

Effects of Divided Attention on fMRI Correlates of Memory Encoding

Melina R. Uncapher and Michael D. Rugg

Abstract

■ Performing a secondary task concurrently with a study task has a detrimental effect on later memory for studied items. To investigate the mechanisms underlying this effect, the processing resources available for an incidental encoding task were varied by manipulating secondary task difficulty. fMRI data were acquired as volunteers ($n = 16$) made animacy decisions to visually presented study words while concurrently performing either an easy or a hard auditory monitoring task. “Subsequent memory effects”—greater activity at study for words later remembered versus words later forgotten—were identified in the left ventral inferior frontal gyrus and the left anterior hippocampus. These effects did not vary according to whether

the encoding task was performed concurrently with the easy or the hard secondary task. However, as secondary task difficulty increased, study-item activity declined and auditory-item activity increased in dorsolateral prefrontal and superior parietal regions that have been implicated in the support of executive and control functions. The findings suggest that dividing attention during encoding influences the probability of engaging the encoding operations that support later episodic memory, but does not alter the nature of the operations themselves. The findings further suggest that the probability of engaging these encoding operations depends on the level of general processing resources engaged in service of the study task. ■

INTRODUCTION

Dividing attention between a study task and a secondary task has a deleterious effect on later memory for the studied items (Naveh-Benjamin, Craik, Gavrilescu, & Anderson, 2000; Naveh-Benjamin, Craik, Perretta, & Tonev, 2000; Craik, Govoni, Naveh-Benjamin, & Anderson, 1996; Baddeley, Lewis, Eldrige, & Thomson, 1984). The detrimental effects of dividing attention at study are found regardless of whether memory is tested with recall or recognition (Craik, Govoni, et al., 1996), and are equally evident on tests of associative and item memory (Naveh-Benjamin, Guez, & Marom, 2003). Furthermore, in studies where recognition judgments were segregated according to whether they were based on an acontextual sense of familiarity, or accompanied by recollection of the encoding episode, divided attention has consistently been found to affect both forms of memory, albeit to a greater extent in the case of recollection (for a review, see Yonelinas, 2002).

The mechanisms by which divided attention interferes with encoding are not fully understood. It seems likely that they involve interference at multiple functional loci within the cascade of processes that lead to the formation of a durable memory representation. One factor that appears to be particularly important, however, is competition between study and secondary tasks for

general, or domain-nonspecific, processing resources (Fernandes & Moscovitch, 2000).

There is a substantial literature on the neural correlates of successful memory encoding as indexed by the functional neuroimaging methodologies of positron emission tomography (PET) and functional magnetic resonance imaging (fMRI). In early studies that employed “blocked” experimental designs, encoding-related activity was operationalized in contrasts between tasks that were associated with relatively good later memory performance versus tasks associated with relatively poor performance. In the majority of such studies (see Rugg, 2002; Wagner, Koutstaal, & Schacter, 1999, for reviews), the critical task manipulation varied whether study items were processed semantically or nonsemantically (a “depth of processing” manipulation; Craik & Lockhart, 1972). A consistent finding in such studies was that tasks associated with relatively better memory performance were also associated with relatively greater activity in several regions of the lateral prefrontal cortex (PFC), implicating these regions in successful (semantically mediated) encoding.

More recently, event-related fMRI has been employed to identify the neural correlates of successful encoding within a *single* encoding task by using the “subsequent memory procedure” (for a review, see Paller & Wagner, 2002). In this procedure, neural activity elicited by a series of study items is back-sorted according to whether the items are remembered or forgotten on a later

University of California at Irvine

memory test. Regions where study activity differs according to later memory are considered candidates for supporting operations underlying successful encoding. Subsequent memory studies that have employed semantic encoding tasks have consistently reported that study items which are later remembered elicit greater activity in the left inferior frontal gyrus (IFG) (e.g., Chee, Westphal, Goh, Graham, & Song, 2003; Otten, Henson, & Rugg, 2001; Wagner, Schacter, et al., 1998), parahippocampal cortex (e.g., Davachi, Mitchell, & Wagner, 2003; Otten, Henson, & Rugg, 2002; Wagner, Schacter, et al., 1998), and hippocampus (e.g., Ranganath, Johnson, & D'Esposito, 2003; Davachi, Maril, & Wagner, 2001; Otten et al., 2001). It has been proposed that the subsequent memory effects observed in the left IFG, particularly its more ventral aspect, reflect the role of this region in semantically mediated processing (Buckner, Logan, Donaldson, & Wheeler, 2000). It is assumed that items which receive more extensive semantic processing (perhaps by virtue of being processed to a greater level of specificity, or being more extensively represented in "semantic working memory"; Gabrieli, Poldrack, & Desmond, 1998), are encoded more effectively. An important implication of this proposal is that the subsequent memory effects in the IFG (and, indeed, in other cortical regions) reflect modulation of processing engaged in service of the study task. Support for the proposal comes from studies demonstrating that the loci of cortical subsequent memory effects vary according to the nature of the study task. For example, Otten and Rugg (2001a) (see also Otten et al., 2001) reported that in contrast to a semantic study task (animacy judgment), a phonological task (syllable judgment) was associated with little or no evidence of subsequent memory effects in the IFG.

The finding that successful memory encoding is associated with a characteristic pattern of neural activity opens the avenue for the employment of neuroimaging methods to investigate the effects of divided attention on encoding. Five blocked-design PET studies have contrasted activity during study tasks performed under conditions of hard versus easy (or no) secondary task (Anderson et al., 2000; Iidaka, Anderson, Kapur, Cabeza, & Craik, 2000; Fletcher, Shallice, & Dolan, 1998; Fletcher, Frith, et al., 1995; Shallice et al., 1994). The most consistent finding across these studies is an attenuation of putative encoding-related activity in the dorsolateral PFC in the vicinity of Brodmann's areas (BA) 9/46. In light of the possible role of this region in domain-general "executive processes" (Wager & Smith, 2003; Collette & Van der Linden, 2002; Szameitat, Schubert, Muller, & Von Cramon, 2002; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001), this finding is consistent with the proposal that divided attention exerts its detrimental effect on encoding by reducing the availability of such processes (Fernandes & Moscovitch, 2000). Because blocked designs do not permit characterization

of activity elicited by individual experimental items, however, such studies cannot address the question of how divided attention modulates encoding-related activity at the level of individual study items.

This question can be addressed with event-related fMRI and the subsequent memory procedure. To date, one study only has investigated the impact of divided attention on fMRI "subsequent memory effects" (Kensinger, Clarke, & Corkin, 2003). Using a semantically oriented encoding task (abstract/concrete judgment) on visually presented words, these authors contrasted subsequent memory effects according to whether volunteers performed the study task concurrently with an easy or a hard secondary task (detection of a change between successively presented auditory patterns that were either rhythmically distinct or rhythmically similar, respectively). Subsequent memory performance was assessed by yes/no recognition performed in conjunction with the same two secondary tasks that were employed at study. fMRI subsequent memory effects were evident in the left ventral IFG and the left anterior hippocampus in the easy secondary task condition, but were absent in these regions in the hard condition. By contrast, the left parahippocampal gyrus and the right inferior PFC demonstrated robust subsequent memory effects in both conditions. Kensinger et al. (2003) also reported a companion behavioral study in which subsequent memory was tested using the "Remember/Know" procedure. The results of this study were interpreted as showing that divided attention impairs later recollection but leaves familiarity unaffected. Accordingly, Kensinger et al. interpreted their fMRI findings as showing that divided attention selectively impairs encoding processes necessary for subsequent recollection, these processes depending upon the left ventral IFG and the anterior hippocampus.

In light of the evidence that divided attention usually impacts recollection and familiarity (Yonelinas, 2002), the present study revisits the question whether and how divided attention modulates fMRI subsequent memory effects. As in Kensinger et al. (2003), subsequent memory effects were investigated under two secondary task conditions that manipulated the attentional resources available for study processing (see Figure 1). To anticipate the results, in contrast to the findings of Kensinger et al. subsequent memory effects in two key regions—the left ventral IFG and the left hippocampus—were unaffected by the attentional manipulation.

RESULTS

Behavioral Data

Study Phase

Subjects were significantly more accurate in their classification of study words under the easy than the hard secondary task condition [82% ($SD = 6$) and 76% ($SD =$

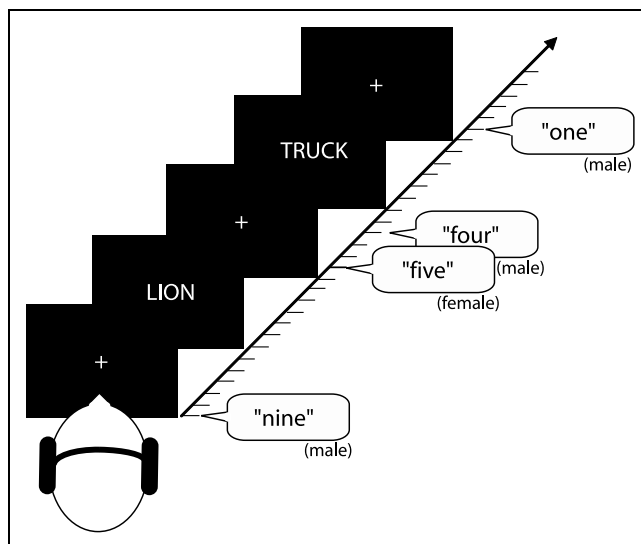


Figure 1. Schematic representation of the study and secondary tasks performed during scanning. Volunteers viewed a series of words, presented one at a time, and indicated via a button press whether each word represented a living or a nonliving thing (study task). Concurrently, volunteers heard a series of numbers, presented one at a time in a male or female voice (secondary task). In the *easy* secondary task condition, a response was required whenever a number was spoken in a female voice, regardless of the identity of the number. In the *hard* secondary task condition, a response was required whenever a number differed in oddity or evenness from the previous number, regardless of voice. Easy and hard secondary tasks were performed in alternating blocks.

9), respectively; $t(15) = 3.43, p < .005$]. Response times (RTs) for correctly judged study items, conditionalized on subsequent memory, are reported in Table 1, along with the standard deviations of the RT distributions in each condition. Effects on RTs of secondary task (easy vs. hard) and later memory classification (hits vs. misses, collapsed across confidence) were assessed using analysis of variance (ANOVA). RTs were significantly slower under the hard than the easy secondary task [$F(1,15) = 19.10, p < .001$], but showed neither an effect of subsequent memory [$F(1,15) = 1.62, p > .2$] nor a Task difficulty \times Subsequent memory interaction [$F(1,15) = 2.63, p > .1$]. A further ANOVA contrasted the standard deviations of study RT distributions according to task condition and subsequent memory. RTs were more variable under the hard than the easy secondary task condition [$F(1,15) = 16.47, p < .001$], but once again showed neither an effect of subsequent memory [$F(1,15) < 1$] nor a Task difficulty \times Subsequent memory interaction [$F(1,15) = 1.01$]. Together, these analyses indicate that whereas study-item RTs were slower and more variable in the hard secondary task condition, neither effect interacted with later memory performance. Thus, the fMRI subsequent memory effects reported below do not merely reflect gross differences in efficiency of the processing at study of items later remembered versus forgotten.

Table 1. Mean Reaction Times and Reaction Time Standard Deviations (msec) of Correctly Judged Study Items According to Whether They were Later Remembered (Hits) or Forgotten (Misses)

	Subsequent Hits		Subsequent Misses	
	Mean	Standard Deviation	Mean	Standard Deviation
Easy	865 (67)	199 (52)	860 (68)	305 (96)
Hard	1016 (150)	182 (61)	1063 (232)	320 (180)

Recognition Memory

To assess memory accuracy in a manner relevant to the fMRI analyses, performance was collapsed across confidence. Mean hit rate for items studied concurrently with the easy secondary task was 0.71 ($SD = 0.13$), whereas the hit rate for items studied in the hard condition was 0.65 ($SD = 0.14$). The correct rejection rate was 0.73 ($SD = 0.14$). The discrimination index, Pr (Probability of hit – Probability of false alarm; Snodgrass & Corwin, 1988), was used to assess memory accuracy. Pr was significantly lower when words were encoded under hard than under easy secondary task conditions [$Pr_{\text{Easy}} = .43 (SD = 0.12)$ vs. $Pr_{\text{Hard}} = .38 (SD = .10)$; $t(15) = 2.77, p < .01$].

fMRI Data

The analyses of the fMRI data were aimed at (i) identifying effects of the secondary task manipulation on item-related activity in the primary (study) and secondary tasks; (ii) characterizing the influence of the secondary task manipulation on subsequent memory effects in the two regions identified by Kensinger et al. (2003) as sensitive to divided attention, namely, the left ventral IFG and the anterior hippocampus; (iii) determining whether any other regions demonstrate subsequent memory effects that were attenuated in the hard relative to the easy secondary task.

Global Task Effects

We conducted two analyses to determine the effects of the task difficulty manipulation on activity elicited by study and secondary task items. The first analysis focused on the activity elicited by study items, without regard to subsequent memory performance, and contrasted the activity according to secondary task condition. The second analysis contrasted the activity elicited by the auditory items according to secondary task condition. Regions where the outcome of these analyses overlapped were identified by inclusive masking, as described below.

Study task. Regions where activity elicited by study words was attenuated in the hard relative to the easy

secondary task are illustrated in Figure 2A and listed in Table 2. These regions included the left dorsolateral PFC (BA 9) and the right lateral parietal cortex (BA 40). Regions where study-item activity was enhanced under the hard secondary task condition are also given in the table. They include the left IFG (BA 47) and the right fusiform gyrus (BA 20).

Secondary task. Only one region, the medial PFC (BA 10), demonstrated greater activity in response to easy relative to hard auditory items (Table 3). Regions where auditory-item activity demonstrated the reverse effect are shown in Figure 2B, and listed in Table 3. These regions included the bilateral dorsolateral PFC (BA 46/9) and the medial superior PFC (BA 6/8).

Overlap between global task effects. The foregoing analyses identified seemingly overlapping regions where activity elicited by study items diminished, and activity elicited by auditory items increased, as a function of increasing secondary task difficulty. Inclusive masking was employed to identify more precisely the extent of this overlap, thereby identifying where the secondary task manipulation gave rise to an apparent “tradeoff” between processing of the primary and the secondary task items. To give a conjoint significance level of $p < .001$ for the outcome of the masking procedure, the relevant single-sided contrasts were each thresholded at $p < .01$. This procedure revealed (Figure 2C) that the two effects overlapped not only in the bilateral dorsolateral PFC regions identified in Table 3 (centers of mass

of the overlap for the right and left dorsolateral PFC at 56, 9, 38 and $-56, 9, 38$, respectively), but also in the bilateral parietal cortex (BA 40), regions not identified in the more conservatively thresholded analyses of auditory-item activity reported above. Repeating that analysis at a reduced threshold ($p < .005$) did, however, identify these parietal regions: left: $-42, -45, 45$ ($Z = 3.46$) and right: $48, -39, 45$ ($Z = 2.98$). The centers of mass of the overlapping task effects in the right and left parietal cortex were at $45, -38, 47$ and $-42, -45, 44$, respectively.

Relation of secondary task effects to memory performance. In light of the tradeoff effects between study-item and auditory-item activity described above, we performed two correlational analyses. We predicted that if fewer neural resources were allocated to study items in the hard relative to the easy task condition, there should be a corresponding decline in later memory performance. Therefore, an analysis was conducted to identify regions where the size of the decline in study-item activity was correlated with the size of the decline in later memory performance. We also predicted that if relatively more neural resources were allocated to auditory items in the hard relative to the easy task condition, this too would lead to a decline in later memory performance for study items. Thus, a second analysis identified regions where the size of the enhancement in auditory-item activity in the hard relative to the easy condition correlated with memory decline. The SPMs expressing these two correlations were each

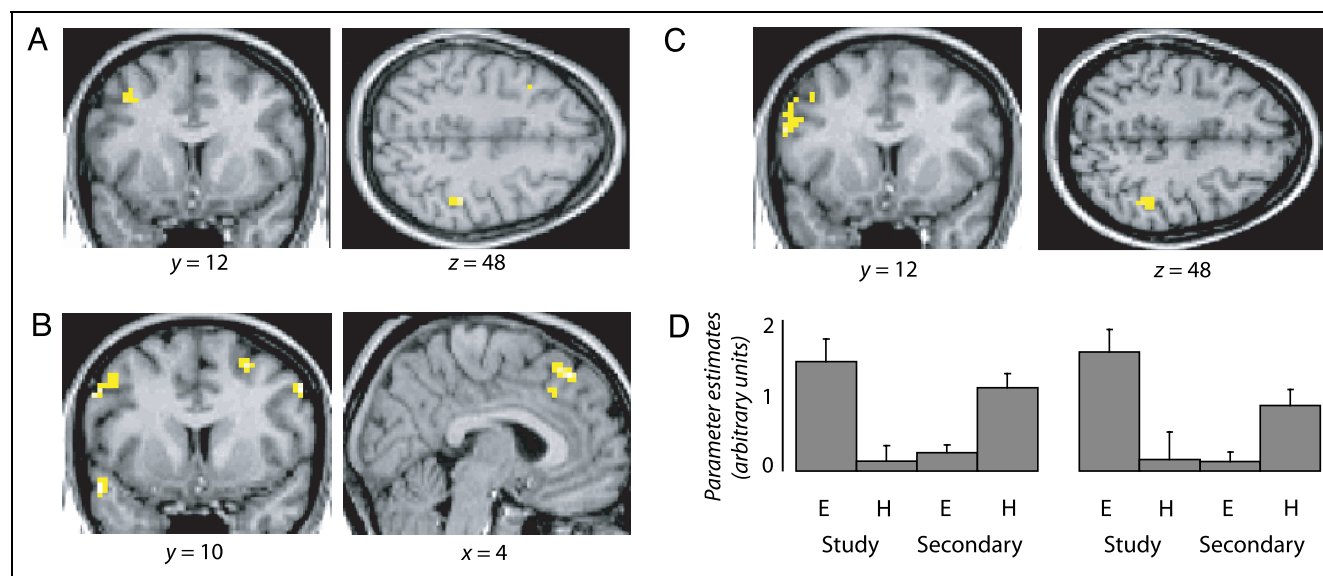


Figure 2. Regions showing (A) attenuated activity for visual study task items and (B) enhanced activity for auditory secondary task items in the hard relative to the easy divided attention condition. (C) Left dorsolateral prefrontal and right parietal areas where contrasts illustrated in A and B overlapped (see text). (D) Means (and standard errors) of parameter estimates of the cluster of overlapping voxels in the left dorsolateral prefrontal (left) and right parietal (right) regions illustrated in C. E = easy, H = hard divided attention condition; Study = study task; Secondary = secondary task. Contrasts are thresholded in A and B at $p < .001$, and in C at a conjoint $p < .001$. All effects are overlaid on normalized T1-weighted structural sections from a single randomly selected subject.

Table 2. Peak Voxels of Clusters where Study Item Activity Varied According to Secondary Task Condition

	<i>Location</i> (<i>x, y, z</i>)	<i>Peak Z</i> (<i>No. of Voxels</i>)	<i>Region</i>	<i>Approximate</i> <i>Brodmann's Area</i>
Easy > Hard	-39, 6, 33	3.60 (5)	Left dorsolateral prefrontal cortex	9
	60, -15, 42	3.72 (6)	Right precentral gyrus	6
	9, -9, 39	3.76 (6)	Right cingulate gyrus	24
	42, -36, 48	3.77 (5)	Right lateral parietal cortex	40
Hard > Easy	-39, 27, 3	3.48 (6)	Left inferior frontal gyrus	47
	48, -54, 9	3.42 (6)	Right superior temporal gyrus	39
	36, -39, -21	4.30 (12)	Right fusiform gyrus	20
	-36, -87, 0	4.46 (24)	Left middle occipital gyrus	18

thresholded at $p < .0005$. The decrement in study-item activity predicted the decrement in memory performance in the ventral anterior cingulate cortex (BA 24/32; 3, 27, -6; $Z = 3.80$). More strikingly, the enhancement of *auditory*-item activity predicted the decrement in later memory performance in the bilateral anterior hippocampus (see Figure 3; peak voxels for these effects were the right hippocampus: 27, -12, -15; $Z = 3.60$ and the left hippocampus: -27, -9, -21; $Z = 3.73$). The strength of this correlation is evident in Figure 3B.

Subsequent Memory Effects

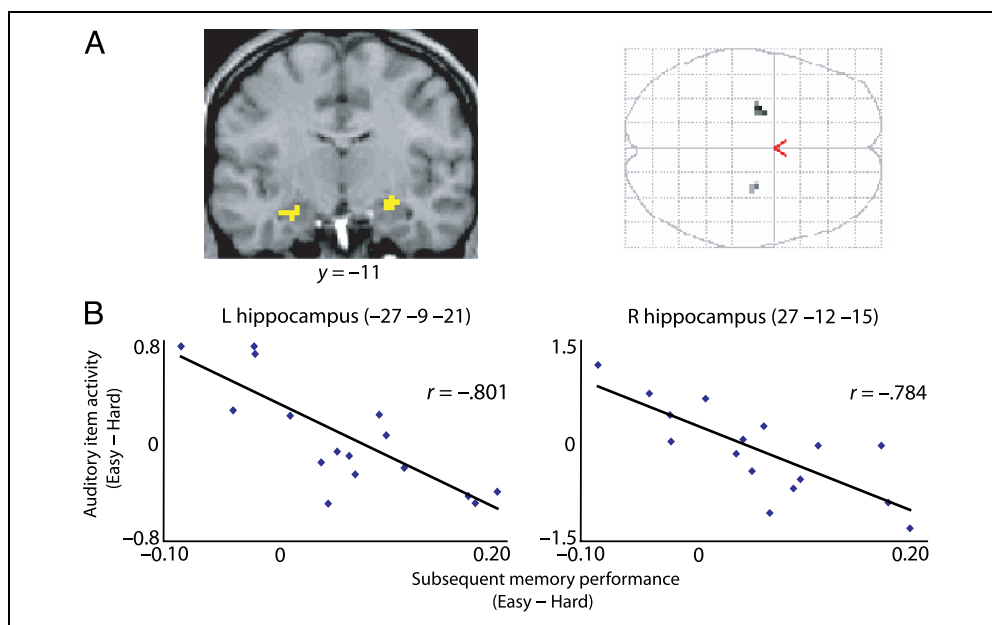
Regions defined a priori. Collapsed across secondary task conditions, subsequent memory effects survived

small-volume correction in both the ventral IFG and anterior hippocampal regions of interest (ROIs) centered on the coordinates derived from Otten et al. (2001) (see Methods). The loci of the peak voxels in the ventral IFG and the hippocampus were -36, 39, -15 ($Z = 3.21$, $p < .025$ corrected) and -21, -21, -9 ($Z = 3.35$, $p < .01$ corrected), respectively. These effects are illustrated in Figure 4A. To investigate the influence of divided attention on subsequent memory effects in the two regions, mean parameter estimates of the effects were computed across all voxels in each region where the main effect of subsequent memory exceeded $p < .01^1$ (see Figure 4B). ANOVAs on these means revealed no hint of a Subsequent memory \times Task difficulty interaction in either region (both $p > .3$).

Table 3. Peak Voxels of Clusters where Auditory Item Activity Varied According to Secondary Task Condition

	<i>Location</i> (<i>x, y, z</i>)	<i>Peak Z</i> (<i>No. of Voxels</i>)	<i>Region</i>	<i>Approximate</i> <i>Brodmann's Area</i>
Easy > Hard	9, 54, 6	3.82 (6)	Right medial frontal gyrus	10
Hard > Easy	57, 9, 39	4.07 (5)	Right dorsolateral prefrontal cortex	9
	57, 18, 30	3.53 (7)	Right dorsolateral prefrontal cortex	9/46
	-54, 9, 39	3.77 (7)	Left dorsolateral prefrontal cortex	9
	-48, 21, 27	4.05 (33)	Left dorsolateral prefrontal cortex	46/9
	9, 30, 54	4.23 (32)	Superior/medial frontal gyri	6/8
	-45, 9, 45	3.46 (5)	Left middle frontal gyrus	8
	-36, -3, 60	3.64 (9)	Left middle frontal gyrus	6
	24, 15, 57	4.02 (18)	Right superior frontal gyrus	6
	-60, -60, -3	3.49 (6)	Left middle temporal gyrus	21/37
	-54, 12, -18	4.29 (11)	Left middle/superior temporal gyri	21/38
	24, -60, 57	3.99 (5)	Right precuneus	7
	-12, -81, -27	3.56 (5)	Left cerebellum	

Figure 3. (A) Bilateral hippocampal regions where auditory-item activity correlated across subjects with magnitude of differential memory performance for items studied in the two secondary task conditions. Left: coronal T1-weighted section from the same subject as depicted in Figure 1 ($p < .001$ for display). Right: maximum intensity projection illustrating the specificity of the effects ($p < .0005$). (B) Scatterplots illustrating the relationship between the difference in hippocampal activity for easy versus hard secondary task conditions (abscissa), and the difference in memory performance between the two conditions (ordinate – more positive scores reflect lower performance in the hard relative to the easy condition).



In a complementary voxel-level analysis, we employed inclusive masking to identify voxels where subsequent memory effects overlapped between the two secondary task conditions. This was achieved by inclusively masking the subsequent memory effects for the two conditions (each thresholded at $p < .05$, giving a conjoint significance of $p < .018$). The outcome of this procedure is illustrated in Figure 4C, where overlap between effects

is evident in both the ventral IFG and the hippocampus. The center of mass of the overlap was at $-36, 38, -15$ for the ventral IFG, and at $-24, -21, -13$ for the hippocampus. The conjoint probability of significance for these subsequent memory effects for parameter estimates averaged across all overlapping voxels was $p < .002$ in the hippocampus, and $p < .0001$ in the ventral IFG.

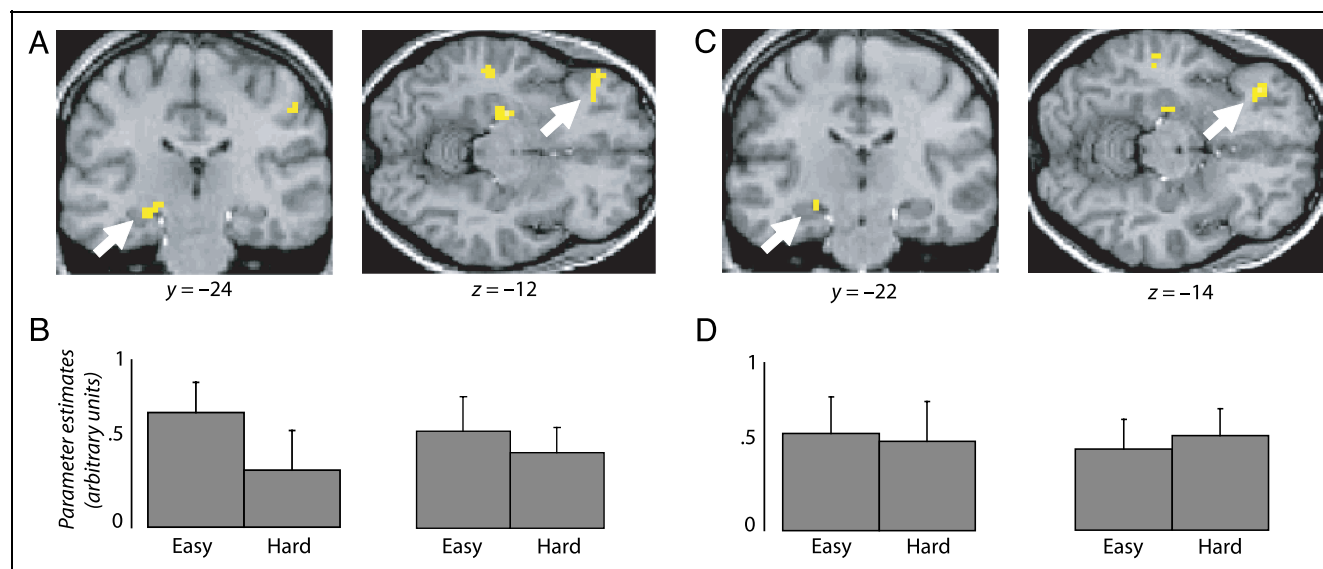


Figure 4. (A) Main effect of subsequent memory ($p < .005$) overlaid on T1-weighted sections from the same subject as in Figure 1. Arrows indicate effects in the left anterior hippocampus and the ventral IFG. (B) Mean parameter estimates (and standard errors) for hippocampal (left) and IFG (right) ROIs according to the secondary task condition. (C) Left anterior hippocampal and IFG voxels where simple effects of subsequent memory in each secondary task condition overlapped (conjoint threshold $p < .018$). (D) Parameter estimates from cluster of overlapping voxels in the hippocampus (left) and the IFG (right).

Together, the results of these analyses converge to indicate that subsequent memory effects in both the ventral IFG and the anterior hippocampal formation demonstrated subsequent memory effects that were insensitive to secondary task load.

Secondary Task × Subsequent Memory Effect Interaction

At the chosen threshold, there were no regions where subsequent memory effects were attenuated during the hard relative to the easy secondary task. Even at the liberal threshold of $p < .01$, there was no evidence of a Task difficulty × Subsequent memory interaction in the vicinity of the hippocampus or the left lateral PFC (cf. Kensinger et al., 2003).

DISCUSSION

Behavioral Data

Performance on the study task was less accurate and slower during concurrent performance of the hard relative to the easy secondary task, consistent with the expectation that the former task would compete more strongly with the study task for processing resources. Also as expected, subsequent memory was significantly worse when the study task was combined with the hard than with the easy secondary task. Although modest (0.054 decrement in proportion correct), this difference is roughly comparable to the divided attention effect in the fMRI study of Kensinger et al. (2003), who reported a difference in proportion correct between easy and hard secondary task conditions of 0.08. The divided attention effects in the two studies are even more similar when, as was the case in Kensinger et al., later memory performance is assessed for all study items (giving a decrement of 0.07), rather than just those items attracting a correct classification response. Therefore, it is unlikely that the disparate fMRI findings between the previous study and the present one (see below) can be attributed to differences between the studies in the size of the divided attention effect on subsequent memory performance.

fMRI Data

Replicating several previous studies that have employed semantically oriented study tasks (e.g., Kensinger et al., 2003; Morcom, Good, Frackowiak, & Rugg, 2003; Otten et al., 2001), reliable subsequent memory effects were present in both the left ventral IFG and left anterior hippocampal formation. In striking contrast to the findings of Kensinger et al. (2003), there was no evidence that the effects in either region were modulated by the divided attention manipulation. Moreover,

an exploratory whole-brain analysis failed to identify voxels demonstrating a Task × Subsequent memory interaction anywhere in the vicinity of these regions, even at a lenient statistical threshold.

There are several possible reasons for the discrepancies between the findings of Kensinger et al. (2003) and the present study. These include differences in secondary tasks (auditory pattern discrimination vs. digit comparison), the presence versus the absence of a secondary task at test, and the inclusion in the former study, and exclusion in the present one, of study items attracting incorrect or omitted classification responses. The last of these factors is unlikely to be important: A reanalysis of our fMRI data including all study items as events of interest yielded findings qualitatively equivalent to those obtained with analyses limited to correct responses only. We suspect that the most salient difference between the two studies may be the manner in which study and secondary task items were presented. In the present study, the onsets of study (visual) and secondary (auditory) stimuli were separated by a minimum of 300 msec, such that the presentation of a secondary task item, whether “target” or “nontarget,” never coincided with a study item. By contrast, in Kensinger et al., the transition between auditory patterns that signaled a “target” event occurred only when a study item was in view, and volunteers were explicitly warned of this contingency (E. Kensinger, personal communication, October 2004). Thus, the strategies adopted by volunteers in the two studies in their efforts to divide attentional resources between the two tasks likely differed markedly. For example, the simultaneous presentation of study and secondary task stimuli in Kensinger et al. would have led to higher across-modality perceptual interference than was the case in the present study, especially for the harder of their two secondary tasks which required a difficult perceptual discrimination. By contrast, the major cause of the across-task interference between the study and the hard secondary task in the present experiment likely arose from the need to maintain an auditory item in memory while processing a study item, rather than from perceptual conflict. Thus, the hard secondary task in the present study may have provided more opportunity for a strategy of attentional switching or time-sharing than did the hard secondary task of Kensinger et al.

Returning to the present findings, what are their implications for an understanding of how divided attention interferes with memory? A popular interpretation of the subsequent memory effects observed in the left ventral IFG is that the effects reflect the benefit to subsequent memory of more elaborate or more differentiated semantic processing of study items (Buckner et al., 2000; Gabrieli et al., 1998). The products of such processing presumably supply part of the cortical input to the hippocampal formation, likely accounting for the association found in the present and previous studies

between left prefrontal and left hippocampal subsequent memory effects. According to this account, subsequent memory effects in the left ventral IFG and the hippocampal formation are a consequence of modulation of domain-specific processes recruited in service of the study task. Our secondary task manipulation would have had little impact on these processes (we assume that digit classification is highly automated, and makes minimal demands on the semantic control or selection mechanisms held to be supported by the left IFG; Wagner, Pare-Blagoev, et al., 2001). Rather, by virtue of the requirement to continuously maintain, update, and monitor digit information, the primary locus of interference between the hard secondary task and the study task would have been at the level of executive and control processes that integrate and coordinate cognitive operations supporting a specific task goal. From this perspective, there is no reason to expect the secondary task manipulation to impact domain-specific semantic processes such as those supported by the left ventral IFG. Thus, encoding should still be modulated according to the extent that an item receives relatively extensive semantic processing. The current findings suggest that when attention was shared between a study item and the hard secondary task, the probability that an item received such processing was reduced. That is, subsequent memory was harmed in the hard secondary task condition not because of a reliance on encoding operations qualitatively different (and less effective) than those engaged in the easy condition (as was seemingly the case in Kensinger et al., 2003), but because the *same* operations were engaged less frequently (although to the same magnitude) than when the secondary task was easy.

The results of the analyses of task effects on activity elicited by study and auditory items are consistent with the foregoing proposal. These analyses revealed overlap between regions where study-item activity was reduced and auditory-item activity enhanced, in the hard relative to the easy secondary task condition. One interpretation of this finding is that it reflects regions where the two classes of item competed for common processing resources, the demands of the hard secondary task being met by withdrawal of resources otherwise available to the study task. Crucially, the regions where such overlap was identified—the dorsolateral prefrontal and lateral parietal cortex—are among those consistently identified as supporting task-general executive and control processes (e.g., Wager & Smith, 2003; Collette & Van der Linden, 2002; Szameitat et al., 2002).

An alternative account of these “task tradeoff effects” is that they reflect competition not for executive processes, but for domain-specific verbal processes required by both the study task and the hard secondary task. This interpretation is motivated by the fact that the easy and hard secondary tasks varied not only in their difficulty, but also in the type of processing that

was required, with only the latter requiring verbal analysis of the items. Thus, it is possible that the study task and the hard secondary task depended upon a common verbal process, hence, a common neural resource. We favor our first account of the tradeoff effects on two grounds. First, the dorsolateral and lateral parietal regions exhibiting these effects have been associated with executive processing in studies employing both verbal and nonverbal tasks and stimuli (Wager & Smith, 2003). Second, the PET studies investigating the effects of divided attention on word encoding that were cited in the Introduction all employed nonverbal secondary tasks. Nonetheless, divided attention was associated with attenuation of encoding-related activity in regions of the dorsolateral PFC close to, or overlapping with, the regions that exhibited task tradeoff effects in the present study.

Intriguingly, the dorsolateral PFC and right parietal regions exhibiting task tradeoff effects overlap not only with regions implicated in executive processing, but also with some of the regions identified by Otten and Rugg (2001b) as loci of what have been referred to as “subsequent forgetting effects” (Wagner & Davachi, 2001); that is, regions where relatively greater study activity is associated with *failure* on a subsequent memory test. Otten and Rugg suggested that these effects might reflect the consequences of diverting cognitive resources away from processes beneficial to encoding toward other processes—anticipation of an upcoming task cue, for example—that although relevant for task performance do not benefit encoding (see Daselaar, Prince, & Cabeza, 2004, for an alternative interpretation of subsequent forgetting effects). This proposal is reminiscent of the account offered here to explain the effects of the present secondary task manipulation; namely, that encoding suffers to the extent that task-general processes supported by the dorsolateral PFC and the lateral parietal cortex are divided between the study and secondary tasks. It will be of considerable interest to determine whether these apparent parallels between fMRI subsequent forgetting effects and divided attention effects are more than coincidental.

A final aspect of the present findings warranting discussion concerns the correlation between the divided attention effect on memory performance and the difference in activity elicited by easy and hard auditory items. The correlation indicated that across subjects, the greater the enhancement of anterior hippocampal activity in the hard condition, the greater was the corresponding decrement in later memory performance (see Figure 3). This finding suggests that encoding of study items was modulated according to the extent that the anterior hippocampus was differentially engaged by the secondary tasks. One possibility is that volunteers differed in the extent that they relied upon (hippocampally mediated) episodic memory rather than working memory to perform the hard secondary

task, the demands of which necessitated that items be retained in memory across successive study trials. Whatever the explanation for this finding, it is noteworthy that the hippocampal regions exhibiting the correlation with memory performance are anterior to the (left-sided) region that demonstrated the subsequent memory effect for study items. This implies that an area can play a role in encoding without that role necessarily being indexed by a detectable subsequent memory effect. It is possible to envisage several scenarios under which this could happen. To take just one, if later memory performance is determined by the *type* of information derived from a study item rather than merely the amount of information, a region necessary for encoding, but indifferent to the type of the information being encoded, might well respond equally to subsequently remembered and forgotten items. Regardless of the precise explanation for the present findings, they indicate that a complete understanding of the neural correlates of encoding will require experimental strategies other than just the subsequent memory procedure.

In conclusion, the findings of the present study suggest that there are at least some circumstances in which the detrimental effects of divided attention on episodic encoding are mediated not through a shift to different, less efficient encoding processes (cf. Kensinger et al., 2003), but through modulation of the probability of engaging the same encoding processes that support memory when attention is undivided. The findings further suggest that the basis of this modulation is the relative availability of domain-general processing resources. In agreement with Fernandes and Moscovitch (2000), the findings suggest that as the resources available to a study task diminish, so does the likelihood of successful encoding.

METHODS

This study was approved by and performed in accordance with the Institutional Review Board of the University of California at Irvine (UCI).

Participants

Seventeen volunteers (6 men; 19 to 31 years of age, mean of 22.8) gave informed consent to participate in the experiment. All volunteers reported themselves to be right-handed, in good general health, with no history of neurological disease or other contraindications for MR imaging, and to have learned English as their first language. Volunteers were recruited from the UCI community and were remunerated for their participation. One volunteer's data were not analyzed due to technical problems, which resulted in too few (less than five) confidently recognized items per session.

Stimulus Materials

Primary Task Stimuli

Stimuli were drawn from a pool of 460 words (4–9 letters long; mean written frequency between 1 and 30 counts per million; Kucera & Francis, 1967). This pool was used to create six lists of 62 items each, with half the words in each list representing animate objects and the other half inanimate objects. Study lists of 240 critical items were created from four of the lists, the extra eight items serving as buffers. Half the critical items were presented under easy concurrent task conditions and the other half were presented under hard concurrent task conditions. The remaining two word lists were used to create a list of 120 new items, with the extra four items used as buffers. Word lists were rotated between study and test conditions across subjects. A separate practice study list of 84 items was created from the remainder of the word pool.

All words were presented visually in white upper case letters on a black background centered on fixation. They subtended maximum horizontal and vertical visual angles of 8° and 1.5°, respectively. During the study phase, words were presented via VisuaStim (Resonance Technology, Northridge, CA, USA) XGA MRI-compatible head-mounted display goggles with a field of view of 30° visual angle and a resolution of 640 × 480 pixels. During the test phase, words were presented on a computer monitor with equivalent display parameters (e.g., size, font, and background/text colors).

Secondary Task Stimuli

Auditory stimuli consisted of the numbers “one” through “ten,” each spoken by a man and a woman. Stimuli spoken by a woman were obtained from the American English Spoken Lexicon (<http://wave.ldc.upenn.edu/cgi-bin/aesl/aesl>). Stimuli spoken by a man were recorded in the laboratory, edited to maintain a constant decibel level and filtered to remove ambient noise (<http://audacity.sourceforge.net>). Auditory stimuli were presented binaurally via MR-compatible headphones and did not exceed 500 msec in duration. Presentation volume was adjusted in the scanner to a comfortable listening level for each volunteer prior to scanning.

From the 20 auditory stimuli (1–10 in male voice; 1–10 in female voice), a pool of 375 items was created. One-third were in the female voice and the distribution of each digit spoken in the two voices was equal in each case. The pool was pseudorandomized (see below) eight times to create four lists for each concurrent task condition (easy and hard) that were rotated across subjects. Each list occupied the same time frame as one of the visually presented study lists described above. The probability of occurrence of a target item (see below) in each list was .33. Additional lists of 260 (86

target) auditory stimuli were used for each difficulty condition during the practice study session.

Experimental Tasks and Procedures

Procedure at Study

Scanning occurred during the study phase only. Instructions and practice sessions were given outside the scanner. The study phase of the experiment proper consisted of two consecutive scanning sessions. In each session, the study phase was performed in two blocks: one in conjunction with the easy secondary task, and another in conjunction with the hard task. The ordering of the secondary tasks blocks was consistent across sessions and counterbalanced across subjects. The study task was identical for both easy and hard conditions: Volunteers were instructed to make animacy decisions to visually presented words and depress buttons with their index (“animate”) and middle (“inanimate”) fingers of one hand accordingly. The secondary task for the easy condition required volunteers to depress a button with the index finger of the opposite hand whenever auditorily presented numbers were spoken by a woman, regardless of the identity of the number (a behavioral pilot study revealed that relative to study without any concurrent task, pairing the study task and the easy secondary task had no effect on subsequent memory for the study items). The hard secondary task required a button press whenever the currently presented and immediately preceding number were incongruent with respect to oddity or evenness (e.g., “one” preceded by “eight”), regardless of voice. Assignment of hand to the two tasks was counterbalanced across subjects. Volunteers were instructed to place equal emphasis on the study and secondary tasks, and to respond as quickly and as accurately as possible.

The beginning of each block was indicated by a 10-sec cue (“Female?” or “Odd/Even change?” for easy and hard conditions, respectively), followed by a central fixation cross. Word stimuli were presented for 300 msec, replacing a baseline fixation cross that was present throughout the interword interval. The word stimulus onset asynchrony (SOA) was stochastically distributed with a minimum SOA of 3200 msec modulated by the addition of one-third (120) randomly intermixed null trials (Josephs & Henson, 1999). Word stimuli were presented in pseudorandom order, with no more than three trials of one item-type (animate, inanimate, or null) occurring consecutively. Each block began with two buffer words and ended with a single buffer, and consisted of 60 critical words (for a total of 240 critical study items across four blocks). Auditory stimuli were presented one at a time with an SOA that varied randomly between 630 and 1800 msec (mean = 840 msec), and were timed such that the presentation of study stimuli and auditory stimuli did not overlap. Auditory

stimuli were presented in pseudorandom order such that no more than two target trials occurred consecutively. Each auditory block consisted of 375 auditory stimuli, 125 of which were targets.

Procedure at Test

Recognition memory was tested outside the scanner approximately 15 min after the conclusion of the last study block. Instructions were to judge whether each test word had been presented in any of the study blocks and to signal level of confidence in the judgment. One of four keys was depressed to indicate whether the word was (i) confidently judged as old, (ii) nonconfidently judged as old, (iii) confidently judged as new, or (iv) nonconfidently judged as new. Responses were made with the index and middle fingers of each hand, with one hand assigned to “old” and the other to “new” responses. Hand assignment was counterbalanced across subjects. Middle fingers were always used to indicate confident responses. Volunteers were instructed to respond quickly without sacrificing accuracy.

The recognition test was administered in three consecutive blocks with short rest periods. All 240 critical words presented during the study phase (old items) were presented, interspersed among 120 unstudied words (new items). One additional new buffer item was added to the beginning of each test block. On each trial, a white fixation cross was presented on a black background for 2000 msec, the screen blanked for 100 msec and the test word presented for 300 msec. A response was required during the following 2400 msec interval during which the screen remained blanked. Old and new items were presented pseudorandomly with no more than three trials of one item-type occurring consecutively. Words were presented in the same font and size as during the study phase.

fMRI Scanning

A Philips Eclipse 1.5-T MR scanner (Philips Medical Systems, Andover, MA, USA) was used to acquire both T1-weighted anatomical volume images (256 × 256 matrix, 1 mm³ voxels, SPGR sequence) and T2*-weighted echo-planar images [64 × 92 matrix, 2.6 × 3.9 mm pixels, echo time (TE) of 40 msec] with blood oxygenation level dependent (BOLD) contrast. Each EPI volume comprised thirty 3-mm-thick axial slices separated by 1 mm, positioned to give full coverage of the cerebrum and most of the cerebellum. Data were acquired in two sessions, each composed of 247 volumes with a repetition time (TR) of 2.7 sec/volume. Volumes within sessions were acquired continuously in a descending interleaved order. The first four volumes of each session were discarded to allow tissue magnetization to achieve a steady state. The 3.2-sec SOA for critical study items

allowed for an effective sampling rate of the hemodynamic response of 2 Hz.

Data Analysis

Data preprocessing and statistical analyses were performed with Statistical Parametric Mapping (SPM2, Wellcome Department of Cognitive Neurology, London, UK: www.fil.ion.ucl.ac.uk; Friston, Holmes, et al., 1995) implemented in MATLAB6 (The Mathworks, USA). All volumes were realigned spatially to the first volume, and the time series for voxels within each slice were realigned temporally to the acquisition of the middle slice in time. Inspection of movement parameters generated during spatial realignment indicated that no volunteer moved more than 2 mm in any direction during any session. Resulting images were spatially normalized to a standard EPI template on the basis of the Montreal Neurological Institute (MNI) reference brain (Cocosco, Kollokian, Kwan, & Evans, 1997) and resampled into 3-mm³ voxels using nonlinear basis functions (Ashburner & Friston, 1999). Normalized images were smoothed with an isotropic 8-mm full-width half-maximum (FWHM) Gaussian kernel. The T1 anatomical volumes were coregistered to the mean EPI volume and normalized to a standard T1 template of the MNI brain.

Statistical analyses were performed in two stages of a mixed effects model. Study task and secondary (auditory) task stimuli were presented as discrete, nonoverlapping events (see Figure 1), permitting analyses to be conducted in a fully event-related design. In the first stage, neural activity elicited by the study and secondary task items was modeled by delta functions (impulse event) at stimulus onset. These functions were then convolved with a canonical hemodynamic response function (HRF) and its temporal and dispersion derivatives (Friston, Fletcher, et al., 1998) to yield regressors in a General Linear Model that modeled the BOLD response to each event type. The two derivatives model variance in latency and duration, respectively. Analyses of the parameter estimates pertaining to these derivatives added no theoretically meaningful information to that contributed by the HRF, and are not reported (results are available from the corresponding author upon request).

Six event-types of interest were defined for each study session: words studied under easy concurrent task conditions later recognized (*easy hits*) or not recognized (*easy misses*), words studied under hard concurrent task conditions later recognized (*hard hits*) or not recognized (*hard misses*), and auditory stimuli in each task condition (*easy auditory items* and *hard auditory items*). Only words that received correct classifications on the study task were included. Words that were incorrectly classified, or for which a response was omitted, were modeled as events of no interest, as were buffer items. To maximize the number of trials in each

condition, and to maintain comparability with Kensinger et al. (2003), activity elicited by subsequently recognized study items was collapsed over the factor of recognition confidence. [An analysis confined to items recognized with high confidence (cf. Otten et al., 2001; Otten & Rugg, 2001a) revealed a qualitatively similar pattern of findings to that described below. These results are available from the corresponding author upon request.] An additional regressor modeled the 10-sec duration task cues. Also employed were six regressors per session modeling movement-related variance (three rigid-body translations and three rotations determined from the realignment stage) and a session-specific constant term modeling the mean over scans. The time series in each voxel were high-pass-filtered to 1/128 Hz to remove low-frequency noise and scaled within-session to a grand mean of 100 across both voxels and scans. Parameter estimates for events of interest were estimated using a General Linear Model. Nonsphericity of the error covariance was accommodated by an AR(1) model, in which the temporal autocorrelation was estimated by pooling over suprathreshold voxels (Friston, Glaser, et al., 2002). The parameters for each covariate and the hyperparameters governing the error covariance were estimated using Restricted Maximum Likelihood (ReML). Effects of interest were tested using linear contrasts of the parameter estimates. These contrasts were carried forward to a second stage in which subjects were treated as a random effect. Unless otherwise specified, only effects surviving a threshold of $p < .001$, uncorrected for multiple comparisons and including five or more contiguous voxels, were interpreted. Contrasts where differences in either direction were of interest were thresholded at $p < .0005$, so as to maintain a two-tailed threshold of $p < .001$. The peak voxels of clusters exhibiting reliable effects are reported in MNI coordinates.

Regions of overlap between the outcomes of two contrasts were identified by inclusively masking the relevant SPMs. The statistical significance of the resulting SPM was computed using Fisher's method of estimating the conjoint significance of the independent tests (Lazar, Luna, Sweeney, & Eddy, 2002; Fisher, 1950).

We were specifically interested in determining the effects of divided attention on subsequent memory effects in two regions—the ventral IFG and the anterior hippocampal formation—which have been consistently identified in prior studies of episodic memory encoding and which were a focus of the findings of Kensinger et al. (2003). We therefore defined two ROIs a priori, each a sphere with a radius of 6 mm, centered on coordinates reported by a study utilizing the same word pool and study task as here (Otten et al., 2001). The coordinates were $-36, 36, -9$ for the ventral IFG, and $-27, -15, -12$ for the anterior hippocampal formation. The significance of effects within these ROIs was evaluated after small-volume correction for multiple

comparisons with the False Discovery Rate procedure (Nichols & Hayasaka, 2003; Worsley et al., 1996).

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Reprint requests should be sent to Melina R. Uncapher, Center for the Neurobiology of Learning and Memory, University of California at Irvine, Irvine, CA 92697-3800, or via e-mail: mball@uci.edu.

The data reported in this experiment have been deposited with the fMRI Data Center archive (www.fmridc.org). The accession number is 2-2005-119PD.

Note

1. Identical findings were obtained if analyses were restricted to parameter estimates of peak voxel in each region.

REFERENCES

- Anderson, N. D., Iidaka, T., Cabeza, R., Kapur, S., McIntosh, A. R., & Craik, F. I. (2000). The effects of divided attention on encoding- and retrieval-related brain activity: A PET study of younger and older adults. *Journal of Cognitive Neuroscience, 12*, 775–792.
- Ashburner, J., & Friston, K. J. (1999). Nonlinear spatial normalization using basis functions. *Human Brain Mapping, 7*, 254–266.
- Baddeley, A., Lewis, V., Eldridge, M., & Thomson, N. (1984). Attention and retrieval from long-term memory. *Journal of Experimental Psychology: General, 113*, 518–540.
- Buckner, R. L., Logan, J., Donaldson, D. I., & Wheeler, M. E. (2000). Cognitive neuroscience of episodic memory encoding. *Acta Psychologica, 105*, 127–139.
- Chee, M. W., Westphal, C., Goh, J., Graham, S., & Song, A. W. (2003). Word frequency and subsequent memory effects studied using event-related fMRI. *Neuroimage, 20*, 1042–1051.
- Cocosco, C., Kollokian, V., Kwan, R. S., & Evans, A. (1997). Brainweb: Online interface to a 3D MRI simulated brain database. *Neuroimage, 5*, S425.
- Collette, F., & Van de Linden, M. (2002). Brain imaging of the central executive component of working memory. *Neuroscience and Biobehavioral Reviews, 26*, 105–125.
- Craik, F. I., Govoni, R., Naveh-Benjamin, M., & Anderson, N. D. (1996). The effects of divided attention on encoding and retrieval processes in human memory. *Journal of Experimental Psychology: General, 125*, 159–180.
- Craik, F. I. M., & Lockhart, R. S. (1972). Levels of processing: A framework for memory research. *Journal of Verbal Learning and Verbal Behavior, 11*, 671–684.
- Daselaar, S. M., Prince, S. E., & Cabeza, R. (2004). When less means more: Deactivations during encoding that predict subsequent memory. *Neuroimage, 23*, 921–927.
- Davachi, L., Maril, A., & Wagner, A. D. (2001). When keeping in mind supports later bringing to mind: Neural markers of phonological rehearsal predict subsequent remembering. *Journal of Cognitive Neuroscience, 13*, 1059–1070.
- Davachi, L., Mitchell, J. P., & Wagner, A. D. (2003). Multiple routes to memory: Distinct medial temporal lobe processes build item and source memories. *Proceedings of the National Academy of Sciences, U.S.A., 100*, 2157–2162.
- Fernandes, M. A., & Moscovitch, M. (2000). Divided attention and memory: Evidence of substantial interference effects at retrieval and encoding. *Journal of Experimental Psychology: General, 129*, 155–176.
- Fisher, R. A. (1950). *Statistical methods for research workers* (11th ed.). London: Oliver and Boyd.
- Fletcher, P. C., Frith, C. D., Grasby, P. M., Shallice, T., Frackowiak, R. S., & Dolan, R. J. (1995). Brain systems for encoding and retrieval of auditory-verbal memory. An in vivo study in humans. *Brain, 118*, 401–416.
- Fletcher, P. C., Shallice, T., & Dolan, R. J. (1998). The functional roles of prefrontal cortex in episodic memory: I. Encoding. *Brain, 121*, 1239–1248.
- Friston, K. J., Fletcher, P. C., Josephs, O., Holmes, A., Rugg, M. D., & Turner, R. (1998). Event-related fMRI: Characterizing differential responses. *Neuroimage, 7*, 30–40.
- Friston, K. J., Glaser, D. E., Henson, R. N., Kiebel, S., Phillips, C., & Ashburner, J. (2002). Classical and Bayesian inference in neuroimaging: Applications. *Neuroimage, 16*, 484–512.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J. B., 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., Poldrack, R. A., & Desmond, J. E. (1998). The role of left prefrontal cortex in language and memory. *Proceedings of the National Academy of Sciences, U.S.A., 95*, 906–913.
- Iidaka, T., Anderson, N. D., Kapur, S., Cabeza, R., & Craik, F. I. (2000). The effect of divided attention on encoding and retrieval in episodic memory revealed by positron emission tomography. *Journal of Cognitive Neuroscience, 12*, 267–280.
- Josephs, O., & Henson, R. N. (1999). Event-related functional magnetic resonance imaging: Modelling, inference and optimization. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, 354*, 1215–1228.
- Kensinger, E. A., Clarke, R. J., & Corkin, S. (2003). What neural correlates underlie successful encoding and retrieval? A functional magnetic resonance imaging study using a divided attention paradigm. *Journal of Neuroscience, 23*, 2407–2415.
- Kucera, H., & Francis, W. (1967). *Computational analysis of present-day American English*. Providence: Brown University Press.
- Lazar, N. A., Luna, B., Sweeney, J. A., & Eddy, W. F. (2002). Combining brains: A survey of methods for statistical pooling of information. *Neuroimage, 16*, 538–550.
- Morcom, A. M., Good, C. D., Frackowiak, R. S., & Rugg, M. D. (2003). Age effects on the neural correlates of successful memory encoding. *Brain, 126*, 213–229.
- Naveh-Benjamin, M., Craik, F. I., Gavrilesco, D., & Anderson, N. D. (2000). Asymmetry between encoding and retrieval processes: Evidence from divided attention and a calibration analysis. *Memory & Cognition, 28*, 965–976.
- Naveh-Benjamin, M., Craik, F. I., Perretta, J. G., & Tonev, S. T. (2000). The effects of divided attention on encoding and retrieval processes: The resiliency of retrieval processes. *Quarterly Journal of Experimental Psychology, Section A, 53*, 609–625.
- Naveh-Benjamin, M., Guez, J., & Marom, M. (2003). The effects of divided attention at encoding on item and associative memory. *Memory & Cognition, 31*, 1021–1035.
- Nichols, T., & Hayasaka, S. (2003). Controlling the familywise error rate in functional neuroimaging: A comparative

- review. *Statistical Methods in Medical Research*, *12*, 419–446.
- Otten, L. J., Henson, R. N. A., & Rugg, M. D. (2001). Depth of processing effects on neural correlates of memory encoding: Relationship between findings from across- and within-task comparisons. *Brain*, *124*, 399–412.
- Otten, L. J., Henson, R. N. A., & Rugg, M. D. (2002). State- and item-related neural correlates of successful memory encoding. *Nature Neuroscience*, *5*, 1339–1344.
- Otten, L. J., & Rugg, M. D. (2001a). Task-dependency of the neural correlates of episodic encoding as measured by fMRI. *Cerebral Cortex*, *11*, 1150–1160.
- Otten, L. J., & Rugg, M. D. (2001b). When more means less: Neural activity related to unsuccessful memory encoding. *Current Biology*, *11*, 1528–1530.
- Paller, K. A., & Wagner, A. D. (2002). Observing the transformation of experience into memory. *Trends in Cognitive Sciences*, *6*, 93–102.
- Ranganath, C., Johnson, M. K., & D'Esposito, M. (2003). Prefrontal activity associated with working memory and episodic long-term memory. *Neuropsychologia*, *41*, 378–389.
- Rugg, M. D. (2002). Functional neuroimaging of memory. In A. Baddeley, B. Wilson, & M. Kopelman (Eds.), *Handbook of memory disorders* (2nd ed.). Hoboken, NJ: Wiley.
- Shallice, T., Fletcher, P., Frith, C. D., Grasby, P., Frackowiak, R. S., & Dolan, R. J. (1994). Brain regions associated with acquisition and retrieval of verbal episodic memory. *Nature*, *368*, 633–635.
- Snodgrass, J. G., & Corwin, J. (1988). Pragmatics of measuring recognition memory—applications to dementia and amnesia. *Journal of Experimental Psychology: General*, *117*, 34–50.
- Szameitat, A. J., Schubert, T., Muller, K., Von Cramon, D. Y. (2002). Localization of executive functions in dual-task performance with fMRI. *Journal of Cognitive Neuroscience*, *14*, 1184–1199.
- Wager, T. D., & Smith, E. E. (2003). Neuroimaging studies of working memory: A meta-analysis. *Cognitive, Affective and Behavioral Neuroscience*, *3*, 255–274.
- Wagner, A. D., & Davachi, L. (2001). Cognitive neuroscience: Forgetting of things past. *Current Biology*, *11*, R964–R967.
- Wagner, A. D., Koutstaal, W., & Schacter, D. L. (1999). When encoding yields remembering: Insights from event-related neuroimaging. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, *354*, 1307–1324.
- Wagner, A. D., Pare-Blagoev, E. J., Clark, J., & Poldrack, R. A. (2001). Recovering meaning: Left prefrontal cortex guides controlled semantic retrieval. *Neuron*, *31*, 329–338.
- Wagner, A. D., Schacter, D. L., Rotte, M., Koutstaal, W., Maril, A., Dale, A., Rosen, B. R., & Buckner, R. L. (1998). Building memories: Remembering and forgetting verbal experiences as predicted by brain activity. *Science*, *281*, 1188–1191.
- Worsley, K. J., Marret, S., Neelin, P., Vandal, A. C., Friston, K. J., & Evans, A. C. (1996). A unified statistical approach for determining significant voxels in images of cerebral activation. *Human Brain Mapping*, *4*, 58–73.
- Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, *46*, 441–517.