linear model (Ollinger et al., 2001; Burock & Dale, 2000). The parameter estimates for this model (calculated using the least-squares solution to the general linear model) are estimates for the temporally evolving response magnitude at each of the 10 points in peristimulus time, selectively averaged across all occurrences of that peristimulus time interval. This approach has recently been implemented by Poldrack and colleagues as an add-on

toolbox to the SPM analysis software (SPM ROI Toolbox, <http://spm-toolbox.sourceforge.net>).

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The data reported in this experiment have been deposited in The fMRI Data Center (<http://www.fmridc.org>). The accession number is 2-2002-112HA.

Note

1. Note that this study was conducted in the spring of 2001, prior to world events that might have altered people's judgments about President Bush.

REFERENCES

- Ackerly, S. S., & Benton, A. L. (1947). Report of case of bilateral frontal lobe defect. *Research Publications: Association for Research in Nervous and Mental Disease*, 27, 479–504.
- Anderson, N. H. (1968). Likableness ratings of 555 personality-trait words. *Journal of Personality and Social Psychology*, 9, 272–279.
- Antrobus, J. S., Singer, J. L., Goldstein, S., & Fortgang, M. (1970). Mindwandering and cognitive structure. *Transactions of the New York Academy of Sciences*, 32, 242–252.
- Bower, G. H., & Gilligan, S.-G. (1979). Remembering information related to one's self. *Journal of Research in Personality*, 13, 420–432.
- Buckner, R. L., Kelley, W. M., & Petersen, S. E. (1999). Frontal cortex contributes to human memory formation [Review]. *Nature Neuroscience*, 2, 311–314.
- Burock, M. A., & Dale, A. M. (2000). Estimation and detection of event-related fMRI signals with temporally correlated noise: A statistically efficient and unbiased approach. *Human Brain Mapping*, 11, 249–260.
- Cohen, J. D., MacWhinney, B., Flatt, M., & Provost, J. (1993). PsyScope: A new graphic interactive environment for designing psychology experiments. *Behavioral Research Methods, Instruments, and Computers*, 25, 257–271.
- Conway, M. A., & Dewhurst, S. A. (1995). The self and recollective experience. *Applied Cognitive Psychology*, 9, 1–19.
- 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.
- Craik, F. I. M., & Tulving, E. (1975). Depth of processing and the retention of words in episodic memory. *Journal of Experimental Psychology: General*, 104, 268–294.
- Demb, J. B., Desmond, J. E., Wagner, A. D., Vaidya, C. J., Glover, G. H., & Gabrieli, J. D. E. (1995). Semantic encoding and retrieval in the left inferior prefrontal cortex: A functional MRI study of task difficulty and process specificity. *Journal of Neuroscience*, 15, 5870–5878.
- Donaldson, D. I., Petersen, S. E., Ollinger, J. M., & Buckner, R. L. (2001). Dissociating state and item components of recognition memory using fMRI. *Neuroimage*, 13, 129–142.
- Friston, K. J., Fletcher, P., Josephs, O., Holmes, A., Rugg, M. D., & Turner, R. (1998). Event-related fMRI: Characterizing differential responses. *Neuroimage*, 7, 30–40.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J.-P., Frith, C. D., & Frackowiak, R. S. J. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping*, 2, 189–210.
- Gabrieli, J. D. E., Desmond, J. E., Demb, J. B., Wagner, A. D., Stone, M. V., Vaidya, C. J., & Glover, G. H. (1996). Functional magnetic resonance imaging of semantic memory processes in the frontal lobes. *Psychological Science*, 7, 278–283.
- Greenwald, A. G., & Banaji, M. R. (1989). The self as a memory system: Powerful, but ordinary. *Journal of Personality and Social Psychology*, 57, 41–54.
- 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.
- Gusnard, D. A., & Raichle, M. E. (2001). Searching for a baseline: Functional imaging and the resting human brain. *Nature Reviews Neuroscience*, 10, 685–694.
- Ingvar, D. H. (1979). "Hyperfrontal" distribution of the cerebral grey matter flow in resting wakefulness; on the functional anatomy of the conscious state. *Acta Neurologica Scandinavica*, 60, 12–25.
- James, W. (1890). *Principles of psychology* (vol. 1). New York: Henry-Holt and Co.
- Kapur, S., Craik, F. I. M., Tulving, E., Wilson, A. A., Houle, S., & Brown, G. M. (1994). Neuroanatomical correlates of encoding in episodic memory: Levels of processing effects. *Proceedings of the National Academy of Sciences, U.S.A.*, 91, 2008–2011.
- Keenan, J. M., & Baillet, S. D. (1980). Memory for personally and socially significant events. In R. S. Nickerson (Ed.), *Attention and performance* (vol. 8, pp. 651–669). Hillsdale, NJ: Erlbaum.
- Klein, S. B., & Kihlstrom, J. F. (1986). Elaboration, organization, and the self-reference effect in memory. *Journal of Experimental Psychology: General*, 115, 26–38.
- Klein, S. B., & Loftus, J. (1988). The nature of self-referent encoding: The contributions of elaborative and organizational processes. *Journal of Personality and Social Psychology*, 55, 5–11.
- Maki, R. H., & McCaul, K. D. (1985). The effects of self-reference versus other reference on the recall of traits and nouns. *Bulletin of the Psychonomic Society*, 23, 169–172.
- Markus, H. (1977). Self-schemata and processing information about the self. *Journal of Personality and Social Psychology*, 35, 63–78.
- Mottaghy, F. M., Krause, B. J., Schmidt, D., Hautzel, H., Herzog, H., Shah, N. J., Halsband, U., & Muller-Gartner, H. W. (2000). Comparison of PET and fMRI activation patterns during declarative memory processes. *Nuclear Medicine*, 39, 196–203.
- Ollinger, J. M., Shulman, G. L., & Corbetta, M. (2001). Separating processes within a trial in event-related functional MRI. *Neuroimage*, 13, 210–217.

- Raczkowski, D., Kalat, J. W., & Nebes, R. (1974). Reliability and validity of some handedness questionnaire items. *Neuropsychologia, 12*, 43–47.
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences, U.S.A., 98*, 676–682.
- Rogers, T. B., Kuiper, N. A., & Kirker, W. S. (1977). Self-reference and the encoding of personal information. *Journal of Personality and Social Psychology, 35*, 677–688.
- Shulman, G. L., Fiez, J. A., Corbetta, M., Buckner, R. L., Miezin, F. M., Raichle, M. E., & Petersen, S. E. (1997). Common blood flow changes across visual tasks: II. Decreases in cerebral cortex. *Journal of Cognitive Neuroscience, 9*, 648–663.
- Stuss, D. T., & Benson, D. F. (1986). *The frontal lobes*. New York: Raven Press.
- Symons, C. S., & Johnson, B. T. (1997). The self-reference effect in memory: A meta-analysis. *Psychological Bulletin, 121*, 371–394.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain* (M. Rayport, Trans.). New York: Thieme Medical Publishers.
- Teasdale, J. D., Dritschel, B. H., Taylor, M. J., Proctor, L., Llyod, C. A., Nimmo-Smith, I., & Baddeley, A. D. (1995). Stimulus-independent thought depends on central executive resources. *Memory and Cognition, 23*, 551–559.
- Wagner, A. D., Schacter, D. L., Rotte, M., Koutstaal, W., Maril, A., Dale, A. M., Rosen, B. R., & Buckner, R. L. (1998). Building memories: Remembering and forgetting verbal experiences as predicted by brain activity. *Science, 281*, 1188–1191.
- Wheeler, M. A., Stuss, D. T., & Tulving, E. (1997). Toward a theory of episodic memory: The frontal lobes and autoegetic consciousness. *Psychological Bulletin, 121*, 331–354.