

Brain regions associated with successful and unsuccessful retrieval of verbal episodic memory as revealed by divided attention

Myra A. Fernandes^{a,*}, Morris Moscovitch^{b,c}, Marilyne Ziegler^c, Cheryl Grady^{b,c}

^a Department of Psychology, 200 University Ave. W., University of Waterloo, Waterloo, Ont., Canada N2L 3G1

^b Rotman Research Institute, Baycrest Centre for Geriatric Care, Toronto, Ont., Canada

^c Department of Psychology, University of Toronto, Toronto, Ont., Canada

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Abstract

Which brain regions are implicated when words are retrieved under divided attention, and what does this tell us about attentional and memory processes needed for retrieval? To address these questions we used fMRI to examine brain regions associated with auditory recognition performed under full and divided attention (DA). We asked young adults to encode words presented auditorily under full attention (FA), and following this, asked them to recognize studied words while in the scanner. Attention was divided at retrieval by asking participants to perform either an animacy task to words, or odd-digit identification task to numbers presented visually, concurrently with the recognition task. Retrieval was disrupted significantly by the word-, but not number-based concurrent task. A corresponding decrease in brain activity was observed in right hippocampus, bilateral parietal cortex, and left precuneus, thus demonstrating, for the first time, involvement of these regions in recognition under DA at retrieval. Increases in activation of left prefrontal cortex (PFC), associated with phonological processing, were observed in the word- compared to number-based DA condition. Results suggest that the medial temporal lobe (MTL) and neo-cortical components of retrieval, believed to form the basis of episodic memory traces, are disrupted when phonological processing regions in left PFC are engaged simultaneously by another task. Results also support a component–process model of retrieval which posits that MTL-mediated retrieval does not compete for general cognitive resources but does compete for specific structural representations.

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1. Brain regions associated with successful and unsuccessful retrieval of verbal episodic memory as revealed by divided attention

Manipulating attention by having participants engage in two attention-demanding tasks simultaneously can be used to determine which memory processes draw on cognitive resources for their operation, and to incorporate that knowledge into theories of memory. Dividing attention has been shown to affect encoding much more than retrieval, leading researchers to conclude that the former, and not the latter, requires a general attentional system for optimal performance (Anderson,

Craik, & Naveh-Benjamin, 1998; Baddeley, Lewis, Eldridge, & Thomson, 1984; Craik, Govoni, Naveh-Benjamin, & Anderson, 1996; Fernandes & Moscovitch, 2000; Naveh-Benjamin, Craik, Guez, & Dori, 1998). In line with these behavioural findings, neuroimaging studies have shown that neural activation in the prefrontal cortex (PFC) is reduced by dividing attention during encoding (Iidaka, Anderson, Kapur, Cabeza, & Craik, 2000; Kensinger, Clarke, & Corkin, 2003; Shallice et al., 1994), but not during retrieval (Iidaka et al.).

However, recent behavioural research suggests that large disruptions in episodic memory also can occur from divided attention (DA) conditions at retrieval, specifically when the concurrent task uses material, and/or processing, similar to that used in the memory task. For example, a decrement in verbal memory of about 30% from full attention levels is observed when the concurrent task is word-based, whereas an

* Corresponding author. Tel.: +1 519 885 1211x2142; fax: +1 519 746 8631.

E-mail address: mafernan@watarts.uwaterloo.ca (M.A. Fernandes).

equally demanding digit-based, or picture-based, task produces a decrement of only 10–15% (Fernandes & Moscovitch, 2000, 2002, 2003). Unlike the general effect observed from DA at encoding, which produces an approximate 50% decline in subsequent memory performance, across numerous types of distracting tasks, effects from DA at retrieval depend on the material or type of processing required in the distracting task. In this study, we use fMRI to examine the neural basis of the interference effect at retrieval, and consider the relevance of those findings for theories of memory.

It has been proposed that the large interference effects from DA at retrieval occur primarily as a result of competition for neo-cortical representations, which likely code phonology (Fernandes & Moscovitch, 2003; Fernandes, Priselac, & Moscovitch, 2005; Moscovitch, Fernandes, & Troyer, 2001). The present experiment tests this hypothesis and, in addition, highlights other brain regions that may be implicated. Differences in activation between those DA conditions that affect retrieval (i.e. word-based distracting task), and those that do not (digit-based distracting task), are expected in neocortical sites associated with verbal representation (semantic, orthographical and/or phonological), as well as in medial temporal lobe (MTL) and related structures associated with reactivation of the memory trace.

An alternative account is that large memory costs at retrieval result from competition for general attentional resources. Such resources, believed to be mediated by dorsolateral PFC, are needed to coordinate the online processing of dual-tasks (Anderson et al., 2000; Craik, 2001; D'Esposito et al., 1995; Iidaka et al., 2000), which may be more difficult as the similarity increases, between materials, and/or processing, in the distracting and memory tasks. This idea is consistent with Baddeley's (1992) hypothesis that the ability to coordinate concurrent tasks relies on the central executive (CE) of his working memory model, whose operation requires resources mediated by the PFC. If true, greater activation should be observed in dorsolateral PFC when attention is divided than full, and specifically, it should be greater when materials and/or processing requirements in the distracting task are similar (word-based) to that in the memory task, than different (digit-based distracting task). fMRI allows us to test these hypotheses, and to identify the brain regions associated with varying levels of proficiency of auditory recognition, during full and divided attention conditions.

2. Materials and methods

2.1. Participants

Twelve normal healthy participants (seven female; two left-handed), from 20 to 30 years of age (mean age = 26.33, S.D. = 3.36), with a mean of 16.5 years (S.D. = 2.33) of education completed the study after giving informed consent. All procedures were approved by a joint ethics committee of the University of Toronto, and the Baycrest Centre for Geriatric

Care. All participants spoke English fluently, and were free from psychiatric or neurological disease.

2.2. Behavioural task materials

All word stimuli, for the recognition and animacy tasks, were medium to high frequency words chosen from Francis and Kucera (1982). Word frequencies ranged from 20 to 100 occurrences per million. For each of the four study phases, participants heard a list of 50 unrelated words while in the scanner, presented at a rate of 1 word every 2 s. Encoding was not scanned.

During the recognition task, words were presented auditorily at a rate of 1 every 2 s, through Avotec headphones, and participants made a button-press to "old" words only. In each block, half of the words were old; these were presented pseudo-randomly throughout each block. Volume of presentation was adjusted individually for each participant, prior to the study phase, such that items could be heard over the noise produced by the scanner.

Items in the distracting tasks were presented visually at a rate of 1 every 2 s, on a white background, with black lettering or numbering, shown centrally through Avotec goggles adjusted for the acuity of each participant. The animacy task consisted of visual presentation of words with a mean of six letters, representing animals (e.g. kitten) and man-made objects (e.g. hammer). Participants responded when the visually presented word represented a non-living object. Stimuli for the odd-digit task consisted of visual presentation of two-digit numbers flanked by two Xs on either side, chosen from a table of random numbers (Kirk, 1995). Participants responded when the visually presented digit was odd. In each block, half of the items were targets requiring a button-press; these were presented pseudo-randomly throughout each block.

For the auditory baseline task, participants heard either the word "word" or "press", and made a button-press for the latter. In the visual baseline task, either a string of "OOOOOO" or "XXXXXX" was seen and participants made a button-press to the latter. For all tasks involving auditory presentation, participants responded by pressing a button with the index finger of the left hand, and for all tasks involving visual presentation responses were made with the right index finger, using two fMRI-compatible response pads (Lightwave Technologies, Surrey, BC, Canada).

2.3. Study procedure

Stimulus presentation and response recording were controlled by an IBM PC, using E-Prime v.1.0 software (Psychology Software Tools Inc., Pittsburgh, PA). Participants performed a practice session, outside of the scanner, consisting of a block of each task, and also a block for each of the dual-task conditions. They also performed a sample run in which blocks were presented randomly, as in the scanner. For each block in the practice and scanner session, 10 items were presented at a rate of 1 item every 2 s, preceded by 4 s

of short instructions, making blocks 24 s in length. For the dual-task conditions, onset of the auditory recognition and visual distracting task was simultaneous. Participants were told that, in DA blocks, they should divide their attention equally between the two tasks, and for each, they should respond as quickly and accurately as possible.

While in the scanner, prior to each of the four runs, participants heard a list of 50 unrelated words presented at a rate of 1 word every 2 s through Avotec headphones. This encoding phase was not scanned. The retrieval phase was scanned. For each participant, two of the runs were “short”, consisting of seven blocks presented pseudo-randomly: three of the recognition task under full attention (FA), two of the recognition task performed under divided attention, with the animacy distracting task (DA animacy), and two of the recognition task performed under DA with the odd-digit task (DA digits). A block of the FA recognition task was presented in between DA blocks. The other two runs were “long”, consisting of 19 blocks presented pseudo-randomly: 2 of the animacy task performed singly, 2 of the odd-digit task performed singly, 2 of the FA recognition task, 2 of the DA animacy, 2 of the DA digits, 5 of the auditory baseline, and 4 of the visual baseline task. Blocks of the auditory and visual baselines alternated in between the other tasks. The order of runs alternated between short and long, in a counterbalanced fashion across participants. Prior to each scanning run, a blank screen was presented for 20 s, to control for transient signal changes in brain magnetization.

Including long runs allowed us to examine behavioural performance of the distracting tasks performed singly, as well as under dual-task conditions. However, the time lag between when words were studied and tested, in the latter half of long runs, would be much longer (>4 min) than in behavioural paradigms investigating effects of DA on memory (Fernandes & Moscovitch, 2000, 2002, 2003; Naveh-Benjamin et al., 1998), where study and test were separated by approximately 1–2 min. Such a lengthy delay in the long runs may diminish memory overall, making it difficult to interpret interference effects from the dual-task manipulations. Thus, we had participants also perform the short runs, which included only blocks involving memory, and not single-task performance of the distracting tasks, or the auditory or visual baselines.

2.4. fMRI data acquisition

Data were acquired with a Signa 1.5 Tesla magnet with a standard coil (CV/i hardware, LX8.3 software; General Electric Medical Systems, Waukesha, WI). A standard high-resolution, 3D T1-weighted fast spoiled gradient echo image (TR = 35 ms; TE = 6.0 ms; flip angle = 35°; acquisition matrix = 256 × 256 × 124; FOV = 22 × 16.5 cm; 124 axial slices; slice thickness = 1.4 mm) was first obtained to register functional maps against brain anatomy. Functional imaging was performed to measure brain activation by means of the blood oxygenation level-dependent (BOLD) effect (Ogawa,

Lee, Kay, & Tank, 1990) with optimal contrast. Functional scans were acquired with a single-shot T2*-weighted pulse sequence with spiral readout (TR = 2500 ms; TE = 40 ms; flip angle = 80°; effective acquisition matrix = 64 × 64 × 26; FOV = 20 cm; 26 slices; slice thickness = 5.0 mm), including off-line gridding and reconstruction of the raw data (Glover & Lai, 1998). For the two short runs, we collected 76 time-points, and for the long runs, 191 time points per run.

2.5. fMRI data analysis

Processing and analysis were performed using the Analysis of Functional Neuroimages (AFNI, version 2.56a) software package (Cox, 1996; Cox & Hyde, 1997). In the pre-processing stage, the initial eight volumes in each run, in which transient signal changes occur as brain magnetization reaches a steady state, were excluded from all analyses. Time series data were spatially co-registered to correct for head motion using a 3D Fourier transform interpolation. Each volume in the time series was aligned to an earlier fiducial volume from the first imaging run in the scanning session. The alignment parameters were computed by an iterative weighted least squares fit to the base volume. The peak range of head motion was less than 1.3 mm for all participants. Implementation was done using the 3dvolreg program from AFNI.

In the individual analysis for each participant, general linear tests (GLTs), with one linear constraint, were conducted to test whether the responses in the DA animacy and DA digits condition differed in magnitude, and consequently, to distinguish different regions of BOLD signal change based on differences in processing across conditions. For each condition, the response was estimated at seven time points (0 TR through 6 TR) and the magnitude of the response was computed by summing the response parameters over all time lags. The data itself determined the functional form of the estimated response. The output consisted of the estimated response, along with the statistical significance of the fit of the response to the original fMRI data, for each voxel in the dataset. In addition to the regression coefficients, *t*-statistics for each response parameter, and partial *F*-statistics for each condition were computed, along with an overall *F*-statistic for the model. The implementation was done using the 3dDeconvolve program from AFNI software.

We performed two analyses: in the first, we used either the single-task animacy or single-task digits condition as baseline for the DA animacy and DA digits condition, respectively; data from the two long runs only were used here, as single-task conditions were not included in the short runs. This analysis, using the single tasks as baseline was chosen to control for the possibility that any differences observed between DA conditions were not due to differences in the brain regions called upon to carry out the two different secondary tasks (animacy and digit decisions). In addition, we

used the dataset from the long runs to consider activation in the FA condition using the auditory task (present in only the long runs) as baseline. In the second analysis, we used the FA condition as the baseline in the contrast of interest, DA digits versus DA animacy. This analysis was conducted on data from all four runs, concatenated. Because our research questions were aimed specifically at the effects of dual-tasks on brain regions contributing to memory, we used the FA recognition blocks, common across short and long runs, as the baseline in these analyses to create activation maps (as described above) of the BOLD signal for each participant, for the DA animacy and DA digits tasks.

For each participant, the output of the regression was then converted into units of percentage change relative to baseline, thus preventing changes in the baseline to artificially add variance in the ANOVA group analysis. For both analyses, the resulting individual activation images were spatially normalized to a Talairach template (Talairach & Tournoux, 1988) using AFNI, and smoothed with a Gaussian filter of 6 mm full-width-at-half-maximum (FWHM) to increase the signal-to-noise ratio. This was done to permit subsequent group analysis. Using the FA task as baseline, a voxel-wise, mixed model, two-factor ANOVA with Condition (DA animacy and DA digits) as a fixed factor, A, and participants as a random factor, B, was conducted. The output contained multiple sub-bricks, consisting of the main effect of Factor A, means for each of the two levels of Factor A, and results from the defined contrast (DA digits versus DA animacy). Separate ANOVAs were conducted using data from the long runs, with respective single-tasks as baselines for each DA condition, and the auditory task as baseline for the FA condition. For both analyses, the statistical cutoff for significant signal change in the contrast of interest was set at $p \leq .005$ (see tables), and the minimum cluster size was 50 mm^3 , with a connectivity radius of 1 mm.

Finally, to enable us to compare the pattern of activation in regions of interest, previously reported to be important for memory (Cabeza & Nyberg, 2000; Fernandes & Moscovitch,

2000, 2002, 2003; Moscovitch, 1992), we used the Talairach atlas (Talairach & Tournoux, 1988) in AFNI to define Brodmann Areas 10, 45, 9/46, hippocampus, parahippocampus and precuneus, bilaterally; these regions of interest were also checked manually by authors MF and CG. For the FA, DA animacy, and DA digits conditions, the coordinate corresponding to the peak t -value within each of the defined regions is noted in Table 5, and its percentage signal change is shown in Figs. 1–3, using the appropriate baseline from the long runs for each (i.e. auditory baseline used for FA, single-task digits for DA digits, and single-task animacy for DA animacy).

3. Results

3.1. Behavioural data

3.1.1. Memory performance

There was no effect of run type on recognition measures in any condition, thus behavioural data were collapsed across runs, for common block types (i.e. FA, DA animacy, DA digits). Hit rate and false alarm rate are shown in Table 1 (each out of 50 overall), along with the hit rate minus false alarm rate for a measure of overall performance on the recognition test. Analyses were done for each of these three dependent measures, and the same pattern was found regardless. Thus, we report only the statistics for the analysis using overall performance on the recognition test (hereafter referred to as recognition accuracy). Also shown in Table 1 is the mean reaction time (RT) for correctly recognized words, in each condition.

Data were analyzed using a within-participants (FA, DA digits, DA animacy) ANOVA. There was a main effect of recognition condition, $F(2, 22) = 28.33$, $p < .001$. Planned comparisons showed recognition accuracy in the DA animacy condition was significantly lower than in the FA condition, $F(1, 11) = 89.66$, $p < .001$, but accuracy in the DA digits and FA conditions did not differ. Recognition accuracy was also

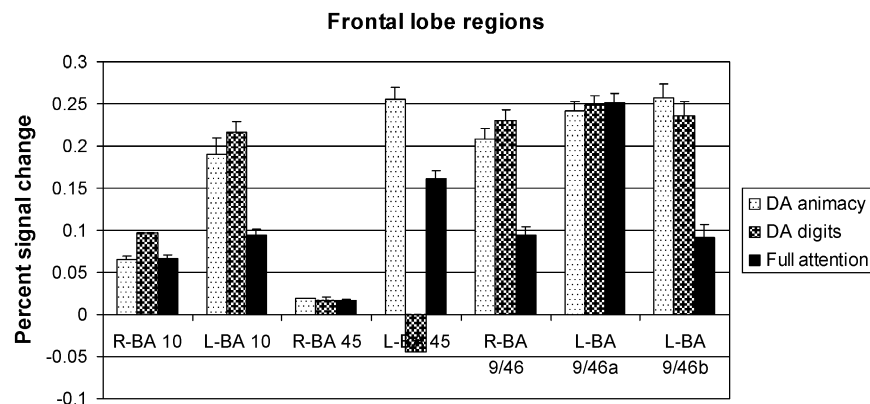


Fig. 1. Percent signal change in ROIs within the frontal lobe noted in Table 5, in the full attention, divided attention with digits (DA digits), and divided attention with animacy (DA animacy) conditions. Error bars indicate standard errors. L: left, R: right. Only two areas differentiated the DA conditions: activity in right BA 10 was higher in the DA digit condition, and activity in the left inferior frontal gyrus (BA 45) was greater in DA animacy. See Table 5 for peak coordinates within each ROI.

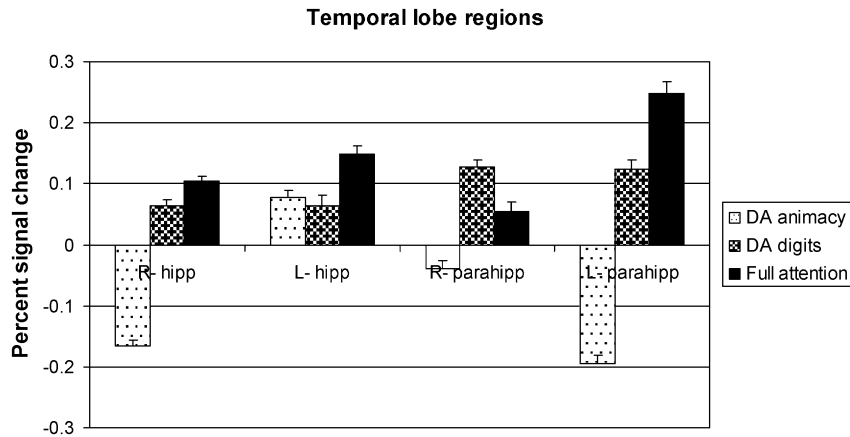


Fig. 2. Percent signal change in ROIs within the temporal lobe noted in Table 5, in the full attention, divided attention with digits (DA digits), and divided attention with animacy (DA animacy) conditions. Error bars indicate standard errors. L: left, R: right, hipp: hippocampus, parahipp: parahippocampus. Activity in right hippocampus was significantly increased in the FA condition (relative to the auditory baseline), was less so in the DA digits condition, and was significantly reduced in the DA animacy condition (using single-task baselines for each DA condition). A similar pattern is seen, across conditions, in the left parahippocampal gyrus. Activity in the left hippocampus did not increase significantly in either DA condition, although an increase was seen in FA. See Table 5 for peak coordinates within each ROI.

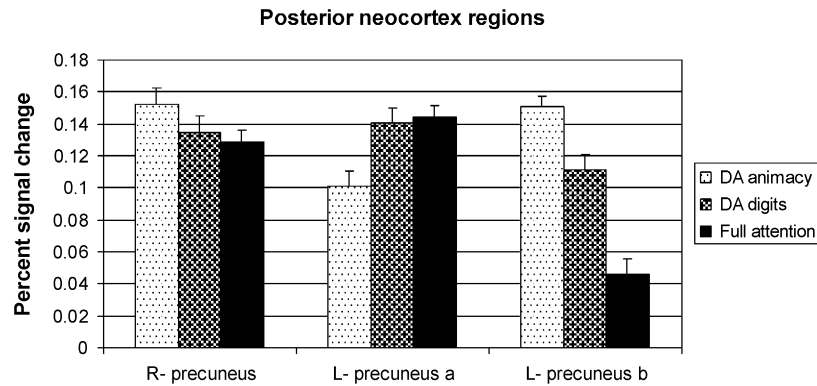


Fig. 3. Percent signal change in ROIs within the posterior neocortex noted in Table 5, in the full attention, divided attention with digits (DA digits), and divided attention with animacy (DA animacy) conditions. Error bars indicate standard errors. L: left, R: right. The precuneus was active across all three memory conditions, in both hemispheres. Activity in one region of left precuneus (−22, −50, 43) was increased during both DA conditions, but more so for DA digits. A more inferior region of left precuneus (−13, −58, 19) was more active in the DA animacy compared to DA digits condition. See Table 5 for peak coordinates within each ROI.

significantly lower in the DA animacy compared to DA digits condition, $F(1, 11) = 26.62, p < .001$. The same analysis was applied to RTs for correctly recognized words. There was a significant effect of Recognition condition, $F(2, 22) = 17.22, p < .001$. RTs were significantly slower under both DA conditions compared to FA ($F(1, 11) = 6.74$, and 51.67 , for the DA digits and DA animacy conditions, respectively, $p < 0.005$).

RTs were significantly longer in the DA animacy compared to DA digits condition, $F(1, 11) = 7.94, p < .05$.

3.1.2. Distracting task performance

Table 2 shows performance on the visually presented animacy and digits task performed singly, and under dual-task conditions. Accuracy rate was calculated as hit rate

Table 1
Measures of recognition task performance, and percentage change in performance from full to divided attention conditions

Measure	Full attention	DA animacy	DA digits
Hit rate	.69 (.11)	.57 (.10)	.66 (.17)
False alarm rate	.10 (.04)	.17 (.07)	.10 (.05)
Recognition accuracy (hit rate – false alarm rate)	.59 (.13)	.40 (.15)	.57 (.19)
Percentage decline in recognition accuracy		34.98 (18.79)	5.39 (19.47)
RT	1114 (66)	1271 (68)	1182 (62)
Percentage increase in RT		12.21 (5.51)	5.42 (7.81)

Note: DA: divided attention; RT: reaction time in ms. Standard deviation shown in parentheses

Table 2
Accuracy rate and reaction time in ms on distracting tasks, and percentage change from single-task to divided attention conditions

Measure	Single-task		Divided attention	
	Animacy	Digits	Animacy	Digits
Accuracy rate (hit rate minus false alarm rate)	.91 (.07)	.99 (.02)	.86 (.08)	.98 (.03)
Percentage decline in accuracy			5.51 (9.21)	0.20 (4.41)
RT	742.92 (99.25)	623.08 (78.96)	1046.71 (95.88)	914.50 (128.71)
Percentage increase in RT			8.64 (10.32)	6.49 (7.66)

Note: DA: divided attention; RT: reaction time in ms. Standard deviation shown in parentheses

minus false alarm rate. There was an effect of Task, with poorer performance on the animacy compared to digits task, $F(1, 11) = 30.47$, $p < .001$, but no effect of Attention. The Task \times Attention interaction was significant, and showed greater disruption, compared to single-task performance, in the DA animacy than DA digits condition, $F(1, 11) = 5.28$, $p < .05$. However, the percentage decline from single to dual-task performance is quite small overall in the DA animacy condition (only 5%), therefore, we do not think our finding of greater memory interference in the DA animacy condition (35% decline, see Table 1) could be accounted for by differences in distracting task difficulty alone.

The same analysis was also applied to distracting task RTs, performed singly and under DA conditions. There was a significant effect of Task and Attention ($F(1, 11) = 30.83$, and $F(1, 11) = 76.29$, p 's $< .001$, respectively), with slower responses on the animacy than digits task, and under DA than single-task conditions. The interaction of these factors, however, was non-significant, and the percentage increase in RT from single to dual-task conditions did not differ.

We also examined correlations between memory and distracting task performance. We found no indication that memory interference in either DA condition was related to performance in the distracting task. The correlation between memory interference and interference on the distracting tasks was $r = .28$ for DA animacy, and $r = -.01$ for DA digits, p 's $> .05$.

3.1.3. fMRI group data

Tables 3 and 4 show the brain regions with a significant percent change in BOLD signal, when the two DA conditions are compared, using either the corresponding single-tasks as baselines or the FA task as baseline, respectively (see Section 2 for details on baselines; see supplemental material on the web for table using the auditory task, and data from the long runs only, as baseline, Appendix A). For each, the x , y , z coordinates of the peak region, the Brodmann Area (BA), and the t -statistic associated with that peak are shown. Also shown is the t -statistic (and corresponding p -value) for each of these regions, contrasting each DA task to its baseline. This allows us to see if the difference in each region, identified by the

Table 3
Coordinates and t -statistics in brain regions showing differences in activation in the DA digits compared to DA animacy condition, using single-task digits and single-task animacy as the baseline condition for each, respectively

Brain region (BA)	Coordinates			DA digits vs. DA animacy	DA task vs. single task		
	x	y	z	(DA _{dig} -S _{dig})-(DA _{anim} -S _{anim})	DA _{dig} -S _{dig}	DA _{anim} -S _{anim}	
DA digits > DA animacy							
Right middle frontal (BA10)	40	55	4	3.79*	6.491**	1.13	
Right hippocampus (BA 28)	34	-26	-8	4.58**	1.334	-5.14**	
Left cingulate (BA 31)	-20	-38	35	3.86*	3.64*	-1.82	
DA animacy > DA digits							
Right superior frontal (BA 6)	12	16	57	-3.84*	-0.60	4.82**	
Right inferior frontal (BA 45)	57	21	21	-4.03*	-1.87	3.82**	
Left inferior frontal (BA 45)	-50	28	19	-4.97**	-1.46	5.58**	
Left middle temporal (BA 21)	-56	-16	-14	-3.53*	-1.03	3.96**	
Left middle temporal (BA 38)	-45	6	-34	-3.96*	-1.64	3.96**	
Left precuneus (BA 31)	-13	-58	18	-4.67**	0.13	6.74**	
Left cuneus (BA 19)	-15	-85	33	-4.36**	-0.45	5.72**	
Left thalamus	-5	-33	6	-3.56*	0.54	5.58**	
Right cerebellum	37	-66	-46	-3.72*	-0.34	4.93**	
Left cerebellum	-31	-21	-34	-3.84*	-2.42	3.02	

Note: data from long runs only; DA: divided attention; the Talairach coordinates represent the peak for the given region, for the t -value of the DA digits by DA animacy interaction (positive values represent greater activation for DA digits vs. DA animacy, negative values represent greater activation for DA animacy vs. DA digits); BA: Brodmann's Area according to the atlas of Talairach and Tournoux (1988); DA_{dig}-S_{dig}: t -value for DA digits vs. single-task digits; DA_{anim}-S_{anim}: t -value for DA animacy vs. single-task animacy.

* $p < .005$.

** $p < .001$.

Table 4

Coordinates and *t*-statistics in brain regions showing differences in activation in the DA digits compared to DA animacy condition, using the full attention task as baseline

Brain region (BA)	Coordinates			DA digits vs. DA animacy	Task vs. full attention	
	<i>x</i>	<i>y</i>	<i>z</i>	(DA _{dig} -FA)-(DA _{anim} -FA)	DA _{dig} -FA	DA _{anim} -FA
DA digits > DA animacy						
Left superior frontal (10)	-26	44	1	5.02*	0.42	-6.68**
Left anterior cingulate (24)	-2	28	13	5.03*	0.38	-6.74**
Left cingulate (23)	-14	-16	31	5.65**	1.92	-6.07**
Right cingulate (23)	7	-29	33	5.12*	3.97*	-3.29
Right lingual (18)	20	-75	-7	5.64**	6.38**	-1.60
Right superior temporal (22)	32	-51	12	6.83**	9.26**	-0.40
Left fusiform (37)	-39	-48	-1	4.00*	4.33*	-1.32
Left parahippocampus (36)	-31	-40	-8	3.93*	2.23	-3.33
Right hippocampus (28)	33	-27	-9	4.18*	0.61	-5.30**
Left lentiform (41)	-28	-25	6	4.68*	3.81*	-2.81
Left precuneus (7)	-22	-50	44	5.08*	16.31**	9.14**
Left insula	-40	-20	16	5.34*	3.91*	-3.65*
Left inferior parietal (40)	-40	-30	33	4.50*	7.90**	1.53
Right inferior parietal (40)	43	-56	42	4.40*	2.44	-3.78*
Left superior parietal (7)	-31	-58	44	5.19*	17.98**	10.63**
Right superior parietal (7)	14	-62	54	4.01*	10.79**	3.53*
Left cerebellum	-8	-45	-40	4.64*	4.14*	-2.41
DA animacy > DA digits						
Left inferior frontal (45)	-52	28	14	-5.35**	-2.75	4.82**
Left inferior frontal (46)	-44	36	11	-5.44*	-5.80**	1.90
Right supplementary motor	3	10	48	-4.69*	4.18*	10.82**
Left supramarginal (40)	-56	-49	27	-4.02*	0.32	6.00**
Left superior temporal (22)	-37	10	-18	-5.12*	-5.47**	1.78

Note: data from all runs; DA: divided attention; FA: full attention; the Talairach coordinates represent the peak for the given region, for the *t*-value of the DA digits by DA animacy interaction (positive values represent greater activation for DA digits vs. DA animacy, negative values represent greater activation for DA animacy vs. DA digits); BA: Brodmann's Area according to the atlas of Talairach and Tournoux (1988); DA_{dig}-FA: *t*-value for DA digits vs. full attention; DA_{anim}-FA: *t*-value for DA animacy vs. full attention.

* $p < .005$.

** $p < .001$.

interaction, is due to an increase or decrease in activation in the DA digits, or DA animacy task, relative to baseline. Brain regions showing signal change were similar regardless of whether the analysis was conducted using the single-tasks, or FA task as baseline, though some differences exist (and are noted below). To enable us to also look for common areas of activation in regions of interest, we used the Talairach atlas (Talairach & Tournoux, 1988) in AFNI to define Brodmann Areas 10, 9/46, 45, hippocampus, parahippocampus and precuneus, bilaterally. For the FA, DA animacy, and DA digits conditions, the coordinate corresponding to the peak *t*-value within each of the defined regions is noted in Table 5. Figs. 1–3 show the peak percent signal change for each region of interest (ROI) within the frontal, temporal, and posterior neocortex regions.

In the temporal lobes, there was an asymmetry in key regions believed to play a role in memory retrieval, which differentiated the DA conditions. We found greater right temporal activity during DA digits and greater left temporal activity during DA animacy. Specifically, activity in right hippocampus was higher in the DA digits relative to the DA animacy condition, regardless of the baseline used for analysis (see Fig. 1). This difference between the two DA conditions was due to significant reductions in activity in the

right hippocampus, in DA animacy, relative to either baseline task (see Tables 3 and 4). Table 5 shows that activity in right hippocampus was increased significantly in the FA condition (relative to the auditory baseline), was less so in the DA digits condition, and was significantly reduced in the DA animacy condition (using single-task baselines for each DA condition). A similar pattern is seen, across conditions, in the left parahippocampal gyrus, consisting of a difference between DA conditions (Table 4) due to a decrease in activity in DA animacy (Table 5). Interestingly, activity in the left hippocampus did not increase significantly in either DA condition, although an increase was seen in FA (see Table 5).

Also notable, when using the FA task as the baseline, activity in the right lingual and right superior temporal regions during DA digits was significantly increased compared to that in the DA animacy condition (Table 4). In contrast to this pattern of greater right temporal activity during DA digits, activity was higher in left middle temporal (using single-task baselines), and in left superior temporal and supramarginal regions (using the FA task as baseline) in the DA animacy compared to DA digits condition (though, of note, an increase in activation for DA digits compared to DA animacy was seen in a superior region of left fusiform (-39, -48, -1) when the FA condition was used as the baseline; see Table 4).

Table 5
Coordinates and *t*-statistics in regions of interest for each experimental condition, using the appropriate baseline for each

Region of interest	FA–aud		DA _{dig} –S _{dig}		DA _{anim} –S _{anim}	
	Coordinates	<i>t</i> -stat	Coordinates	<i>t</i> -stat	Coordinates	<i>t</i> -stat
BA 10						
Right	42, 56, 2	3.56*	41, 57, 5	4.69**	40, 57, –5	3.75*
Left	–42, 58, 8	3.514*	–42, 53, 2	4.61**	–42, 50, 4	2.69 ⁺
BA 45						
Right	63, 19, 18	3.60*	64, 20, 18	8.43**	64, 19, 18	7.35**
Left	–49, 24, 19	4.73**	–50, 30, 21	–0.96	–50, 29, 21	5.59**
BA 9/46						
Right	50, 14, 32	2.49 ⁺	50, 12, 32	5.72**	48, 10, 34	4.80**
Left a	–44, 17, 22	6.16**	–44, 19, 23	6.87**	–45, 19, 23	6.40**
Left b	–30, 54, 27	1.69	–30, 53, 27	4.07**	–32, 49, 26	4.54**
Hippocampus						
Right	33, –35, –5	3.89**	29, –40, 4	2.18 ⁺	33, –26, –7	–5.18**
Left	–28, –22, –14	3.12*	–30, –23, –14	1.15	–27, –27, –14	1.80
Parahippocampus						
Right	33, –45, –6	1.07	33, –45, –6	2.88 ⁺	33, –46, –6	–0.84
Left	–19, –26, –7	3.56*	–35, –35, –11	2.46 ⁺	–25, –12, –13	–4.36**
Precuneus						
Right	16, –60, 27	4.80**	17, –64, 26	3.92**	16, –64, 27	4.28**
Left a	–23, –59, 36	5.26**	–22, –50, 43	4.03**	–24, –50, 43	2.89 ⁺
Left b	–11, –65, 29	1.36	–16, –60, 29	3.45*	–13, –58, 19	6.88**

Note: data from long runs only; DA: divided attention; FA: full attention; S: single task; aud: auditory baseline; the Talairach coordinates represent the peak for the given region; for the *t*-statistics shown, positive values represent increases and negative values decreases in activation, relative to each task's appropriate baseline; BA: Brodmann's Area according to the atlas of Talairach and Tournoux (1988); FA–aud: *t*-value for full attention vs. auditory baseline; DA_{dig}–S_{dig}: *t*-value for DA digits vs. single-task digits; DA_{anim}–S_{anim}: *t*-value for DA animacy vs. single-task animacy. Bold font represents coordinates and *t*-statistics within 1 cm of those that differentiate the DA digits and DA animacy conditions, in at least one of the two reported ANOVAs.

⁺ *p* < .05.

* *p* < .005.

** *p* < .001.

Activity in areas believed to be involved in mediating content, or representations that form the memory trace, in parietal cortex, including bilateral inferior parietal regions (BA 40), was generally higher in the DA digits than DA animacy condition. Activity in BA 7, particularly left precuneus and superior parietal cortex, was also increased during both DA conditions relative to FA, but again, more so for DA digits (see Table 4). There was, however, an area in left precuneus that was more active in the DA animacy compared to DA digits condition (see Tables 3 and 5). Despite these differences, the precuneus was active across all three memory conditions, in both hemispheres (Table 5).

With respect to areas believed to be involved in executive functions, in the frontal lobes, differences in signal between the two DA conditions were found primarily in anterior frontal cortex (BA 10), and in inferior frontal regions (BA 45), bilaterally (see Tables 3 and 4). In the analysis results shown in Table 3, activity in right BA 10 was increased to a greater degree in the DA digits than DA animacy condition. Table 5 shows that activity in the same approximate region of right BA 10 also was increased in the FA condition relative to the auditory baseline. Using the FA task as baseline, activity in left BA 10 was significantly reduced during DA animacy (see Table 4).

Another frontal region differentiating the DA conditions, was left inferior frontal (BA 45), which showed an increase during DA animacy (see Fig. 2). Peak coordinates were similar regardless of baseline used in the analysis (–50, 28, 19 using single-task, and –52, 28, 14 using FA baselines). Notably, an increase in activity is seen in the FA condition at similar coordinates in BA 45 (see Table 5).

Left dorsolateral cortex (BA 46) showed a significant difference between DA animacy and DA digits, using FA as baseline, but this was due to a significant reduction in the DA digits condition, rather than increase in the DA animacy condition (see Table 4). As shown in Table 5, the FA and both DA conditions show increases in more dorsolateral portions of left BA 9/46 (using the auditory and single-task baseline). There were additional areas, within left dorsolateral cortex, as well as a region within right dorsolateral cortex that were active in both DA tasks, but not in the FA condition.

4. Discussion

In this study, we used the dual-task paradigm to isolate specific brain regions mediating good and poor retrieval under DA in order to determine the components of memory and

attention, and their interaction at retrieval. Behaviourally, we showed that recognition performance was significantly disrupted, compared to full attention, by a word-, but not digit-based, concurrent task, replicating our previous results using free recall (Fernandes & Moscovitch, 2000, 2003). Brain imaging results indicate support for our initial hypothesis of interference at the level of phonological and word form representations, with increased activation under DA animacy in a network of areas that mediate these processes (left inferior frontal, left temporal, left supramarginal cortex).

We also found that the DA animacy task led to decreased activity in a group of regions involved in memory retrieval (hippocampus, precuneus and parietal cortex), and which may be critical for successful memory performance. Behavioural and brain results did not support the alternative hypothesis, that differences in demand for CE processing resources, mediated by the frontal lobes, and required under the DA animacy compared to DA digits condition, underlie the memory interference effect.

4.1. Memory systems

This study is the first to document the involvement of the hippocampal region in recognition under DA conditions at retrieval. As such, it is in agreement with other studies in which activity in the hippocampal region has been associated with successful episodic retrieval (Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Grasby et al., 1993; Nyberg, McIntosh, Houle, Nilsson, & Tulving, 1996; Schacter, Savage, Alpert, Rauch, & Albert, 1996; Stark & Squire, 2000). Decreased hippocampal activation is associated with decreased retrieval in our study, and is consistent with similar observations by Anderson et al. (2004), who report a reduction in right hippocampal activity under conditions in which participants suppressed unwanted memories, and in which such items are remembered poorly. Thus, increases in hippocampal activation, as seen in the FA and DA digits condition, are associated with better memory and decreases in hippocampal activity, as seen in the DA animacy condition, are associated with poorer memory.

Increases in right hippocampal blood flow have been observed in other studies of memory (Grady et al., 1995; Schacter et al., 1995, 1996; Squire et al., 1992). Rugg, Fletcher, Frith, Frackowiak, & Dolan (1996) suggested that this right hippocampal activity reflects the role of this structure in memory for visually coded information. It is curious that in our study, retrieval for auditorily presented verbal materials was associated with significantly increased activation in both the right and left hippocampus in the FA condition, but no change in activation in left hippocampus in either DA condition (see Fig. 2). Given that memory in this experiment was for verbal materials, one might expect activation of the left hippocampus in the DA as well as FA conditions. We do see, on the other hand, a slight increase in activity in the right hippocampus in the DA digits condition, and significantly decreased activation in the right hippocampus in the DA animacy condition

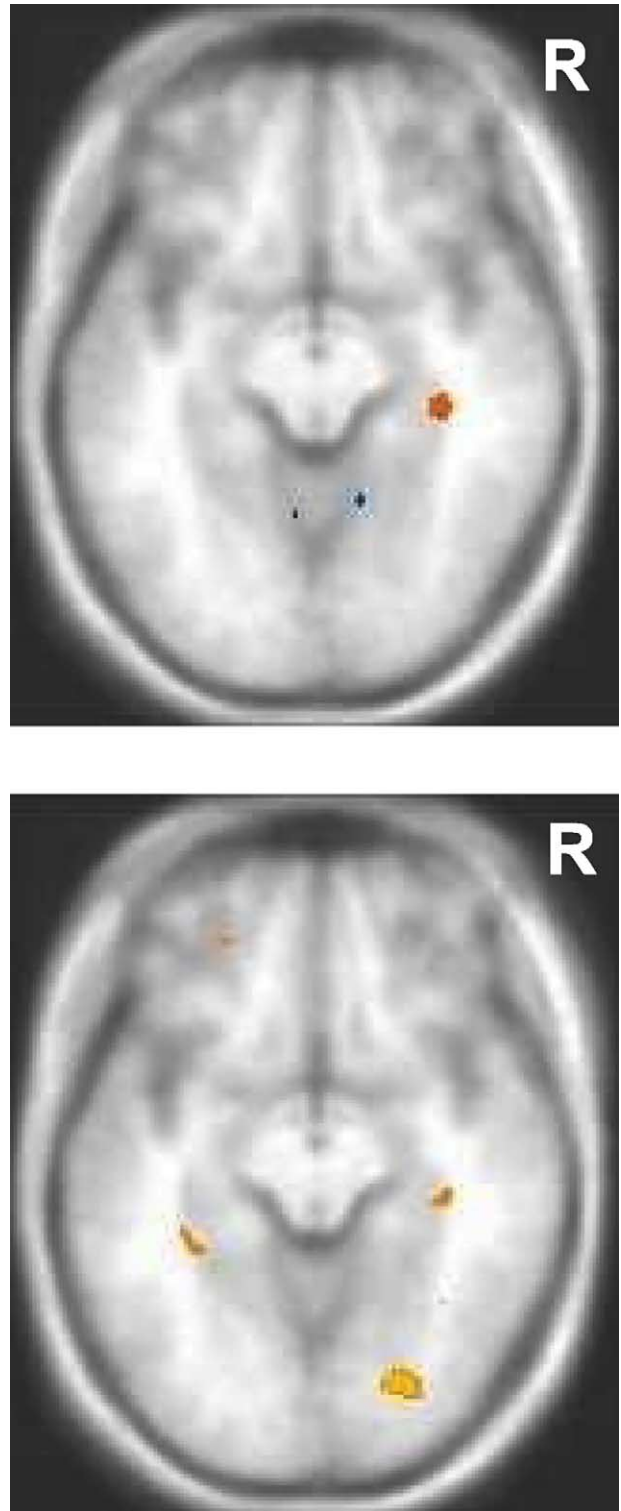


Fig. 4. Brain regions in medial temporal lobes showing greater activation in DA digits relative to DA Animacy. Displayed are axial sections ($z = -8$, $p < .005$) of the averaged neuroanatomical brain from 12 participants. The top figure shows activations using the single task as baseline and the bottom figure shows activations using the FA task as baseline. In both analyses, the orange areas show activations that were significantly greater in the DA digits relative to DA animacy condition in right hippocampus ($34, -26, -8$ using single task and $33, -27, -9$ using FA task as baseline).

(see Fig. 4). Of note, the left parahippocampus showed the same pattern as right hippocampus, with significant activation under FA, less during DA digits, and a significant reduction during DA animacy. While there is no obvious explanation as to why these changes occur in the right hemisphere, and not in the left, it is clear that DA reduced hippocampal activity, particularly in the DA animacy condition, and that this pattern of activation in the brain paralleled memory performance behaviourally.

It is, nonetheless, possible that increased hippocampal activity at retrieval is related to concurrent encoding of targets and lures, rather than to memory retrieval. Because an equal number of old and new words were presented in each block, activation associated with novel items, which is known to increase hippocampal activity (Habib, McIntosh, Wheeler, & Tulving, 2003), is confounded with retrieval-associated activation to repeated, old items. By this account, however, no differences in hippocampal activity should have been observed between the DA animacy condition and the DA digits condition, because concurrent encoding of novel items and retrieval of old items is common to both conditions. Because we observed hippocampal deactivation in the DA animacy condition, relative to the DA digits condition, we believe the pattern of hippocampal activity observed in this study is explained best as resulting from the effects of the word-based distracting task on memory retrieval.

In addition to the hippocampus, other regions that consistently are part of an episodic memory network, also show modulations in activity which vary with interference condition. Activation in precuneus and parietal cortex has been found reliably in several studies during retrieval (Buckner et al., 1995; Iidaka et al., 2000; Krause et al., 1999; Shallice et al., 1994). If optimal memory performance depends on the degree of activation in these areas, as suggested by Kapur et al. (1995), then the differences in memory under DA conditions may result from differences in activation of these structures. Consistent with this hypothesis, our study showed significantly greater activity in left BA 7 (precuneus) and bilateral BA 40 (parietal cortex) in the DA digits compared to DA animacy condition, relative to the FA baseline. Dobbins, Rice, Wagner, & Schacter (2003) likewise found that increased activity in the parietal cortex was associated with successful, compared to unsuccessful, performance. If the precuneus represents reactivation of stored engrams, as has been proposed by Roland and Gulyas (1995) and Krause et al. (1999), it suggests that it is the reactivation of stored memories of words, likely via the hippocampus, that is hampered in the DA animacy condition. Lesion studies support this idea, as damage in areas of posterior cingulate and precuneus can cause severe memory impairment (Rudge & Warrington, 1993; Valenstein, Bowers, Varfaellie, Day, & Watson, 1987).

4.2. Phonological systems

The pervasive increase in left prefrontal cortex activation during the DA animacy condition (see Fig. 5) overlaps with

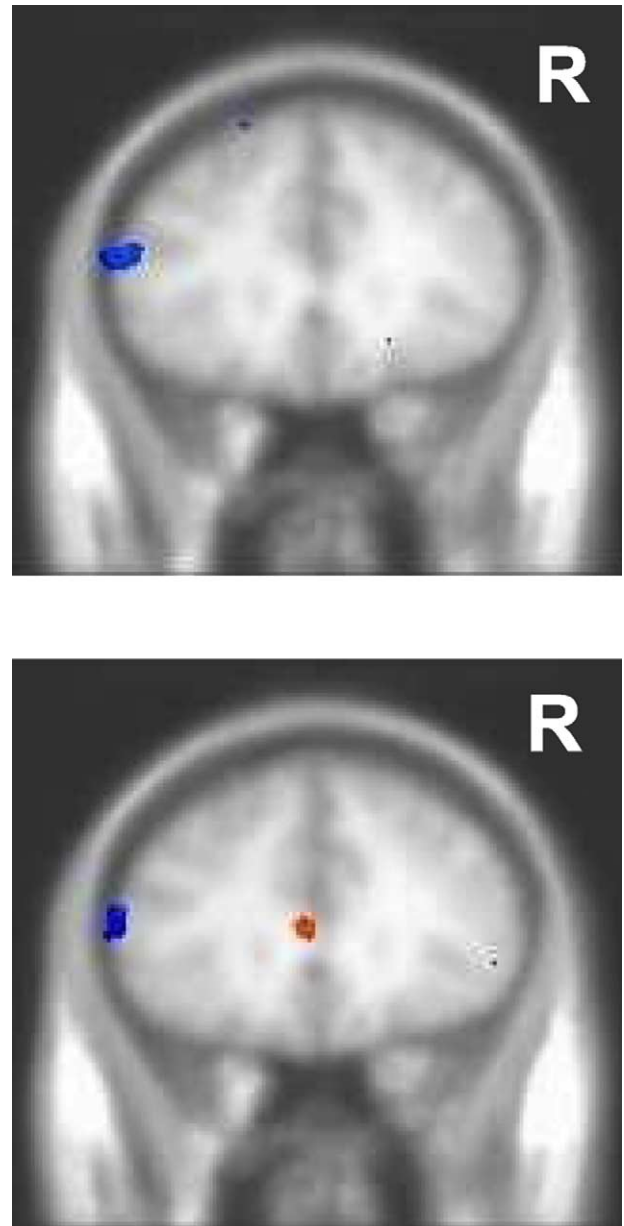


Fig. 5. Brain regions in frontal lobes showing greater activation in DA animacy relative to DA digits. Displayed are coronal sections ($y = 28$, $p < .005$) of the averaged neuroanatomical brain from 12 participants. The top figure shows activations using the single tasks as baseline and the bottom figure shows activations using the FA task as baseline. In both analyses, the blue areas show activations that were significantly greater in the DA animacy relative to DA digits condition in left inferior frontal ($-50, 28, 19$ using single task and $-52, 28, 14$ using FA task as baseline).

regions previously shown to be implicated in semantic retrieval (see Cabeza & Nyberg, 2000) and phonological working memory (WM) tasks (Crosson et al., 1999). It has been suggested that the anterior region of left inferior PFC is involved in semantic processing during retrieval whereas the posterior part of left inferior PFC plays a role in the maintenance and/or access to lower level phonological or lexical information (Dobbins, Foley, Schacter, & Wagner, 2002).

Both regions may play roles in specifying the cues necessary for retrieval in our task. Though activation in our study overlapped both regions, the greater increase in activity in the DA animacy condition relative to the DA digits condition was closer to the more posterior regions of left inferior PFC. This finding is consistent with our view, based on behavioural studies, that the primary locus of interference in the DA animacy condition is at the phonological level (Fernandes et al., 2004) though some semantic interference likely also occurs (Fernandes & Moscovitch, 2002). The results also suggest that visually presented words in the DA animacy condition may have privileged access to phonological representations, as compared to visually-presented digits. These interpretations are supported further by our finding that activation during the DA animacy, as compared to the FA and the DA digits condition, was greater in the left supramarginal gyrus (BA 40) as well as the left inferior frontal cortex (BA 45), areas involved in storage and processing of phonological (but not semantic) information, respectively (Awh et al., 1996; Paulesu, Frith, & Frackowiak, 1993).

4.3. Executive systems

We can provide evidence, both behaviourally, and in the fMRI data, to support our claim that the difference in memory interference observed in the divided attention (DA) animacy compared to DA digits condition is not due to differences in task difficulty, thus arguing against the alternative, resource-based account for the effect. We found that performance on the animacy task was worse overall than on the digits task, however, we do not believe this difference can account for our finding of greater memory interference from the former than latter distracting task for several reasons. There was no correlation between memory and distracting task performance during either DA condition. The percentage decline in performance, from single to dual-task conditions was quite small in the DA animacy condition (only 5%). The slowing in RT from single to dual-task conditions did not differ across the animacy and digits distracting tasks. Furthermore, recent behavioural work examining latency to respond on each distracting task, while concurrently engaged in a continuous auditory tone identification task, showed the slowing in RT under dual-task conditions was similar for the digits as for the animacy task, indicating the relative resource demands of these tasks are matched (Fernandes & Moscovitch, 2003). Moreover, behavioural studies showed that the magnitude of memory interference, using these same distracting tasks, did not differ in older adults classified with either low or high levels of frontal lobe function (Fernandes, Davidson, Glisky, & Moscovitch, 2004), arguing against the hypothesis that differences in memory interference across conditions can be accounted for by differences in resource demands of the two tasks.

In the present study, fMRI showed that in the brain, those regions in the PFC, such as the DLPFC, known to be involved in executive functions, did not show consistent changes in

activation across the DA conditions, as would be predicted if the distracting tasks differed in overall level of difficulty. For these reasons, we do not think our finding of greater memory interference in the DA animacy condition could be accounted for by differences in distracting task difficulty alone.

With one exception, there were no differences, in our study, in the right dorsolateral prefrontal regions typically activated during retrieval of episodic memories (i.e. BA 9 and 46) (Buckner, Raichle, Miezin, & Petersen, 1996; Cabeza & Nyberg, 2000; Fletcher, Shallice, Frith, Frackowiak, & Dolan, 1998; Ungerleider, 1995). We noted several areas within BA 9/46 in both hemispheres showing activations in the two DA conditions, but not in the FA condition. These areas may be related to processes needed for general coordination of dual-tasks over single-tasks. Only one DLPFC region showed a significant difference in activity across DA conditions. Using FA as the baseline, there was a significant reduction in left BA 46 (−44, 36, 11), in the DA digits condition, and a non-significant increase in the DA animacy condition. That there were no consistent differences in dorsolateral prefrontal activity across DA conditions suggests that memory interference in the DA animacy condition cannot be attributed to differences in resource-demanding strategic processes mediated by the PFC. The one difference between conditions, in DLPFC brain activation, is not one that favours the DA animacy condition as being more difficult or resource demanding. Thus, differences in memory interference cannot be accounted for by differences in task difficulty, post-retrieval monitoring, or general executive function, including the processing demands in dual-task conditions, which presumably are associated with the management of concurrent tasks, and believed to be mediated by DLPFC (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991; Iidaka et al., 2000; Johannsen et al., 1997; Klingberg, 1998; Madden et al., 1997).

5. Conclusions

Our results are the first to identify changes in brain activity, under DA at retrieval, that are related to memory performance. Our findings suggest that the concurrent animacy task disrupted memory directly by suppressing or interfering with temporal lobe function, specifically in the hippocampus, and related episodic memory structures in a network that includes the left precuneus, and parietal cortex. The reduction in activity likely occurs because there is competition between the DA animacy and memory tasks primarily for phonological, but also for semantic, representations in anterior and posterior neocortex. These representations either specify the cues needed to recover information from the hippocampus and related structures, or instantiate the retrieved memories, or both. That there was little variation in activation of the regions of PFC known to be implicated in executive functions during retrieval, suggests, in accordance with the component–process model (Fernandes & Mosco-

vitch, 2000, 2002, 2003; Moscovitch, 1992) that the ecphoric (cue-engram interaction, Tulving, 1983) process itself requires few general processing resources, though some of the pre- and post-ecphoric processes draw on them.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at 10.1016/j.neuropsychologia.2004.11.026.

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