

Neuroanatomical Correlates of Veridical and Illusory Recognition Memory: Evidence from Positron Emission Tomography

Daniel L. Schacter,¹ Eric Reiman,^{2,3}
Tim Curran,⁴ Lang Sheng Yun,^{3,5} Dan Bandy,³
Kathleen B. McDermott,⁶ and Henry L. Roediger III⁷

¹Department of Psychology
Harvard University
Cambridge, Massachusetts 02138

²Department of Psychiatry
University of Arizona
Tucson, Arizona 85721

³Positron Emission Tomography Center
Good Samaritan Regional Medical Center
Phoenix, Arizona 85006

⁴Department of Psychology
Case Western Reserve University
Cleveland, Ohio 44106

⁵Department of Computer Science and Engineering
Arizona State University
Tempe, Arizona 85287

⁶Department of Radiology
Washington University School of Medicine
St. Louis, Missouri 63110

⁷Department of Psychology
Washington University
St. Louis, Missouri 63130

subjects. The experimental analysis of memory distortions is usually traced to the British psychologist Bartlett (1932), who reported that people sometimes misremember stories they recently studied. Cognitive psychologists have also demonstrated that memory distortions occur in experimental paradigms that use sentences (e.g., Bransford and Franks, 1971), passages of text (Sulin and Dooling, 1974), and sequences of slides (Lof-tus et al., 1978).

Another type of memory distortion that has been extensively examined in cognitive studies is known as false recognition, which was first demonstrated experimentally by Underwood (1965) in experiments using words as target materials. When making old/new recognition judgments about whether words had appeared earlier in a list, subjects sometimes falsely recognized as “old” new words that were semantically or physically related to previously presented items. For example, after studying *table*, people claimed that they recognized as old an associated (but not previously presented) word such as *chair* more often than an entirely unrelated word such as *cloud*. Subsequent research confirmed the existence of false recognition (e.g., Anisfeld and Knapp, 1968), and contemporary investigators continue to investigate the phenomenon (cf. Brainerd et al., 1995; Ceci, 1995; Hintzman, 1988; Wallace et al., 1995).

In the experimental paradigm developed by Underwood (1965), where nonpresented words are preceded by a single associate, the magnitude of the false recognition effect is typically quite small. Roediger and McDermott (1995) have recently described a paradigm for producing a much more robust false recognition effect. Roediger and McDermott revived and modified a procedure initially reported by Deese (1959), who found that after studying a long series of words that are all high associates of a nonpresented target word, subjects frequently falsely recalled the nonpresented target. For example, after studying *candy*, *sugar*, *chocolate*, and other semantic associates of *sweet*, subjects frequently produced the word *sweet* on a recall test. Roediger and McDermott replicated this finding (see also McDermott, 1996) and extended it to recognition memory. They found that subjects frequently and confidently claimed to recognize the nonpresented word *sweet* after studying a list of semantic associates. Indeed, subjects falsely recognized nonpresented words such as *sweet* almost as often as they recognized words that had appeared previously on the study list (see also Payne et al., 1996; Schacter et al., 1996d).

Little is known about the brain systems that are involved in false memories (for discussion, see Johnson et al., 1993; Moscovitch, 1995a; Phelps and Gazzaniga, 1992; Schacter, 1996b; Squire, 1995), and no information is available about patterns of brain activity that might distinguish between veridical and illusory recollections. However, with the recent application of brain imaging techniques such as positron emission tomography (PET) to the study of various forms of memory (e.g., Andreasen et al., 1995; Blaxton et al., 1996; Cahill et al., 1996; Martin et al., 1996; Moscovitch et al., 1995; Schacter et al.,

Summary

Memory distortions and illusions have been thoroughly documented in psychological studies, but little is known about the neuroanatomical correlates of true and false memories. Vivid but illusory memories can be induced by asking people whether they recall or recognize words that were not previously presented, but are semantically related to other previously presented words. We used positron emission tomography to compare brain regions involved in veridical recognition of printed words that were heard several minutes earlier and illusory recognition of printed words that had not been heard earlier. Veridical and illusory recognition were each associated with blood flow increases in a left medial temporal region previously implicated in episodic memory; veridical recognition was distinguished by additional blood flow increases in a left temporoparietal region previously implicated in the retention of auditory/phonological information. This study reveals similarities and differences in the way the brain processes accurate and illusory memories.

Introduction

People sometimes remember events that never happened. Memory distortions and illusions can provide theoretical insights into the nature of remembering and also have important implications for such everyday activities as eyewitness identification and the accuracy of memories retrieved in psychotherapy (for recent reviews, see Johnson et al., 1993; Roediger, 1996; Schacter, 1995, 1996a). Most scientific information about illusory memories comes from cognitive studies of human

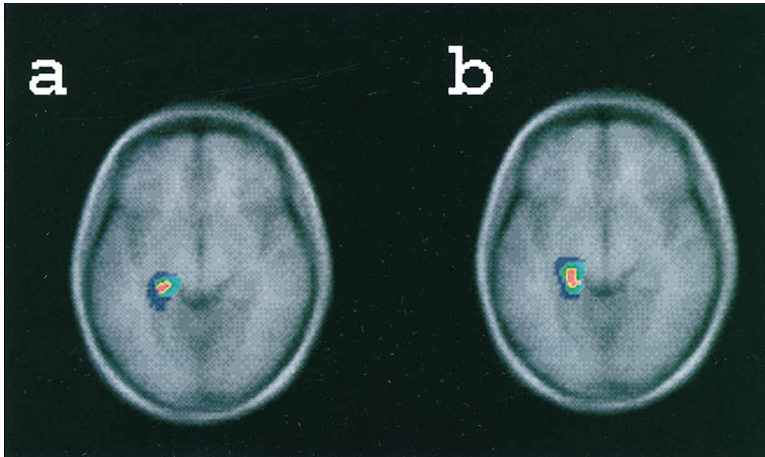


Figure 1. Blood Flow Increases in the Left Medial Temporal Lobe during Veridical and Illusory Word Recognition

The true and false target conditions were each distinguished from the passive fixation baseline by increased blood flow in the left parahippocampal gyrus, as indicated in (a) and (b), respectively. (The true and false target conditions were also distinguished from the passive fixation baseline by significantly increased blood flow bilaterally in occipital and prefrontal regions on this section and others, which are not shown, but appear to be related to visual stimulation and decision making, respectively.) For each comparison, automated algorithms were used to characterize significant increases in regional blood flow (those with a critical z -value > 2.58 , $p < 0.005$ uncorrected for multiple comparisons) and superimpose the increases onto an aver-

age of 12 spatially standardized brain MRIs. The section in each figure corresponds to a section 8 mm below a horizontal plane through the anterior and posterior commissures in a standard brain atlas (Talairach and Tournoux, 1988). Increases in parahippocampal blood flow are shown in red, green, and blue, which correspond to z -values greater than 2.58, 2.33, and 1.64, and uncorrected probabilities less than 0.005, 0.01, and 0.05, respectively.

1996a; Shallice et al., 1994; Squire et al., 1992; Tulving et al., 1994; for reviews, see Buckner and Tulving, 1995; Ungerleider, 1995), and the development of reliable methods for experimentally producing robust false recognition (Roediger and McDermott, 1995), it is now possible to examine directly the neuroanatomical correlates of both veridical and illusory memories. In this article, we report an experiment that uses PET measurements of regional cerebral blood flow, a marker of local neuronal activity, to address these issues.

We adapted the false recognition paradigm developed by Roediger and McDermott (1995) to the demands of PET scanning in order to examine activity in brain regions associated with veridical recognition of previously studied words and illusory recognition of semantic associates. Some clues concerning the possible neuroanatomical substrates of illusory memories in this paradigm are provided by an experiment showing that amnesic patients with medial temporal lobe damage exhibit reduced levels of veridical recognition of previously presented words and false recognition of non-presented associates (Schacter et al., 1996d). In addition, recent PET studies have demonstrated that the conscious recollection of recently studied materials is associated with increased blood flow in the vicinity of the medial temporal lobe (Nyberg et al., 1996b; Schacter et al., 1995, 1996a, 1996c). Taken together, these findings led us to hypothesize that illusory recollections, like veridical ones, should be associated with activity in the medial temporal lobes.

Evidence and theory from cognitive research also provide a basis for hypothesizing about brain regions that may distinguish veridical and illusory recognition in our experimental paradigm. Johnson and colleagues theorized that recollections of actual events contain sensory details not found in memories for imagined or suggested events (Johnson and Raye, 1981), and several behavioral studies have provided evidence confirming this idea (e.g., Johnson et al., 1988; Schooler et al., 1986). In a behavioral study that used the same experimental

paradigm described here, Norman and Schacter (submitted) employed rating scales that probe what kinds of information subjects remember about words they call “old” on a recognition test (i.e., words they remember appearing earlier on the study list). Norman and Schacter found that people indicated remembering significantly more about the sound of words, and thoughts they had when rehearsing words, during veridical than illusory recognition (see also Mather et al., submitted). Accordingly, we hypothesized that activity in regions of the superior temporal lobe involved with auditory or phonological memory might distinguish the two types of recognition.

To investigate these issues, we exposed subjects prior to scanning to a series of 20-word lists, each comprised of semantic associates of a nonpresented “false target.” After a 10 min break, subjects were given separate 1 min PET scans during which they made old/new recognition decisions about either previously heard words (true targets), semantic associates of previously heard words (false targets), or words that were neither previously presented nor semantic associates of true targets (true target controls and false target controls, presented in separate scans). An additional baseline scan was included in which subjects passively fixated on a cross-hair displayed at central fixation (see Table 1 for schematic of the experimental design).

Results

Behavioral Data

Analysis of recognition responses during PET scanning revealed significant levels of both veridical recognition (68% old responses to true targets compared with 33% old responses to true target controls [$p < 0.001$]) and illusory recognition (58% old responses to false targets compared with 33% old responses to false target controls [$p < 0.001$]; subjects also made nonsignificantly more old responses to true targets than to false targets

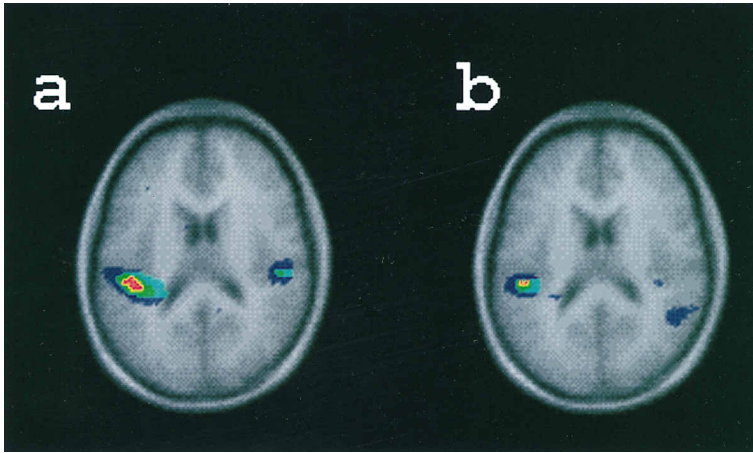


Figure 2. Blood Flow Increases in Temporoparietal Cortex Distinguish Veridical from Illusory Word Recognition

The true target condition was distinguished from the true target control (a), the passive fixation baseline (data not shown), and the false target condition (b) by blood flow increases in the vicinity of the left superior temporal gyrus, temporal plane, and supramarginal gyrus and by smaller increases in the right (a and b each depict all significant blood flow increases on the section displayed). In contrast, the false target condition was not distinguished from either the false target control or passive fixation condition by blood flow increases in the temporoparietal region shown in (a) and (b) ($p > 0.05$). For each comparison, automated algorithms were used to characterize significant increases in regional blood flow (those with a critical z-value > 2.58 ,

$p < 0.005$ uncorrected for multiple comparisons) and superimpose the increases onto an average of 12 spatially standardized brain MRIs. The section in each figure corresponds to a section 20 mm above a horizontal plane through the anterior and posterior commissures in a standard brain atlas (Talairach and Tournoux, 1988). Increases in temporoparietal blood flow are shown in red, green, and blue, which correspond to z-values greater than 2.58, 2.33, and 1.64, and probabilities less than 0.005, 0.01, and 0.05 uncorrected for multiple comparisons, respectively.

[$p = 0.072$], but this trend does not affect the interpretation of our results). The absolute magnitude of the false recognition effect was somewhat smaller than in previous purely behavioral studies (Payne et al., 1996; Roediger and McDermott, 1995; Schacter et al., 1996d), probably reflecting changes in the experimental procedure that are necessitated by the demands of PET scanning. Nonetheless, the fact that levels of veridical and illusory recognition were relatively comparable replicates findings from previous studies.

PET Data

Analysis of blood flow increases revealed similarities and differences between veridical and illusory recognition. We first consider data relevant to our a priori hypotheses about medial temporal and superior temporal regions, respectively, and then consider further exploratory analyses.

Medial Temporal Lobes

Consistent with our hypothesis that both true and false recognition would be associated with medial temporal

lobe activity, comparisons of blood flow in the true and false target conditions to the fixation baseline revealed that veridical and illusory recognition were each characterized by significantly increased blood flow in the left medial temporal lobe (i.e., in the vicinity of the left parahippocampal gyrus; results for both veridical and illusory recognition are shown in Table 2 and Figure 1). Post hoc comparisons revealed greater parahippocampal blood flow increases on the left than on the right for both true and false memories ($p < 0.05$).

By contrast, we did not observe significant medial temporal blood flow increases when we compared the true target control and false target control conditions with the fixation baseline, suggesting that the medial temporal increases shown in Table 2 and Figure 1 may be specifically related to recollection of true and false targets, respectively. However, the true target minus true target control and false target minus false target control comparisons did not reveal significant blood flow increases in the parahippocampal or medial temporal regions, although there were bilateral trends for parahippocampal blood flow increases ($0.005 < p < 0.01$) in

Table 1. Summary of the Experimental Procedure

Task	Scan	Materials	Condition
Listen to words	—	Lists of associated words	Study
Fixate on cross-hair	A	Cross-hair	Passive fixation
Old/new recognition	B	Previously studied words	True targets
Old/new recognition	C	Nonstudied words	True target controls
Old/new recognition	D	Nonstudied strong associates of presented words	False targets
Old/new recognition	E	Nonstudied words not preceded by high associates	False target controls

Prior to scanning subjects listened to 24 separate words lists, each containing 20 associates of a nonpresented false target. After presentation of all the lists, there was a 10 min rest break followed by five separate 60 s scans, separated from each other by 10 min rest periods and counterbalanced for order. One was a cross-hair fixation scan (A), which came first for half of the subjects and last for the other half. During each of the other four scans (B–E), subjects saw 12 words and made old/new recognition memory decisions with a key press response concerning true targets from the study list (scan B), true target control words that did not appear on a study list (scan C), false targets that had not been heard during study list presentation but were preceded by a list of associates (scan D), and false target controls that were neither heard during the study list nor preceded by a list of associates (scan E).

Table 2. Blood Flow Increases in Critical Comparisons

Comparison	Region	Brodman Area	X (mm)	Y (mm)	Z (mm)	z-score
True target-passive fixation	L. parahippocampal gyr.	35	-20	-28	-8	2.72
	L. sup. temp./supramarg. gyr.	42, 22, 40	-42	-26	16	3.23
False target-passive fixation	L. parahippocampal gyr.	35	-16	-32	-8	2.78
True target-true target control	L. sup. temp./supramarg. gyr.	42, 22, 40	-42	-28	20	3.00
	L. midinsular cortex	-	-36	2	4	2.66
False target-false target	R. ant. prefrontal	10/11	10	36	-16	3.18
Control	L. orbitofrontal	11	-18	40	-24	3.29
	R. orbitofrontal	11	14	22	-24	3.05
	L. cerebellum	-	-30	-62	-20	3.27
	R. cerebellum	-	12	-34	-12	3.41
True target-false target	L. sup. temp./supramarg. gyr.	42, 22, 40	-42	-28	20	2.62

Location and magnitude of significant blood flow increases for each of the comparisons noted in the table. The location of maximal z-scores was defined according to the brain atlas of Talairach and Tournoux (1988), such that x is the distance in millimeters to the right (+) or left (-) of midline, y is the distance in mm anterior (+) or posterior (-) to the anterior commissure, and z is the distance in millimeters superior (+) or inferior (-) to a horizontal plane through the anterior and posterior commissures. For each comparison except for those involving passive fixation, all significant ($p < 0.005$) activations are reported. For comparisons to passive fixation, significant increases are presented for parahippocampal and temporoparietal areas that are related to our a priori hypotheses.

Abbreviations: L., left; R., right; supramarg., supramarginal; gyr., gyrus; sup., superior; temp., temporal; ant., anterior.

the true target minus true target control comparison. These results are attributable to small, though not significant, parahippocampal blood flow increases in the true target control and false target control conditions relative to passive fixation. Indeed, there was a trend ($0.01 < p < 0.05$) for left parahippocampal activation in the false target control minus passive fixation comparison. Because false alarm rates were substantial in both control conditions (33%), suggesting that some recollection occurred in each condition, these trends likely reflect a weak false recognition response.

Superior Temporal Cortex

Supporting our hypothesis that the two types of recognition might be distinguished by activity in the vicinity of superior temporal cortex, we found that veridical recognition was associated with significant blood flow increases in the left temporoparietal cortex (i.e., in the vicinity of the superior temporal gyrus, the temporal plane, and inferior aspects of the supramarginal gyrus, Brodmann areas [BAs] 42, 22, and 40, respectively; Table 2 and Figure 2), whereas false recognition was not associated with significant blood flow increases or trends in this region. The true target condition was distinguished from both the true target control and passive fixation baseline conditions by significant increases in left temporoparietal blood flow, but the false target condition was not distinguished from either the false target control or the fixation baseline condition by significant blood flow increases or trends in this region. A direct comparison between true and false targets revealed significantly greater blood flow in the left temporoparietal region during veridical than illusory recognition; post hoc comparisons revealed an additional increase in right temporoparietal blood flow ($0.01 < p < 0.05$) that was significantly smaller than in the left ($p < 0.005$). An additional post hoc analysis indicated that the true target minus true target control comparison was distinguished from the false target minus false target control comparison by greater blood flow increases in the left ($0.005 < p < 0.01$) and right ($p < 0.005$) temporoparietal regions.

The failure to observe significant left temporoparietal

blood flow increases during false recognition does not appear to be attributable to increased activity during the false target control condition (i.e., an increase related to some aspect of the words used in this condition). Whereas the true target condition was distinguished from the false target condition by significant blood flow increases in the left temporoparietal region, the true target control condition was not distinguished from the false target control condition by significant blood flow increases or trends in this region.

Although findings concerning the left temporoparietal region appear to be unrelated to any systematic difference in features of words used in the true and false recognition lists, post hoc analyses indicate that false target controls were distinguished from true target controls by significant blood flow increases in the vicinity of posterior cingulate cortex bilaterally, left midinsular cortex, and right temporoparietal cortex. Thus, findings concerning the left midinsular cortex (Table 2) and right temporoparietal region may be at least partly related to differences in word sets.

Exploratory Analyses

Exploratory analyses revealed further similarities and differences between veridical and illusory recognition. Similarities between veridical and illusory recognition were evident in comparison to passive fixation. Specifically, we observed significant blood flow increases in several regions previously linked to episodic word recognition (cf. Andreasen et al., 1995; Buckner and Tulving, 1995; Nyberg et al., 1995; Ungerleider, 1995) in each of the four main experimental conditions (true targets, false targets, true target controls, and false target controls) compared with passive fixation: bilateral dorsolateral/anterior prefrontal cortex (BA 10/46), bilateral cerebellum, left middle temporal gyrus, and precuneus (on the right for true targets and true target controls, and on the left for false targets and false target controls). There were also significant blood flow increases in all four conditions (compared with passive fixation) in bilateral visual cortex (BAs 17-19) and in a superior aspect of the left inferior parietal lobule (BA 40) that is distinct from

the region discussed earlier that distinguishes between veridical and illusory recognition. These increases could reflect aspects of episodic word recognition that are common to the four experimental conditions, or visual, semantic, and phonological word processing, independent of episodic recognition.

Differences between veridical and illusory recognition were observed when the false target condition was compared with the false target control condition and when the true target condition was compared with the true target control condition. The false target minus false target control comparison revealed that blood flow increases in anterior prefrontal cortex (BA 10), orbitofrontal cortex (BA 11), and the cerebellum were associated with illusory recognition (Table 2). However, analysis of the true target minus true target control comparison did not reveal any corresponding changes for veridical recognition. Direct comparisons revealed that illusory recognition was distinguished from veridical recognition by trends for blood flow increases in prefrontal cortex, orbitofrontal cortex, and cerebellum ($0.005 < p < 0.05$).

Further exploratory analyses revealed different patterns of blood flow decreases during veridical and illusory recognition. For veridical recognition, there was a trend ($p < 0.01$) for a blood flow decrease in primary visual cortex bilaterally (BA 17) in the true target condition compared with the true target control condition; for illusory recognition, there were significant blood flow decreases in the right posterior cingulate cortex (BA 30/23) and in the vicinity of the right superior temporal gyrus, temporal plane, and inferior aspects of the supramarginal gyrus (BAs 42, 22, and 40) in the false target condition compared with the false target control condition.

Discussion

This experiment has yielded several novel findings concerning the brain systems involved in true and false recognition. First, consistent with our a priori hypothesis, we documented blood flow increases in the left medial temporal lobe for both veridical and illusory recognition. Second, and also confirming an a priori hypothesis, veridical recognition was distinguished from illusory recognition by blood flow increases in the vicinity of the left superior temporal lobe. Third, exploratory analyses revealed that false recognition was associated with greater blood flow increases in prefrontal cortex, orbitofrontal cortex, and cerebellum than was veridical recognition. We now consider each of these findings in relation to previous research.

In light of earlier data showing low levels of false recognition in amnesic patients with medial temporal lobe damage (Schacter et al., 1996d), and PET studies linking medial temporal regions with successful conscious recollection (Nyberg et al., 1996b; Schacter et al., 1995, 1996a, 1996c), the observed blood flow increases in the left medial temporal lobe constitute a potentially important similarity between veridical and illusory recognition. Our findings, combined with the earlier data from amnesics and PET, raise the possibility that illusory recollections of false targets seem authentic

because they are accompanied by medial temporal lobe activity that is usually linked to veridical conscious recollection (for further discussion of conscious recollection and medial temporal regions, see Moscovitch, 1995b; for illusory familiarity and medial temporal activity, see Milner, 1989). However, this hypothesis must be viewed cautiously because we observed significant medial temporal blood flow increases for true and false targets only in comparison to the fixation baseline. Thus, the possibility remains open that the observed increases are associated with some aspect of the recognition task unrelated to conscious recollection (e.g., visual stimulation or lexical processing), although previous studies of visual word processing have not reported blood flow increases in medial temporal/hippocampal regions (Démonet et al., 1992; Petersen et al., 1989). In addition, as we noted earlier, levels of false recognition to both true target controls and false target controls were quite high (33% false alarms to both), possibly high enough that nonsignificant trends for medial temporal blood flow increases in these conditions made it difficult to detect further increases to true and false targets, respectively. Consistent with this possibility, a previous PET experiment revealed left medial temporal lobe blood flow increases in association with false recognition of nonstudied visual objects (Schacter et al., 1995). Thus, it seems likely that the left parahippocampal blood flow increases we observed are related to episodic memory.

Our data consistently show that blood flow in a left temporoparietal region involving the superior temporal gyrus, temporal plane, and supramarginal gyrus (BAs 42, 22, and 40) was significantly greater during veridical than illusory recognition. Previous PET studies have linked the temporoparietal region that was activated preferentially during veridical recognition with auditory/phonological processing and retention (Howard et al., 1992; Paulesu et al., 1993; Petersen et al., 1989); lesions to the supramarginal gyrus are also known to disrupt phonological analysis and retrieval (Roeltgen and Heilman, 1985). In conjunction with the previously mentioned behavioral experiment showing that subjects remember more auditory information about true targets than false targets (Norman and Schacter, submitted), and earlier behavioral studies showing that memories of perceived events contain sensory details not found in memories for imagined events (Johnson et al., 1988; Schooler et al., 1986), these observations suggest that the preferential activation of the temporoparietal region during veridical recognition reflects the retrieval of auditory or phonological information about previously hearing or rehearsing words, which would be available for true targets but not for false targets. This idea is also consistent with a recent study showing activation of a similar temporoparietal region during retrieval of recently studied words (Schacter et al., 1996a).

However, other possibilities should also be considered. For instance, Nyberg et al. (1995) found activation of the left middle temporal gyrus during visual recognition of words that had been studied auditorily when the encoding task involved a semantic judgment, but not when the encoding task involved a perceptual judgment. Because we used lists of semantically related words, it is possible that the temporoparietal blood flow increases

we observed reflect activation of semantic information during recognition of previously heard words, as in the Nyberg et al. experiment. Similarly, Blaxton et al. (1996) reported that performance of a memory task requiring retrieval of semantic information was associated with blood flow increases in the left middle temporal gyrus and bilaterally in a lateral aspect of the inferior parietal lobule (BA 40). However, if temporoparietal activation in our experiment reflects semantic processing, we would have expected to observe it for false targets, which are semantic associates of studied words. Moreover, Hayman and Rickards (1995) have shown that semantic encoding enhances recall of the sensory modality of auditorily presented words, raising the possibility that Nyberg et al.'s left middle temporal gyrus activation reflects memory for auditory/perceptual information, as opposed to semantic information. Finally, the temporo-parietal region activated in the present study is superior to the middle temporal gyrus activated in the Nyberg et al. and Blaxton et al. experiments, and inferior to the parietal region activated in the Blaxton et al. experiment. Therefore, it is uncertain whether previously reported areas of semantic activation are homologous to the left temporoparietal region that distinguished between veridical and illusory recognition in the present study. Overall, the evidence is consistent with the idea that blood flow increases in this region reflect retrieval of auditory/phonological information rather than semantic information.

Results from the false target versus false target control comparison also revealed that blood flow increases in the vicinity of the frontal pole and orbitofrontal cortex (BAs 10 and 11, respectively) are specifically associated with illusory recognition, including a right anterior frontal region (BA 10) that has been activated in numerous previous studies of episodic retrieval (cf. Andreasen et al., 1995; Blaxton et al., 1996; Buckner, 1996; Moscovitch et al., 1995; Nyberg et al., 1996a; Shallice et al., 1994; Squire et al., 1992; Tulving et al., 1994). This region has been implicated in effortful retrieval processes (Kapoor et al., 1995; Nyberg et al., 1995; Schacter et al., 1996a) that may be related to subjects' attempts to reinstate the context of a recent event (Norman and Schacter, 1996; Schacter, 1996b). Because we observed frontal lobe blood flow increases in each of the four main conditions relative to passive fixation, but failed to observe them in the true target minus true target control comparison, it seems likely that such increases reflect some aspect of the retrieval effort involved in attempting to determine whether a word on the recognition test appeared earlier in the experiment. Our data linking prefrontal activation with false recognition are also consistent with findings from brain-damaged patients that frontal lobe lesions can produce high levels of false recognition and related memory distortions (Curran et al., 1996; Moscovitch, 1995a; Schacter et al., 1996b), perhaps because such patients do not engage in the effortful processes necessary to distinguish accurate from illusory memories.

We also found activation of the cerebellum during illusory recognition (i.e., the false target minus false target control comparison). Increases in cerebellar blood flow have been reported in previous PET studies of episodic memory (Andreasen et al., 1995; Blaxton et al.,

1996; Buckner and Tulving, 1995; Schacter et al., 1996a; Ungerleider, 1995) and other cognitive functions (Fiez, 1996; Middleton and Strick, 1994; Raymond et al., 1996). It has been proposed that the cerebellum is part of a functional circuit that includes prefrontal cortex (Andreasen et al., 1995; Middleton and Strick, 1994) and is critical for effortful processes involved in error detection (Fiez, 1996; Fiez et al., 1992). As with the frontal lobes, we observed cerebellar blood flow increases in each of the four main experimental conditions compared with passive fixation, but not in the true target minus true target control comparison, so it seems likely that such increases are related to retrieval effort. We suggest that blood flow increases in prefrontal cortex and cerebellum reflect subjects' efforts to inhibit (Shimamura, 1995), monitor (Moscovitch, 1995a; Shallice, 1988), or make decisions about the sense of familiarity or recollection associated with false recognition. For example, during false recognition, subjects may be attempting to resolve a conflict between two opposing tendencies: to call a word "old" because they remember other associated words from the list that create an illusory sense of recollecting the nonpresented word, and to call a word "new" because they fail to retrieve auditory/phonological information that is specifically associated with veridical recognition. Frontal and cerebellar blood flow increases during false recognition may reflect this effortful monitoring or decision making process. The fact that levels of veridical and illusory recognition were roughly similar suggests that an absence of auditory/phonological information is not sufficient to overcome the sense of recollection experienced in response to a false target.

This study reveals similarities and differences in the neuroanatomical correlates of veridical and illusory recognition. It provides a foundation for understanding the brain systems that support accurate and mistaken recollections of past events.

Experimental Procedures

Design, Procedure, and Materials

Prior to scanning, subjects listened to 24 lists of words, each containing 20 words that were semantically related to a nonpresented false target; these 24 lists were preceded by a block of 20 unrelated filler words and followed by a block of 20 unrelated filler words. For example, subjects heard *taste, bitter, candy, chocolate, cake, sour, eat, pie*, and other associates of a false target (i.e., *sweet*) that was not previously heard or viewed during the recognition task, or heard *thread, pin, eye, sewing, sharp, point, prick, thimble, pain*, and other associates of another false target that was not previously presented (i.e., *needle*). Studied words, selected from an earlier behavioral experiment (Roediger and McDermott, 1995), and standard association norms (Russell and Jenkins, 1954) were presented at a rate of 1700 ms per word. Each list of 20 associates was presented in order from the first (strongest) associate to the last (weakest) associate. After presentation of each list, subjects responded aloud to simple arithmetic problems for 20 s; after presentation of all 520 words, there was a 10 min rest break, followed by five separate 60 s scans, separated from each other by 10 min rest periods. One was a passive fixation scan, which came first for half the subjects and last for the other half (scan A). Subjects looked at a cross-hair displayed at central fixation for the entire 60 s. During each of the remaining four scans (scans B–E), counterbalanced for order across subjects, subjects saw 12 words presented visually at central fixation for 4500 ms each, separated by a 500 ms interword interval. Subjects made old/new recognition decisions with a key press response and could respond anytime during the 4500 s the stimulus appeared or during

the 500 ms before the next stimulus. Each scan contained either true targets from the study list (scan B), true target controls that had not been presented on a study list (scan C), false targets that had not been heard but were preceded by a list of associates (scan D), or false target controls that had not been heard or preceded by a list of associates (scan E). Separate true and false target controls were used to control for possible differences in word sets. True targets and true target controls were always the tenth most frequent associate of the theme word. False targets and false target controls were always "theme words" to which all other words were associated; the only difference between false targets and false target controls is that the former were preceded by a list of associates prior to scanning and the latter were not. The experiment was counterbalanced across subjects so that individual words appeared equally often as false targets (i.e., they were preceded by a list of associates) or false target controls (i.e., they were not preceded by a list of associates), or they were heard equally often as true targets (i.e., they appeared on the study list) or true target controls (i.e., they were not heard on the study list).

Subjects

Twelve healthy female, right-handed volunteers (mean age = 23 years, SD = 4.8 years) participated in the experiment. All subjects had a normal neurological examination and no evidence of psychiatric disorders using a structured psychiatric interview.

PET Scanning

Five 31-slice PET images of regional cerebral blood flow were obtained using the ECAT 951/31 scanner (Siemens, Knoxville, TN), 45 mCi intravenous bolus injections of ¹⁵O-water, and 60 s scans separated by 10–15 min between scans. PET images were reconstructed with an in-plane resolution of about 10 mm full-width at half-maximum (FWHM) and a slice thickness of about 5 mm FWHM. For data analysis, a Gaussian filter yielded an in-plane resolution of about 20 mm FWHM and a slice thickness of about 10 mm FWHM.

Automated algorithms were used to align the five PET images from each subject, spatially transform them into the coordinates of a standard brain atlas, control for variations in whole-brain measurements, compute z-score maps of significant increases in regional blood flow for each comparison (z-score > 2.58, p < 0.005, uncorrected for multiple comparisons), and superimpose the maps onto an average of 12 spatially standardized brain MRIs (Collins et al., 1994; Friston et al., 1991; Woods et al., 1992; Talairach and Tournoux, 1988). This analysis allowed us to test the hypotheses that veridical and illusory recognition are each associated with blood flow increases in the vicinity of the medial temporal lobe and that veridical recognition is distinguished from illusory recognition by blood flow increases in the vicinity of the superior temporal gyrus; it also allowed us to explore blood flow increases in additional brain regions.

Acknowledgments

We thank Gayle Bessenoff, Sharon Koleske, and Ken Norman for research assistance and Endel Tulving for helpful comments on an earlier draft of the manuscript. Supported by grants from the Charles A. Dana Foundation, Robert S. Flinn Foundation, National Institute on Aging AG08441, and National Institute of Neurological Disorders and Stroke NS26985.

The costs of publication of this article were defrayed in part by the payment of page charges. This article must therefore be hereby marked "advertisement" in accordance with 18 USC Section 1734 solely to indicate this fact.

Received June 17, 1996; revised July 1, 1996.

References

Andreasen, N.C., O'Leary, D.S., Arndt, S., Cizadlo, T., Hurtig, R., Rezai, K., Watkins, G.L., Boles Ponto, L.L., and Hichwa, R.D. (1995). Short-term and long-term verbal memory: a positron emission tomography study. *Proc. Natl. Acad. Sci. USA* 92, 5111–5115.

Anisfeld, M., and Knapp, M. (1968). Association, synonymy, and directionality in false recognition. *J. Exp. Psychol.* 77, 171–179.

Bartlett, F.C. (1932). *Remembering* (Cambridge: Cambridge University Press).

Blaxton, T.A., Bookheimer, S.Y., Zeffiro, T.A., Figliozzi, C.M., Gaillard, W.D., and Theodore, W.H. (1996). Functional mapping of human memory using PET: comparisons of conceptual and perceptual tasks. *Can. J. Exp. Psychol.* 50, 42–56.

Brainerd, C.J., Reyna, V.F., and Kneer, R. (1995). False-recognition reversal: when similarity is distinctive. *J. Memory Language* 34, 157–185.

Bransford, J.D., and Franks, J.J. (1971). The abstraction of linguistic ideas. *Cogn. Psychol.* 2, 331–350.

Buckner, R.L. (1996). Beyond HERA: contributions of specific prefrontal brain areas to long-term memory retrieval. *Psychon. Bull. Rev.* 3, 149–158.

Buckner, R.L., and Tulving, E. (1995). Neuroimaging studies of memory: theory and recent PET results. In *Handbook of Neuropsychology*, F. Boller and J. Grafman, eds. (Amsterdam: Elsevier), pp. 439–466.

Cahill, L., Haier, R.J., Fallon, J., Alkire, M., Tang, C., Keator, D., Wu, J., and McGaugh, J.L. (1996). Amygdala activity at encoding correlated with long-term, free recall of emotional information. *Proc. Natl. Acad. Sci. USA*, in press.

Ceci, S.J. (1995). False beliefs: some developmental and clinical considerations. In *Memory Distortion: How Minds, Brains and Societies Reconstruct the Past*, D.L. Schacter, J.T. Coyle, G.D. Fischbach, M.-M. Mesulam, and L.E. Sullivan, eds. (Cambridge, Massachusetts: Harvard University Press), pp. 91–128.

Collins, D.L., Neelin, P., Peters, T.M., and Evans, A.C. (1994). Automatic 3D intersubject registration of MR volumetric data in standardized Talairach space. *J. Comp. Assist. Tomogr.* 18, 192–204.

Curran, T., Schacter, D.L., Norman, K.A., and Galluccio, L. (1996). False recognition after a right frontal lobe infarction: memory for general and specific information. *Neuropsychologia*, in press.

Deese, J. (1959). On the prediction of occurrence of particular verbal intrusions in immediate recall. *J. Exp. Psychol.* 58, 17–22.

Démonet, J.-F., Chollet, F., Ramsay, S., Cardebat, D., Nespoulous, J.-L., Wise, R., Rascol, A., and Frackowiak, R. (1992). The anatomy of phonological and semantic processing in normal subjects. *Brain* 115, 1753–1768.

Fiez, J.A. (1996). Cerebellar contributions to cognition. *Neuron* 16, 13–15.

Fiez, J.A., Petersen, S.E., Cheney, M.K., and Raichle, M.E. (1992). Impaired non-motor learning and error detection associated with cerebellar damage. *Brain* 115, 155–178.

Friston, K.J., Frith, C.D., Liddle, P.R., Dolan, R.J., Lammertsma, A.A., and Frackowiak, R.S.J. (1991). The relationship between global and local changes in PET scans. *J. Cereb. Blood Flow Metab.* 10, 458–466.

Hayman, C.A., and Rickards, C. (1995). A dissociation in the effects of study modality on tests of implicit and explicit memory. *Memory Cogn.* 23, 95–112.

Hintzman, D.L. (1988). Judgements of frequency and recognition memory in a multiple-trace memory model. *Psychol. Rev.* 95, 528–551.

Howard, D., Patterson, K., Wise, R., Brown, W.D., Friston, K., Weiller, C., and Frackowiak, R. (1992). The cortical localization of the lexicons: positron emission tomography evidence. *Brain* 115, 1769–1782.

Johnson, M.K., and Raye, C.L. (1981). Reality monitoring. *Psychol. Rev.* 88, 67–85.

Johnson, M.K., Foley, M.A., Suengas, A.G., and Raye, C.L. (1988). Phenomenal characteristics of memories for perceived and imagined autobiographical events. *J. Exp. Psychol. Gen.* 117, 371–376.

Johnson, M.K., Hashtroudi, S., and Lindsay, D.S. (1993). Source monitoring. *Psychol. Bull.* 114, 3–28.

Kapur, S., Craik, F.I.M., Jones, C., Brown, G.H., Houles, S., and

- Tulving, E. (1995). Functional role of prefrontal cortex in retrieval of memories: a PET study. *Neuroreport* 6, 1880–1884.
- Loftus, E.F., Miller, D.G., and Burns, H.J. (1978). Semantic integration of verbal information into a visual memory. *J. Exp. Psychol. Hum. Learn. Mem.* 4, 19–31.
- Martin, A., Wiggs, C.L., Ungerleider, L.G., and Haxby, J.U. (1996). Neural correlates of category-specific knowledge. *Nature* 379, 649–652.
- McDermott, K.B. (1996). The persistence of false memories in list recall. *J. Memory Language* 35, 212–230.
- Middleton, F.A., and Strick, P.L. (1994). Anatomical evidence for cerebellar and basal ganglia involvement in higher cognitive function. *Science* 266, 458–461.
- Milner, P.M. (1989). A cell assembly theory of hippocampal amnesia. *Neuropsychologia* 27, 23–30.
- Moscovitch, M. (1995a). Confabulation. In *Memory Distortion: How Minds, Brains, and Societies Reconstruct the Past*, D.L. Schacter, J.T. Coyle, G.D. Fischbach, M.-M. Mesulam, and L.E. Sullivan, eds. (Cambridge, Massachusetts: Harvard University Press), pp. 226–254.
- Moscovitch, M. (1995b). Recovered consciousness: a hypothesis concerning modularity and episodic memory. *J. Clin. Exp. Neuropsychol.* 17, 276–290.
- Moscovitch, M., Kapur, S., Köhler, S., and Houle, S. (1995). Distinct neural correlates of visual long-term memory for spatial location and object identity: a positron emission tomography (PET) study in humans. *Proc. Natl. Acad. Sci. USA* 92, 3721–3725.
- Norman, K.A., and Schacter, D.L. (1996). Implicit memory, explicit memory, and false recollection: a cognitive neuroscience perspective. In *Implicit Memory and Metacognition*, L.M. Reder, ed. (Hillsdale, New Jersey: Erlbaum), in press.
- Nyberg, L., Tulving, E., Habib, R., Nilsson, L.-G., Kapur, S., Houle, S., Cabeza, R., and McIntosh, A.R. (1995). Functional brain maps of retrieval mode and recovery of episodic information. *Neuroreport* 6, 249–252.
- Nyberg, L., Cabeza, R., and Tulving, E. (1996a). PET studies of encoding and retrieval: the HERA model. *Psychon. Bull. Rev.* 3, 135–148.
- Nyberg, L., McIntosh, A.R., Houle, S., Nilsson, L.-G., and Tulving, E. (1996b). Activation of medial temporal structures during episodic memory retrieval. *Nature* 380, 715–717.
- Paulesu, E., Frith, C.D., and Frackowiak, R.S.J. (1993). The neural correlates of the verbal component of working memory. *Nature* 362, 342–345.
- Payne, D.G., Elie, C.J., Blackwell, J.M., and Neuschatz, J.S. (1996). Memory illusions: recalling, recognizing, and recollecting events that never occurred. *J. Memory Language* 35, 261–285.
- Petersen, S.E., Fox, P.T., Posner, M.I., Mintun, M.A., and Raichle, M. E. (1989). Positron emission tomographic studies of the processing of single words. *J. Cogn. Neurosci.* 1, 153–170.
- Phelps, E., and Gazzaniga, M.S. (1992). Hemispheric differences in mnemonic processing: the effects of left hemisphere interpretation. *Neuropsychologia* 30, 293–297.
- Raymond, J.L., Lisberger, S.G., and Mauk, M.D. (1996). The cerebellum: a neuronal learning machine? *Science* 272, 1126–1131.
- Roediger, H.L., III (1996). Memory illusions. *J. Memory Language* 35, 76–100.
- Roediger, H.L., III, and McDermott, K.B. (1995). Creating false memories: remembering words not presented in lists. *J. Exp. Psychol. Learn. Mem. Cogn.* 21, 803–814.
- Roeltgen, D.P., and Heilman, K.M. (1985). Review of agraphia and a proposal for an anatomically-based neuropsychological model of writing. *Appl. Psycholinguistics* 6, 205–230.
- Russell, W.A., and Jenkins, J.J. (1954). Technical Report Number 11, Contract N8 ONR 66216 (Minneapolis, Minnesota: University of Minnesota).
- Schacter, D.L. (1995). Memory distortion: history and current status. In *Memory Distortion: How Minds, Brains and Societies Reconstruct the Past*, D.L. Schacter, J.T. Coyle, G.D. Fischbach, M.-M. Mesulam, and L. E. Sullivan, eds. (Cambridge, Massachusetts: Harvard University Press), pp. 1–43.
- Schacter, D.L. (1996a). *Searching for Memory: The Brain, the Mind, and the Past* (New York: Basic Books).
- Schacter, D.L. (1996b). Illusory memories: a cognitive neuroscience analysis. *Proc. Natl. Acad. Sci. USA*, in press.
- Schacter, D.L., Reiman, E., Uecker, A., Polster, M.R., Yun, L.S., and Cooper, L.A. (1995). Brain regions associated with retrieval of structurally coherent visual information. *Nature* 376, 587–590.
- Schacter, D.L., Alpert, N.M., Savage, C.R., Rauch, S.L., and Albert, M.S. (1996a). Conscious recollection and the human hippocampal formation: evidence from positron emission tomography. *Proc. Natl. Acad. Sci. USA* 93, 321–325.
- Schacter, D.L., Curran, T., Galluccio, L., Milberg, W., and Bates, J. (1996b). False recognition and the right frontal lobe: a case study. *Neuropsychologia*, in press.
- Schacter, D.L., Savage, C.R., Alpert, N.M., Rauch, S.L., and Albert, M.S. (1996c). The role of hippocampus and frontal cortex in age-related memory changes: a PET study. *Neuroreport* 7, 1165–1169.
- Schacter, D.L., Verfaellie, M., and Pradere, D. (1996d). The neuropsychology of memory illusions: false recall and recognition in amnesic patients. *J. Memory Language* 35, 319–334.
- Schooler, J.W., Gerhard, D., and Loftus, E.F. (1986). Qualities of the unreal. *J. Exp. Psychol. Learn. Mem. Cogn.* 12, 171–181.
- Shallice, T. (1988). *From Neuropsychology to Mental Structure* (Cambridge: Cambridge University Press).
- Shallice, T., Fletcher, P., Frith, C.D., Grasby, P., Frackowiak, R.S.J., and Dolan, R.J. (1994). Brain regions associated with acquisition and retrieval of verbal episodic memory. *Nature* 368, 633–635.
- Shimamura, A.P. (1995). Memory and frontal lobe function. In *The Cognitive Neurosciences*, M. Gazzaniga, ed. (Cambridge, Massachusetts: MIT Press), pp. 803–813.
- Squire, L.R. (1995). Biological foundation of accuracy and inaccuracy in memory. In *Memory Distortion: How Minds, Brains, and Societies Reconstruct the Past*, D.L. Schacter, J.T. Coyle, G.D. Fischbach, M.-M. Mesulam, and L.E. Sullivan, eds. (Cambridge, Massachusetts: Harvard University Press), pp. 197–225.
- Squire, L.R., Ojemann, J.G., Miezin, F.M., Petersen, S.E., Videen, T.O., and Raichle, M.E. (1992). Activation of the hippocampus in normal humans: a functional anatomical study of memory. *Proc. Natl. Acad. Sci. USA* 89, 1837–1841.
- Sulin, R.A., and Dooling, D.J. (1974). Intrusion of a thematic idea in retention of prose. *J. Exp. Psychol.* 103, 255–262.
- Talairach, J., and Tournoux, P. (1988). *Co-planar Stereotaxic Atlas of the Human Brain* (New York: Thieme Medical Publishing).
- Tulving, E., Kapur, S., Craik, F.I.M., Moscovitch, M., and Houle, S. (1994). Hemispheric encoding/retrieval asymmetry in episodic memory: positron emission tomography findings. *Proc. Natl. Acad. Sci. USA* 91, 2016–2020.
- Underwood, B.J. (1965). False recognition produced by implicit verbal responses. *J. Exp. Psychol.* 70, 122–129.
- Ungerleider, L.G. (1995). Functional brain imaging studies of cortical mechanisms for memory. *Science* 270, 760–775.
- Wallace, W.P., Stewart, M.T., Sherman, H.L., and Mellor, M.D. (1995). False positives in recognition memory produced by cohort activation. *Cognition* 55, 85–113.
- Woods, R.P., Cherry, S.R., and Mazziotta, J.C. (1992). Rapid automated algorithm for aligning and reslicing PET images. *J. Comp. Assist. Tomogr.* 16, 620–633.