

Separable Routes to Human Memory Formation: Dissociating Task and Material Contributions in the Prefrontal Cortex

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Abstract

■ The present study used fMRI to investigate functional dissociations across frontal regions during incidental memory formation. Subjects were imaged while encoding materials with differential access to phonological codes (nonfamous faces and nameable famous faces) under task conditions that encouraged elaborate (deep) or superficial (shallow) encoding strategies. Results revealed a functional dissociation between dorsal posterior regions of the prefrontal cortex (BA 6/44) that were sensitive to material type

(famous vs. nonfamous), irrespective of the encoding task, and ventral anterior regions of the prefrontal cortex (BA 45/47) that were uniquely sensitive to task demands (deep vs. shallow), regardless of material type. Further, subjects realized a memorial advantage to the extent that they recruited these dissociable frontal regions. These results demonstrate a posterior/anterior dichotomy in the frontal cortex that underlies separable code-based routes to human memory formation. ■

INTRODUCTION

Recent functional neuroimaging studies have highlighted frontal contributions to human memory formation. For instance, studies of intentional memorization have demonstrated a material-specific dissociation across hemispheres (Golby et al., 2001; McDermott, Buckner, Petersen, Kelley, & Sanders, 1999; Kelley et al., 1998; Wagner, Poldrack, et al., 1998). Here, memorization of verbal material (e.g., words) activates frontal regions preferentially in the left hemisphere (along the dorsal extent of the inferior frontal gyrus near Brodmann's area [BA] 6/44), whereas memorization of nonverbal material (e.g., nonfamous faces or texture patterns) activates homologous regions in the right hemisphere. Interestingly, material that encourages reliance on both verbal and nonverbal pictorial codes, such as nameable pictures of objects, recruits frontal regions bilaterally during memorization (Kelley et al., 1998). In keeping with this bilateral activation, memory for these nameable objects is superior to memory for materials that engage these regions unilaterally (Paivio & Csapo, 1973).

Memory formation can also occur incidentally as a by-product of information processing. For example, even when no explicit attempt at memorization is made, tasks that require “deep” or semantic elaboration of words (e.g., “Does ‘honest’ mean the same as ‘trustworthy’?”)

produce better memory than tasks that require “shallow” or surface-based judgments (e.g., “Is ‘SUSHI’ in uppercase letters?”; Craik & Lockhart, 1972). Imaging studies of incidental memory formation have suggested task-specific dissociations within the left hemisphere. Elaborative semantic encoding tasks activate left anterior prefrontal regions more strongly (near BA 45/47) than nonsemantic surface-based encoding tasks (for reviews, see Buckner, Kelley, & Petersen, 1999; Gabrieli, Poldrack, & Desmond, 1998; Fiez, 1997).

Collectively, these findings suggest the hypothesis that certain frontal regions may be sensitive to properties of the to-be-remembered material (e.g., posterior prefrontal cortex or pPFC), whereas other frontal regions may be sensitive to properties of the encoding task (e.g., anterior prefrontal cortex or aPFC). Here we provide direct evidence supporting this distinction. Subjects underwent functional magnetic resonance imaging (fMRI) under two task conditions that placed varying demands on semantic elaboration while incidentally encoding two classes of material (famous or nonfamous faces). For half of the faces, subjects performed a semantic appraisal task in which they judged whether each face was considered to be honest or dishonest. For the remaining half, subjects made a gender classification, indicating whether each face was male or female. Compared with the gender classification task, the honest/dishonest incidental encoding task has been shown to enhance subsequent recognition memory for faces (Bower & Karlin, 1974). Importantly,

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famous and nonfamous faces are stimuli that allow differential access to verbal codes dependent upon pre-experimental associated knowledge, yet their physical attributes remain constant. In other words, certain famous faces can be readily associated with a verbal referent (e.g., a name), whereas nonfamous faces cannot. In this regard, the use of faces permitted a potential dissociation between material-specific and task-specific frontal activity that may not be easily achieved using purely verbal materials such as words. The effects of manipulating task demands and material type are discussed in terms of their functionally dissociable roles during encoding and their impact on subsequent remembering.

RESULTS

Behavioral

Due to an equipment failure, response latencies during the encoding tasks were not recorded from one subject (Experiment 2). The resulting analysis reflects data from the remaining 27 subjects. An analysis of variance (ANOVA) examining main effects of task and material revealed that participants were significantly faster at making “male/female” judgments (“shallow” encoding) than “honest/dishonest” judgments (“deep” encoding) [shallow = 758 msec; deep = 1131 msec; $F(1,25) = 119.4, p < .0001$]. There was no significant difference in response latencies based on material type [nonfamous = 1002 msec; famous = 873 msec; $F(1,25) = 1.9, p = .18$] and no Task \times Material interaction ($F < 1$).

Accurate performance on a surprise yes/no recognition memory test was used to index successful encoding. Subjects viewed old or new faces (either nonfamous or famous) and indicated whether the face had been previously presented during the study phase. Data on the memory test were obtained from all 28 subjects. Significant memory differences (expressed as corrected recognition: proportion of hits minus false alarms) were noted across task manipulations (Figure 1). Faces encoded under “deep” conditions were better remembered than those encoded under “shallow” conditions

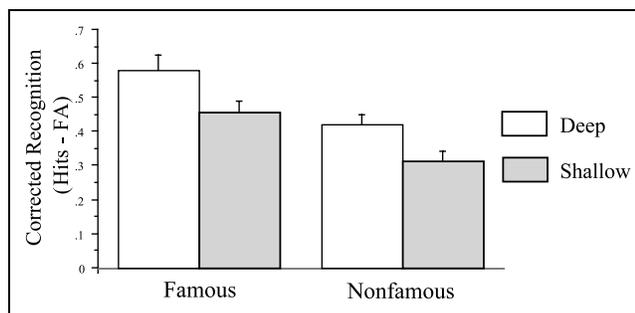


Figure 1. Corrected recognition (expressed as the proportion of hits minus false alarms) is shown for famous and nonfamous faces that were encoded under deep (white) and shallow (gray) task instructions.

[deep = 0.50; shallow = 0.38; $F(1,26) = 31.7, p < .0001$]. Across material types, subsequent memory for famous faces was superior to that following encoding of nonfamous faces [famous = 0.52; nonfamous = 0.37; $F(1,26) = 13.5, p = .005$]. The Task \times Material interaction was not significant ($F < 1$).

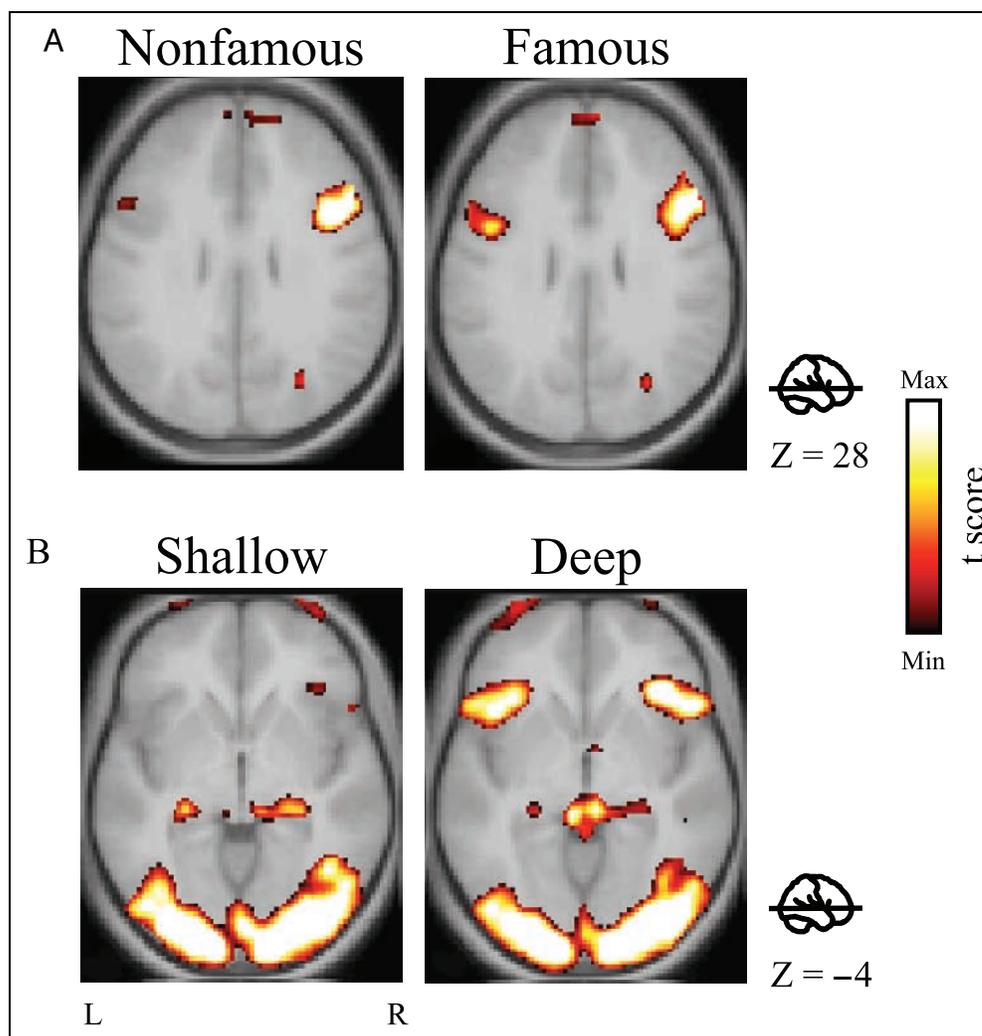
Functional Magnetic Resonance Imaging

To identify frontal regions that were sensitive to each material type, nonfamous faces (Experiment 1) and famous faces (Experiment 2) were collapsed across encoding tasks and contrasted to the baseline fixation task. When compared to fixation, both material types recruited pPFC (BA 6/44) in the right hemisphere regardless of the encoding task. In addition, encoding of famous faces was found to activate the homologous frontal region in the left hemisphere (Figure 2A). To identify frontal regions sensitive to each task condition, “deep” (honest/dishonest judgments) and “shallow” (male/female judgments) encoding conditions were collapsed across material type and contrasted to the baseline fixation task. Deep encoding, regardless of material type, resulted in bilateral activation of aPFC (BA 45/47), whereas shallow encoding did not (Figure 2B).

A central aim of the present study was to test for task/material dissociations in frontal brain regions during memory formation. This was achieved by employing a region-of-interest (ROI) analysis. Specifically, spherical ROIs in frontal cortex were defined in an unbiased manner from a statistical activation map created by comparing *all* face-encoding conditions to the baseline fixation task (see Experimental Procedures). This resulted in the identification of six frontal regions: left BA 6/44, left BA 45, left BA 47, right BA 6/44, right BA 45, and right BA 47. For each subject, signal intensities for each ROI were then calculated separately for each condition and examined statistically using a repeated-measures ANOVA. For each frontal region, effects of task (deep/shallow), material (nonfamous/famous), and the Task \times Material interaction were examined.

The ROI analysis revealed a significant main effect of task (deep > shallow) in aPFC regions [left BA 45: $F(1,26) = 28.7, p < .0001$; left BA 47: $F(1,26) = 24.1, p < .0001$; right BA 45: $F(1,26) = 6.9, p < .05$; and right BA 47: $F(1,26) = 19.9, p < .0001$] (Figure 3). None of these aPFC regions revealed a significant main effect of material type (all F s < 1). Similarly, the Task \times Material interaction was nonsignificant (all F s < 1). By contrast, left pPFC revealed a significant main effect of material (famous > nonfamous) [left BA 6/44: $F(1,26) = 8.9, p < .001$] (Figure 4). There was no significant magnitude difference between tasks ($F < 1$) and no interaction [$F(1,26) = 1.2, p = .30$]. The right pPFC (BA 6/44) was equally active across all four conditions and revealed no significant main effects [material: $F < 1$; task: $F(1,26) = 2.6, p = .12$] and no interaction ($F < 1$).

Figure 2. Axial sections show significant activations in the pPFC and aPFC averaged across subjects in each experiment. Colored pixels exceeded the statistical threshold and are superimposed on corresponding anatomic images. The left side of the images corresponds to the left side of the brain. Z-coordinates indicate the inferior–superior slice position (in mm) above or below the anterior commissure–posterior commissure plane. (A) Activity in the pPFC was material-specific and insensitive to task demands. When both deep and shallow encoding tasks were collapsed and compared with the baseline fixation control condition, famous and nonfamous faces produced robust activation in the right pPFC (BA 6/44). Deep and shallow encoding of famous faces additionally recruited the left hemisphere pPFC homologue of this region. (B) Activity in the aPFC was task-specific and insensitive to material type. When collapsed across material type, deep encoding (i.e., honest/dishonest judgments) was found to engage aPFC bilaterally (BA 45/47). Shallow encoding (i.e., gender classification) did not yield significant activation in these regions.



To explicitly test the hypothesis that pPFC and aPFC yielded dissociable patterns of activation in the left hemisphere, a three-way ANOVA was conducted incorporating task, material, and brain region as factors. Results of this ROI analysis revealed a significant main effect of region (aPFC > pPFC) [$F(1,26) = 11.4$, $p < 0.005$] and task (deep > shallow) [$F(1,26) = 30.2$, $p < .0001$]. Importantly, significant interactions were observed between region and material type [$F(1,26) = 5.8$, $p < .05$] and between region and task [$F(1,26) = 42.5$, $p < .0001$]. The Task \times Material interaction and the three-way interaction were not significant ($F < 1$). A significant three-way interaction would have indicated that either (i) the interaction between region and material was further modulated by the two levels of task, or (ii) the interaction between region and task was further modulated by the two levels of material. Thus, the frontal dissociation that was qualitatively observed in the statistical activation maps (Figure 2) was significant in unbiased ROI analyses. This dissociation can be clearly appre-

ciated in an inflated representation of the left hemisphere (Figure 5).

Exploratory whole-brain analyses revealed that a number of additional brain regions were commonly activated during deep and shallow encoding of nonfamous and famous faces. These included bilateral regions of the primary and extrastriate visual cortex, the fusiform gyrus, the parahippocampal gyrus, the amygdala, the thalamus, the motor cortex, and the supplementary motor area. An additional ROI analysis revealed a significant task effect (deep > shallow) in the left amygdala [$F(1,26) = 7.5$, $p < .05$], with no significant effect of material ($F < 1$) and no interaction ($F < 1$) (Figure 6).

DISCUSSION

The present study provides evidence for functional dissociations both *between* and *within* frontal regions in the left and right hemispheres. Across two separate experiments, subjects incidentally encoded stimulus materials (faces) for which access to verbal codes varied

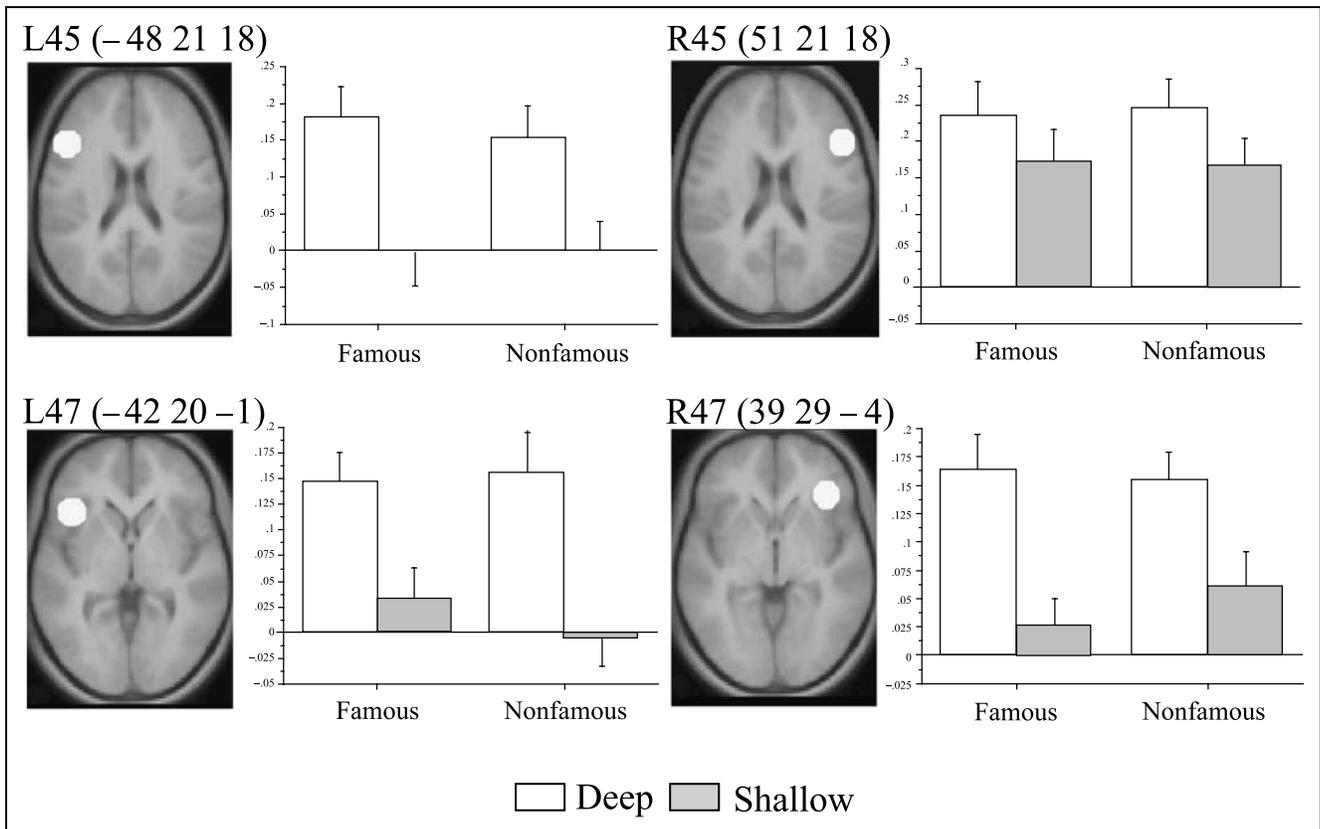


Figure 3. The aPFCs demonstrate task sensitivity regardless of material type. Axial sections display aPFC spherical ROIs superimposed on averaged anatomic images. Brodmann's areas and peak coordinates are listed above each region. Plots to the right of each region display changes in signal amplitude (in percent) across conditions relative to fixation. Error bars indicate standard error of mean (*SEM*). Activity in each aPFC region demonstrated sensitivity to task demands, producing significantly greater activation during deep encoding (white bars) than shallow encoding (gray bars) of famous and nonfamous faces. These regions were not sensitive to material type.

as a function of the pre-experimental knowledge associated with the face, while the physical attributes of the stimuli remained constant. In both studies, subjects performed incidental encoding tasks designed to place

varying demands on semantic elaboration. Clear functional dissociations between material specificity and task specificity were observed in posterior dorsal (pPFC; near BA 6/44) and anterior ventral (aPFC; near BA 45/47)

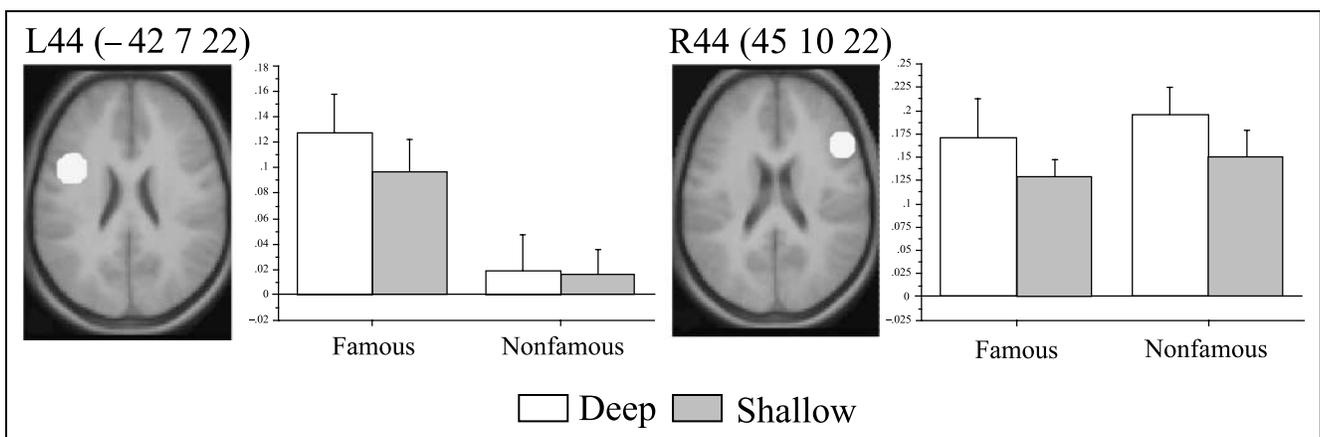


Figure 4. The pPFC demonstrate material sensitivity, regardless of task demands. Axial sections display left and right pPFC spherical ROIs superimposed on averaged anatomic images. Brodmann's areas and peak coordinates are listed above each region. Plots to the right of each region display changes in signal amplitude (in percent) across conditions relative to fixation. Error bars indicate standard error of mean (*SEM*). Activity in the pPFC was sensitive to material type. The left pPFC exhibited significantly greater activation for famous than nonfamous faces during both deep (white bars) and shallow (gray bars) encoding tasks. The right pPFC produced robust activation in response to both famous and nonfamous faces. Neither pPFC region demonstrated a significant effect of task demands.

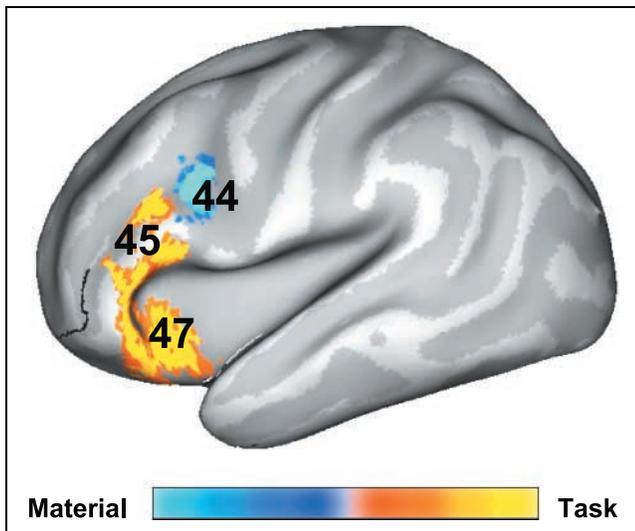


Figure 5. An inflated cortical rendering of an averaged anatomic image (Van Essen et al., 2001) illustrates a functional anatomic distinction between pPFC (BA 44) and aPFC (BA 45/47). A voxel-by-voxel ANOVA examining task effects (within subject) and material effects (between subjects) was used to compute *F*-statistics for each main effect in pPFC and aPFC. Voxels that did not yield a significant main effect of either task or material were excluded from further analysis. A task/material sensitivity measure (*F*-ratio) was then computed for each voxel by dividing the task *F* value by the material *F* value. To facilitate visualization of this measure, *F*-ratios were converted to a logarithmic scale. Thus, voxels that were more sensitive to material type than task demands yielded negative values (blue color scale) and voxels that were more sensitive to task demands than material type yielded positive values (yellow color scale). Voxels at the tail end of the color scales (light blue and bright yellow) were those voxels that exhibited the strongest bias towards material sensitivity and task sensitivity, respectively. Voxels in the pPFC (BA 44) demonstrated greater sensitivity to material type, whereas voxels in the aPFC (BA 45 and 47) demonstrated greater sensitivity to task demands.

regions of the prefrontal cortex. Regions of the pPFC exhibited sensitivity to material type irrespective of the encoding task. In particular, right pPFC responded strongly to both famous and nonfamous faces during deep and shallow encoding; encoding of famous faces additionally engaged the left hemisphere pPFC homologue. By contrast, aPFC exhibited task specificity irrespective of the material type. Recruitment of aPFC bilaterally was observed during deep, but not during shallow, encoding of both material types.

The functional dissociation between task and material specificity observed in the left hemisphere fits nicely within the context of previously reported phonological/semantic processing distinctions. Specifically, tasks that encourage reliance on phonological processing have consistently yielded activation in the pPFC (McDermott, Petersen, Watson, & Ojemann, 2003; Gold & Buckner, 2002; Bokde, Tagamets, Friedman, & Horwitz, 2001; Davachi, Maril, & Wagner, 2001; Roskies, Fiez, Balota, Raichle, & Petersen, 2001; Poldrack et al., 1999; Demonet et al., 1992; Zatorre, Evans, Meyer, & Gjedde, 1992), whereas tasks that emphasize semantic elaboration have

produced activation in the aPFC (McDermott et al., 2003; Bernstein, Beig, Siegenthaler, & Grady, 2002; Fletcher et al., 2002; Gold & Buckner, 2002; Grady, Bernstein, Beig, & Siegenthaler, 2002; Bokde et al., 2001; Otten, Henson, & Rugg, 2001; Roskies et al., 2001; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001; Poldrack et al., 1999; Wagner, Poldrack, et al., 1998; Wagner, Schacter, et al., 1998; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Gabrieli et al., 1996; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996; Demb et al., 1995; Kapur et al., 1994; Petersen, Fox, Posner, Mintun, & Raichle, 1988). For example, Poldrack and colleagues (1999) directly contrasted phonological and semantic processing tasks and observed greater pPFC activation (near BA 44) during a phonemic classification task (syllable counting) and greater aPFC activation (near BA 45/47) during a semantic classification task (deciding whether a word was abstract or concrete). Gold and Buckner (2002) compared an abstract/concrete semantic decision task to a phonological decision task in which subjects decided whether words (or pseudowords) contained short or long vowel sounds and observed a similar pPFC/aPFC dissociation. More recently, McDermott and colleagues (2003) required subjects to attend to either the meanings of semantically related words or the sounds of phonologically similar words (i.e., words that rhymed). Frontal activity engaged during attention to phonological relations was observed in regions of pPFC, whereas frontal activity during semantic relations was noted in aPFC.

Clearly, previous work has often relied on overt task manipulations to vary access to phonology. In the present report, access to phonological codes was linked in a more covert fashion to properties of the stimulus material. Interestingly, human faces represent a stimulus class that is inherently nonverbal and is often associated with right hemisphere pPFC activation (Kelley et al., 1998). Certain famous faces, however, can be readily associated with a phonological label (e.g., can be

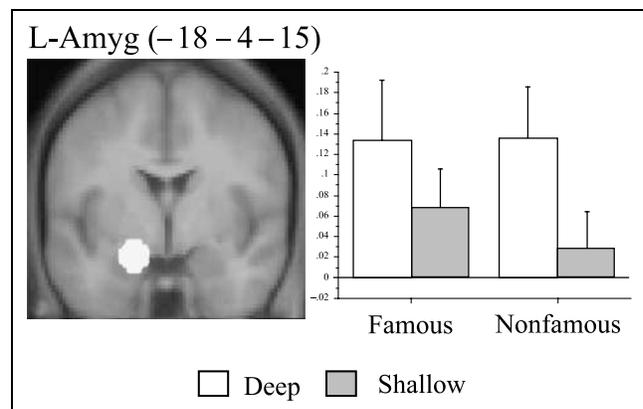


Figure 6. A coronal section displays an ROI in the amygdala that demonstrated greater activity for famous and nonfamous faces during honesty judgments (white bars) than during gender classification (gray bars). The graph displays percent signal change for each condition relative to fixation. Bars indicate standard error of the mean (*SEM*).

named). Here we show additional engagement of left pPFC when faces are those of famous, nameable people. That such a dissociation was observed under both deep and shallow encoding tasks suggests that recruitment of left and right pPFC may be obligatory, dependent on the presence or absence of a verbal or nonverbal code, respectively. Similar bilateral pPFC activity has been observed during intentional memorization of nameable, line-drawn objects, presumably reflecting access to both nonverbal pictorial codes (via right pPFC) and also to verbal, phonological codes (via left pPFC) (Kelley et al., 1998). As such, recruitment of the pPFC need not be predicated solely on the task engaged (see also Kirchoff, Wagner, Maril, & Stern, 2000). Indeed, in the present study, pPFC activity was task-independent. Rather, pPFC activation can, at times, reflect an automatic response to intrinsic properties of the to-be-remembered material.

By contrast, activity in the aPFC was modulated directly through task manipulations. When subjects made subjective/elaborative judgments as to whether a face was perceived to be honest or dishonest, robust aPFC activity resulted. When subjects performed the more superficial gender classification task, aPFC activity was significantly attenuated. A number of models have been proposed to explain the functional role of left aPFC (for review, see Badre & Wagner, 2002). One common theory suggests that the left aPFC (near BA 45/47) plays a critical role in controlled semantic retrieval (Bokde et al., 2001; Roskies et al., 2001; Wagner et al., 2001; Poldrack et al., 1999; Fiez, 1997; Gabrieli et al., 1996; Kapur et al., 1994). An alternative account suggests that the left aPFC (near BA 44/45) functions to select relevant semantic knowledge when response competition between multiple alternatives is high (Thompson-Schill et al., 1997; Thompson-Schill et al., 1998; Thompson-Schill, D'Esposito, & Kan, 1999). More recently, Gold and Buckner (2002) have suggested that the left aPFC participates in controlled processing across multiple information domains when "task conditions involve stimulus-to-representation mappings that are relatively ambiguous" (p. 808) (but see Clark & Wagner, 2003). The present work contrasted a highly constrained task condition with relatively low response ambiguity (gender classification) to a task condition with greater response ambiguity (honesty judgment), as the "correct" response was subjective. Moreover, the aPFC was insensitive to material type even though access to semantic knowledge varied greatly between the famous and nonfamous faces. In this regard, the present results appear to be consistent with the Gold and Buckner account of aPFC function. Such a domain-general account might also help to explain why activation in the aPFC in the present study was strongly bilateral and insensitive to the verbal/ nonverbal nature of the materials.

It is somewhat difficult to reconcile the current findings with a controlled semantic retrieval account of aPFC function, as the present study did not explicitly

require subjects to make use of the additional semantic knowledge available for famous faces. A controlled semantic retrieval account might better explain the present findings if the aPFC activity observed here indexed semantic retrieval effort rather than success. For example, aPFC activity may reflect a sustained response that underlies a particular cognitive state (e.g., making honesty judgments) rather than transient, item-related activity associated with recalling specific semantic knowledge about a particular face. As the present study employed a block-design paradigm, the activations observed here could reflect item-related processes, processes associated with a more global cognitive state, or both. Recent advances in fMRI methodology permit such dissociations (Donaldson, Petersen, Ollinger, & Buckner, 2001) and may provide insight into potential state-related effects in the aPFC.

Left hemisphere activity in the amygdala was also sensitive to task demands, irrespective of material type. The greater left amygdala activation observed during honesty judgments most likely reflects the social appraisal component intrinsic to our deep encoding task. Winston, Strange, O'Doherty, and Dolan (2002) have previously demonstrated a linear relationship between facial trustworthiness and amygdala activity, regardless of whether subjects were explicitly judging trustworthiness. Similarly, researchers have observed left amygdala activation when faces were evaluated as either pleasant or unpleasant (Bernstein et al., 2002; Grady et al., 2002).

While the present results demonstrate how task manipulations (deep vs. shallow) may impact memory via bilateral engagement of the aPFC, recent work with callosotomy (i.e., split-brain) patients has provided evidence for hemispheric specialization during incidental encoding tasks (Miller, Kingstone, & Gazzaniga, 2002). Miller and colleagues presented words and unfamiliar faces to the left and right hemispheres under deep and shallow encoding constraints. Notably, "deep" encoding manipulations benefited the left hemisphere only when words were used as stimuli and benefited the right hemisphere only when unfamiliar faces were used. Similar hemispheric asymmetries in memory performance are noted during intentional memorization of verbal and nonverbal stimulus materials following lesions to left and right hemisphere brain regions (Milner, 1972) and when portions of the left and right hemisphere are anesthetized with sodium amytal (Kelley et al., 2002). Collectively, these findings suggest a hierarchy of memory formation. Information may be initially encoded in left and right hemisphere cortical regions dependent upon material type and may further benefit from either left, right, or bilateral prefrontal recruitment in accordance with task demands. When the hemispheres are disconnected, however, the memorial benefits resulting from task manipulation are only realized if the hemisphere can effectively encode the material type.

The results reported here provide direct support for multiple-code models of memory. Subjects realized a memorial advantage to the extent that left and right pPFC and aPFC frontal regions were recruited (Figure 7). “Shallow” encoding of nonfamous faces activated only the right pPFC and yielded relatively poor subsequent memory performance. Memory performance for nonfamous faces improved when task demands encouraged “deep” encoding which, in turn, was characterized neuroanatomically by the additional recruitment of the aPFC. Interestingly, memory for famous faces that were presented during the “shallow” encoding task was comparable to memory for nonfamous faces that were presented during the “deep” encoding task, yet the neural mechanisms subserving these memories appear to differ. Whereas nonfamous faces benefited from “deep” processing by additionally recruiting the aPFC, famous faces benefited from the obligatory phonological

code by engaging the left pPFC. Following this logic, the greatest memorial advantage was afforded to deeply encoded famous faces, as these faces benefited both from task-specific aPFC activity and material-specific pPFC activity in both hemispheres. Taken together, these results demonstrate functionally separable routes to memory within the prefrontal cortex that depend on both the intrinsic properties of the to-be-remembered materials and the specific cognitive operations engaged during interactions with such materials.

METHODS

Experimental Procedures

Subjects

Thirty-two subjects between the ages of 18 and 29 were recruited from the Dartmouth community. Of the 32 sub-

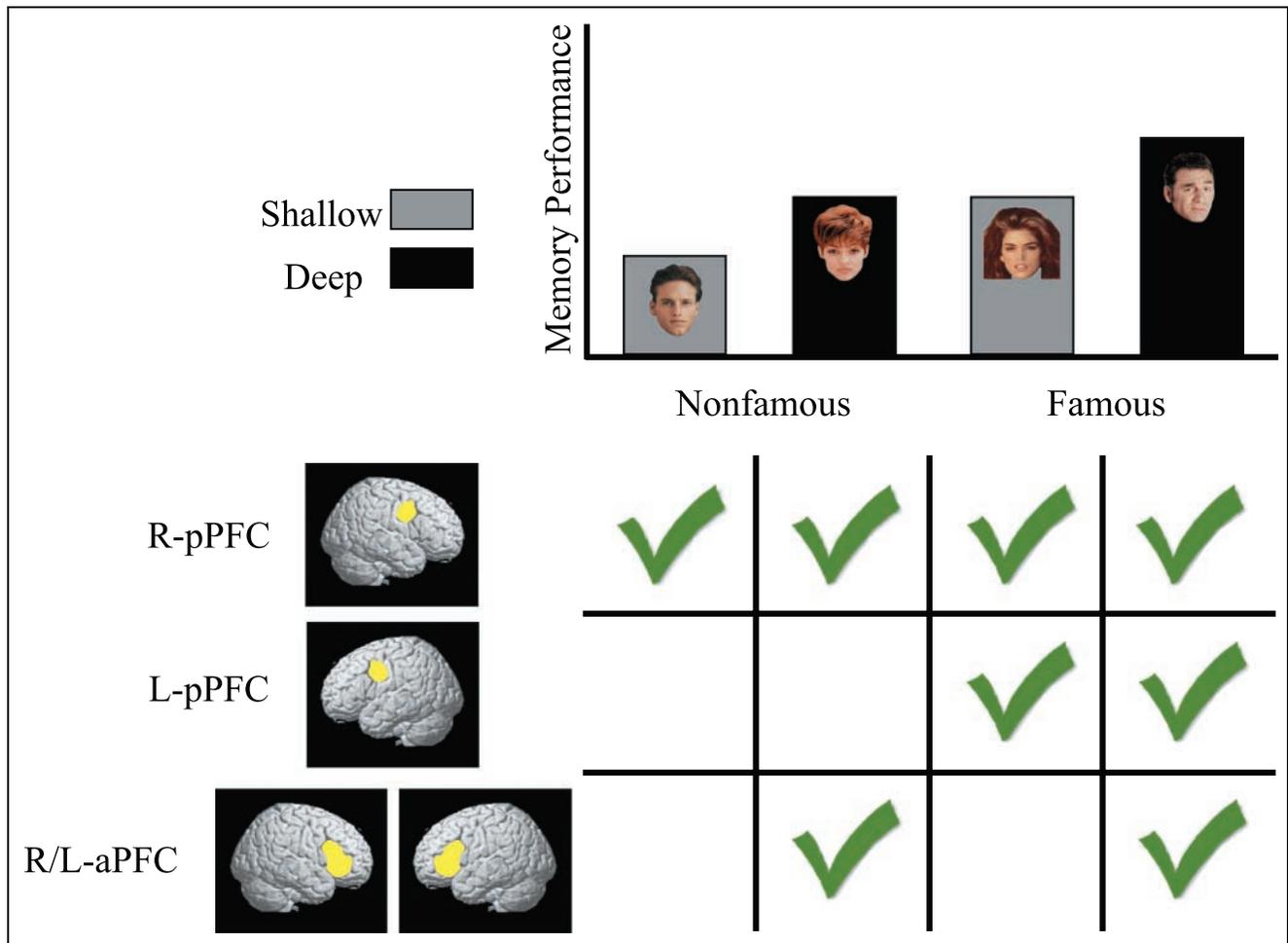


Figure 7. Memory performance benefited to the extent that left and right pPFC and aPFC were engaged during encoding. The graph (top) summarizes memory performance following deep (black) and shallow (gray) encoding of nonfamous and famous faces. Checkmarks below each bar on the graph indicate whether significant activity was noted in corresponding prefrontal regions displayed to the left of the grid. Subsequent memory performance was weakest when the right pPFC was recruited in isolation (shallow encoding of nonfamous faces) and was strongest when both the pPFC and aPFC were engaged bilaterally (deep encoding of famous faces). Memory for deeply encoded nonfamous faces was comparable to memory for famous faces encoded under shallow task demands, although the patterns of frontal recruitment suggest functionally separable routes to memory formation for these items.

jects, two were removed from subsequent analysis due to technical difficulties encountered during the scanning procedure. Two additional participants were removed because of excessive movement during imaging (>1 mm between successive image acquisitions). Results reported here reflect data analyzed from the remaining 28 participants (10 men, 18 women; mean age = 20).

As such, 15 subjects participated in Experiment 1. The remaining 13 subjects participated in Experiment 2. All subjects were strongly right-handed as measured by the Edinburgh Handedness Inventory (Raczkowski, Kalat, & Nebes, 1974). Subjects reported no significant abnormal neurological history and all had normal or corrected-to-normal visual acuity. Subjects were either paid for their participation or received course credit. All subjects gave informed consent in accordance with the guidelines set by the Committee for the Protection of Human Subjects at Dartmouth College.

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 with an Apple G3 Laptop computer running PsyScope software (Cohen, MacWhinney, Flatt, & Provost, 1993). Stimuli were projected onto a screen positioned at the head end of the bore by an Epson (model ELP-7000) LCD projector. Subjects viewed the screen through a mirror mounted on top of the head coil. A fiber-optic, light-sensitive key press that interfaced with the PsyScope Button Box (New Micros, Dallas, TX) was used to record subjects' responses. Cushions were used to minimize head movement.

Imaging

Anatomic 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, TE = 35 msec, flip angle = 90°, 3.75 × 3.75 mm in-plane resolution). During each functional run, 106 sets of axial images (25 slices; 4.5-mm slice thickness, 1 mm skip between slices) were acquired allowing complete brain coverage.

Behavioral Tasks

Two studies were performed. In both studies, subjects performed two incidental encoding tasks, indicating their responses with a two-alternative forced-choice button press. In one task, subjects were required to indicate whether the face they were viewing was that of a male or a female ("shallow" encoding). In the second task, subjects judged whether they thought the face was

that of an honest person or that of a dishonest person ("deep encoding"). Subjects were instructed to be as fast and accurate as possible and were not informed that they would be tested for their memory of these faces.

Subjects were imaged during two functional runs while performing these encoding tasks. Each functional run lasted 265 sec and was comprised of seven blocks; four of these were "task" blocks (two each of the "deep" and "shallow" encoding conditions) and three were "fixation" control blocks. During the fixation control blocks, a cross-hair (plus sign) was present on the screen for the duration of the block, and subjects were instructed to fixate the cross-hair. Task blocks (40 sec duration) were interleaved with fixation blocks (25 sec duration). Sixteen faces were presented during each task block (2000 msec stimulus duration, 500 msec interstimulus interval). Each task block was preceded by a cue lasting for 2500 msec. The cue indicated which task was to be performed in the following block (i.e., "male/female?" or "honest/dishonest?"). Task order was counterbalanced across and within runs.

Following the encoding scans, subjects were given a surprise old-new recognition test for their memory of the faces. This memory test consisted of the 64 "shallow"-encoded faces, the 64 "deep"-encoded faces, and 64 "new" faces that had not been presented during the study trials. Subjects indicated (with a button press) whether each face was old or new.

Face stimuli consisted of high-resolution color pictures of faces. In Experiment 1, subjects viewed only nonfamous faces. In Experiment 2, subjects viewed only famous faces. As such, the overall experimental paradigm represents a 2 × 2 factorial design, with one within-factor (task) and one between-factor (material). Because the study implemented an incidental encoding procedure whereby subjects were unaware of the ensuing memory test, all of the encoding trials needed to be completed prior to the memory test. In this regard, the incidental encoding paradigm placed constraints on the number of faces that could be studied and subsequently remembered. Indeed, behavioral pilot data indicated that overall memory performance suffered significantly when material effects were also incorporated as a within-factor variable. A behavioral norming study was performed on a separate group of 20 individuals to identify faces that were famous and nameable and to ensure that the nonfamous faces were truly nonfamous and non-nameable. The famous faces used in the present study had a mean nameability rating of 83% (range: 60–100%). The nonfamous faces were identical to those used previously by Kelley and colleagues (1998).

Data Analyses

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 realigned within and across runs to correct for head movement, coregistered with each participant's anatomic data, and then transformed into a standard anatomic space (3-mm isotropic voxels) based on the ICBM 152 brain template Montreal Neurological Institute), which approximates the Talairach & Tournoux (1988) atlas space. Normalized data were then high-pass filtered to a maximum of 1/120 Hz, spatially smoothed (6 mm full width at half maximum [FWHM]) using a Gaussian kernel, and globally scaled to permit between-group comparisons. Analyses took place at two levels: formation of statistical images and regional analysis of hemodynamic responses.

Statistical Images

For each participant, a general linear model incorporating task effects (modeled as a box-car function convolved with the canonical hemodynamic response function), a mean, and a linear trend were used to compute *t*-contrast images (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 $p = .001$, uncorrected). An automated search algorithm identified the location of peak activations based on *t* value and cluster size. This analysis allowed several comparisons to be made. First, task effects could be explored by comparing deep-encoding and shallow-encoding conditions to the baseline fixation task (collapsed across material type). Second, material effects could be explored by comparing nonfamous faces and famous faces to fixation (collapsed across task conditions).

Signal Intensities

The present study sought to examine the contributions of anterior and posterior frontal regions during incidental memory encoding. The statistical *t* images (Figure 2) suggested a task/material dissociation between pPFC regions (BA 6/44) and aPFC regions (BA 45/47). To explore the involvement of these regions across conditions in finer detail, a second analysis was conducted to examine signal intensities in these specific regions of interest. To calculate signal intensities in an unbiased manner, spherical ROIs (8-mm radius) were defined based on peaks identified in a mean *t* image that was created by comparing *all* face-encoding conditions to the baseline fixation task (averaged across all subjects). In this way, each condition (nonfamous–deep, nonfamous–shallow, famous–deep, and famous–shallow) contributed equally to the generation of ROIs. This resulted in the identification of six frontal regions: left BA 6/44, left BA 45, left BA 47, right BA 6/44, right BA 45, and right BA 47. For each subject, signal intensities for each ROI

were then calculated separately for each condition and examined statistically using repeated-measures ANOVA.

Acknowledgments

We thank J. Moran, P. Janata, G. Wolford, and T. Laroche for their assistance. This work was supported by a National Institute of Health grant (MH64667) to W.M.K. and the Dartmouth Brain Imaging Center. G.S.W. is an NSERC graduate fellow.

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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 2-2003-113XH.

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