

Neural correlates of auditory recognition under full and divided attention in younger and older adults

Myra A. Fernandes^{a,*}, Anda Pacurar^b, Morris Moscovitch^{b,c}, Cheryl Grady^{b,c,d}

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

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

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

^d Department of Psychiatry, University of Toronto, Toronto, Ont., Canada

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Abstract

We examined how aging affects the pattern of brain activity mediating retrieval under dual-task conditions. We used functional magnetic resonance imaging (fMRI) to measure brain activity in younger and older adults while they were engaged in an auditory verbal recognition test under either full or divided attention (FA or DA). During recognition under FA, older adults had more activity in bilateral dorsolateral prefrontal cortex (PFC). DA with a distracting task requiring animacy judgments to words disrupted memory more than did a task requiring odd-digit judgments to numbers. For both behavioural and brain measures we contrasted the two DA conditions to recognition under FA to identify interference with memory performance. Behaviourally, there were no age differences in the magnitude of memory interference from DA conditions, although recognition performance was poorer overall in older adults. During the DA animacy condition, younger adults showed an increase in recognition latency, and older adults an increase in distracting task costs. Younger adults in this condition showed an increase in left inferior PFC, coupled with a decrease in right hippocampal activity; these effects were diminished in older adults who instead showed an increase in bilateral middle frontal activity. During both DA conditions, older adults showed greater activity in posterior neocortex compared to the younger group. Results indicate that older adults are able to perform as well as younger adults on retrieval tasks under DA conditions due to two alterations in brain activity: a dampening of the changes characterizing younger adults during the DA animacy condition and greater recruitment of additional regions during both DA tasks. © 2006 Elsevier Ltd. All rights reserved.

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The dual-task technique has been used extensively to identify the component-processes and cognitive resources needed for a given task, as well as to determine how aging affects these resources. With respect to memory, having participants engage in an attention-demanding task while attempting to encode or retrieve information, i.e., dividing attention (DA), has a greater effect on encoding than on retrieval (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, functional neuroimaging studies have shown that activation in the prefrontal cortex (PFC) is reduced by dividing attention during encoding

(Fletcher et al., 1995; Iidaka, Anderson, Kapur, Cabeza, & Craik, 2000; Kensinger, Clarke, & Corkin, 2003; Shallice et al., 1994), but not during retrieval (Anderson et al., 2000; Iidaka et al., 2000).

Recent behavioural research suggests, however, that large disruptions in episodic memory can also occur from DA conditions *at retrieval* when the concurrent task uses the same material as that in the memory task. For example, free recall of a list of unrelated words is disrupted more when the concurrent task also involves words, as compared to numbers or pictures (Fernandes & Moscovitch, 2000, 2002, 2003). A decrement in verbal memory of about 30% from full attention levels is observed when the concurrent task is word-based, whereas an equally-demanding digit-based task produces a decrement of only 10–15%. Unlike the *general effect* observed from DA at encoding, which produces an approximate 50% decline in subsequent memory performance regardless of material used in

* Corresponding author. Tel.: +1 519 885 1211x2142; fax: +1 519 746 8631.
E-mail address: mafernan@watarts.uwaterloo.ca (M.A. Fernandes).

the concurrent task, effects from DA at retrieval appear to be *material-specific*. In this study, we used DA and functional neuroimaging to examine whether aging affects general resources, material-specific representations, or both.

Our work on DA is based on a neuropsychological, component-process model of retrieval proposed initially by Moscovitch and Umiltà (1990, 1991) and Moscovitch (1994) (see also Moscovitch & Winocur, 1992). According to that model, episodic retrieval requires at least two main components, one resource-demanding and the other less so. The first is mediated by the prefrontal cortex, and represents resource-demanding processes that are needed to maintain and implement strategic aspects of retrieval such as retrieval mode, search and monitoring, and to coordinate competing task demands. The second component of the model, believed to be mediated by the medial temporal lobes/hippocampus (MTL/H), involves the relatively automatic re-activation of memory traces resulting from their interaction with memory cues, a process termed *ecphory* by Semon (1923) (see also Schacter, Eich, & Tulving, 1978). The memory trace itself is presumed to consist of an ensemble of MTL/H and neocortical neurons, the latter mediating the representations of the memory event itself, with the MTL/H acting as a pointer or index to the neocortical representations to which it is bound. At retrieval, the cue is presumed to activate the MTL/H index, which in turn reactivates the cortical representations leading to recovery of the memory trace.

Because this *ecphoric* process is presumed to require little, if any, resources (Moscovitch, 1994), it is not affected by DA manipulations at retrieval, unless the task material is similar to that being retrieved from memory (Fernandes & Moscovitch, 2000, 2003). Under those circumstances, DA at retrieval is presumed to exert its effect, not by competing for general resources, but by competing for neocortical representations that the distracting task and memory trace (or the *ecphoric* recall process) have in common. Thus, verbal distracting tasks can disrupt the representations that constitute the memory trace for studied words, or those needed for successful recall.

In line with this, our recent behavioural work suggests that material-specific interference effects on verbal retrieval arise primarily as a result of competition for phonological representations (Fernandes & Moscovitch, 2002), and our recent neuroimaging study provides support for this hypothesis (Fernandes, Moscovitch, Ziegler, & Grady, 2005). Recognition memory, during DA conditions with a word-based distracting task, was reduced and there was a corresponding decrease in brain activity in right hippocampus and precuneus. In addition, we observed increased activation in left inferior frontal regions (BA 45) associated with phonological processing, in the word compared to a digit-based DA condition. This suggests that the interaction of the MTL/H with posterior regions, believed to form the basis of the memory trace, is hampered when phonological processing regions in left inferior PFC are engaged simultaneously by another task. That is, DA at retrieval interferes with memory when there is competition for word representations needed for both the memory and the distracting task.

The present experiment was designed to identify the neural correlates of DA at retrieval in older adults. Aging is thought to be associated with memory deficits resulting from a reduction in general processing resources critical for numerous cognitive operations (Craik, 1983; Craik & Byrd, 1982; Rabinowitz, Craik, & Ackerman, 1982). These resources have been conceptualized in many ways, though theorists converge on the idea that changes in brain function, particularly in the frontal lobes, underlie the reduction in resources (e.g. Baddeley & Wilson, 1988; Fuster, 1997; Knight, Grabowecy, & Scabini, 1995; Luria, 1966; Shallice & Burgess, 1991). Given that older adults may have more limited processing resources, one might expect that they would be particularly vulnerable to effects of distraction, but this is not always the case. Several studies have shown that older adults are more susceptible than younger to interference on memory tasks when a concurrent task is performed with encoding (Park, Smith, Dudley, & Lafronza, 1989; Puglisi, Park, Smith, & Dudley, 1988; Salthouse, Rogan, & Prill, 1984), though others fail to find larger decrements in older adults from DA at encoding (Anderson et al., 1998; Baddeley, Logie, Bressi, & Della Sala, 1986; Light & Prull, 1995; Nyberg, Nilsson, Olofsson, & Bäckman, 1997). In contrast to encoding, most studies find that older adults are no more susceptible to memory interference than younger adults when attention is divided at retrieval (Macht & Buschke, 1983; Nyberg et al., 1997; Park et al., 1989; Whiting & Smith, 1997), though performance on the distracting task suffers significantly more in older than younger adults under DA conditions at retrieval (Craik & McDowd, 1987; Macht & Buschke, 1983; Whiting & Smith, 1997). In line with these results, our recent work looking at the effect of aging on interference from DA at retrieval showed that although the number of words recalled, during a free recall test for unrelated word lists, was significantly lower in older compared to younger adults, the *percentage decline* (i.e. interference effect) in performance, from full to DA conditions, was equivalent across age groups (Fernandes, Davidson, Glisky, & Moscovitch, 2004; Fernandes & Moscovitch, 2003), regardless of the materials used in the distracting task.

This last finding is consistent with our suggestion that the locus of interference at retrieval occurs at the level of reactivation of perceptual representations (content of the memory trace), and suggests further that these representations, and the brain regions mediating them, are intact in older adults. That is, if representations are mediated by posterior cortical regions, such as the precuneus, and their interaction with MTL/H, as our previous neuroimaging study suggested, then older adults should have modulations of activity in these regions similar to those seen in younger adults in FA and DA conditions.

Alternatively, older, as compared to younger adults may simply increase activity in bilateral PFC (BA 9/44 and 46/10) under DA conditions, as they have been shown to do during memory retrieval (Cabeza et al., 2004; Cabeza, Grady et al., 1997; Cabeza, McIntosh, Tulving, Nyberg, & Grady, 1997). Increases in PFC activation have been associated with better memory performance in high-performing older adults (Cabeza, Anderson, Locantore, & McIntosh, 2002), leading to the suggestion that such brain activity compensates for age-related changes else-

where in the brain (Grady et al., 1994; Madden et al., 1996, 1997; Rypma & D'Esposito, 2000; Schacter, Savage, Alpert, Rauch, & Albert, 1996). In our previous work, we found no evidence of greater memory interference, behaviourally, in older than in younger adults during DA at retrieval (Fernandes & Moscovitch, 2003). We hypothesized, therefore, that an increase in dorsolateral PFC activity in the older group would be needed to maintain a comparable level in size of memory interference.

To test these ideas we used fMRI to measure brain activity in younger and older adults while they were engaged in verbal memory tasks under either full or divided attention. The distracting tasks were an animacy judgment for words and an odd-digit judgment for numbers. The approach was to examine brain activity during FA to determine baseline age differences in brain areas mediating verbal recognition. We then contrasted activity during DA conditions, using FA as the baseline for these contrasts, to identify those areas whose activity was modulated by the DA tasks. As the behavioral interference in DA is defined relative to FA, using this same approach for the imaging data is analogous to determining the “brain” interference effects. Further, since we expected the behavioral interference effects to be equivalent in younger and older adults, any differences in brain activity during DA between groups would reflect age differences in the way the brain copes with the distracting tasks and not differences in performance level per se.

1. Methods

1.1. Participants

Twelve healthy younger adults (7 females; 2 left-handed), from 20 to 30 years of age (mean age = 26.33, S.D. = 3.36), and 12 healthy older adults (8 females; 1 left-handed), from 65 to 76 years of age (mean age = 71.18, S.D. = 4.07), participated in the experiment after giving informed consent. Data from one male, left-handed senior were excluded from all analyses due to excessive head movement during scanning. Younger adults had a mean of 17 years (S.D. = 2.33) of education and older adults had a mean of 16.4 years (S.D. = 2.16). The National Adult Test of Reading (NART-revised) was used to compute an estimate of full scale IQ (Blair & Spreen, 1989; Nelson, 1982); younger and older adults had mean FSIQ estimates of 114.3 (S.D. = 6.4) and 113.5 (S.D. = 8.2), respectively. All procedures were approved by the ethics committee of Baycrest Centre for Geriatric Care. All participants spoke English fluently, and were free from psychiatric or neurological disease. In the older adult group, one participant was taking cholesterol-reducing medication, one was taking thyroid medication, two were on medication to reduce high blood pressure, and two were taking calcium supplements at the time of testing.

1.2. 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 study phase, participants heard a list of 50 unrelated words (presented via Avotec headphones) while in the scanner, presented at a rate of one word every 2 s. During the recognition task blocks, words again were presented auditorily, and participants made a button-press to “old” words only. 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, on a white background, with black lettering or numbering, shown centrally through MRI-compatible goggles (Silent Vision™, Avotec Inc.) 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, presented randomly, at a rate of one item every 2 s.

Two control tasks were presented, only one of which was used for the current analysis. For the auditory control task, participants heard either the word “word” or “press”, and made a button-press for the latter. In the visual control 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).

1.3. 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, in which they performed 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 (either animacy or odd-digit task) was simultaneous. In all blocks requiring recognition decisions (FA, DA animacy, DA digits), half of the words were old (five targets per block), and in each of the blocks requiring responses to a distracting task (either animacy or digits), half of the items were targets (five targets per block).

While in the scanner, and prior to each of the 4 scanning runs, participants heard a study list of 50 unrelated words. Encoding was not scanned. Following encoding, participants counted backwards silently by threes for approximately 30 s, until the scanning run began. For each participant, two of the scanning 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 with the animacy distracting task (DA animacy), and two of the recognition task performed with the odd-digit task (DA digits). A block of the FA recognition task was presented in between DA blocks. The other 2 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 DA animacy, 2 of DA digits, 5 of the auditory control task, and 4 of the visual control task. Blocks of the auditory and visual controls alternated in between the other tasks. The order of runs alternated between short and long, in a counterbalanced fashion across participants.

Including long runs allowed us to examine behavioural performance of the distracting tasks performed singly, as well as under dual-task conditions (see Fernandes et al., 2005), and the short runs were utilized so that the delay between encoding and recognition was more similar to that used in our earlier studies (Fernandes & Moscovitch, 2000, 2002, 2003). However, for the purposes of the present analysis we included only the FA condition, the two DA conditions and the auditory control task.

1.4. fMRI data acquisition

Data were acquired with a Signa 1.5T magnet with a standard coil (CV/i hardware, LX8.3 software; General Electric Medical Systems, Waukesha, WI). 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 (axial orientation, TR = 2500 ms; TE = 40 ms; flip angle = 80°; effective acquisition matrix = 64 × 26; FOV = 20 cm; number of slices = 26; slice thickness = 5.0 mm; slice spacing = 0). Reconstruction of the data was conducted off-line and included gridding (Glover & Lai, 1998) as well as correction for magnetic field

inhomogeneities and Maxwell gradient terms. For each participant, two short runs of 76 volumes each and two long runs of 191 volumes each were collected.

A standard high-resolution, 3D T1-weighted fast spoiled gradient echo image (axial orientation; TR = 35 ms; TE = 6.0 ms; flip angle = 35°; acquisition matrix = 256 × 124; FOV = 22 cm × 16.5 cm; number of slices = 124; slice thickness = 1.4 mm; slice spacing = 0 mm) was obtained before fMRI acquisition and used to register brain structure and function.

1.5. fMRI data analysis

Image processing and analysis were performed using the Analysis of Functional Neuroimages (AFNI, version 2.25) software package (Cox, 1996; Cox & Hyde, 1997). 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.

In the preprocessing stage, time series data were spatially co-registered to correct for small head motions. For each run, each volume in the time series was aligned volumetrically, using the 3dvolreg program from AFNI, to an earlier reference volume from the first imaging run in the scanning session. Alignment parameters were computed by an iterative weighted least squares fit to the reference volume and then applied using 3D Fourier transform interpolation. The peak range of head motion was less than 1.5 mm for all participants. The co-registration results were also checked visually for additional quality control.

In the analyses stage, two models were considered: the first used the auditory control task as the baseline and identified brain regions active during the FA condition. Data from the long runs only were included in this first analysis. The second used the FA recognition task as the baseline and identified the brain areas active during DA digits and DA animacy. Data from all four runs, concatenated, were used in this second analysis.

For each analysis, deconvolution using the 3dDeconvolve program from AFNI was performed to model the response of the stimulus type considered in the model. The stimulus-input waveform was modeled from the data, but the data itself determined the functional form of the estimated bold response, and as a result the shape of the response varied from voxel to voxel. The output included the estimated response, along with the statistical significance of the model fitting to the original functional data, for each voxel in the data set. In addition to the regression coefficients, an F statistic and t statistic for each response parameter, and partial F statistics for each stimulus type were computed.

For both analyses, the resulting individual activation maps were converted into signal percentage change relative to the baseline considered in the model, and then resampled to a 1 mm × 1 mm × 1 mm grid, transformed into Talairach space (Cox & Hyde, 1997) and spatially smoothed with a Gaussian filter of 6 mm full-width-at-half-maximum (FWHM) to account for the individual variation of the anatomical landmarks and to increase the signal-to-noise ratio. These last three steps were performed to facilitate subsequent group and between-group analyses. The group level analysis, for each of the models of analyses proposed consisted of a voxel-wise, mixed model, two-factor ANOVA with participants as a random factor and task as a fixed factor.

Common areas of activity across younger and older age groups were determined using a conjunction analysis in AFNI, which identified voxels that were activated in both groups. The statistical maps entered into the conjunction analysis were thresholded at $p < 0.005$, uncorrected, with a cluster size $> 50 \text{ mm}^3$, and a connectivity radius of 1 mm. The voxel-by-voxel difference of the mean of the younger age group activation map and the mean of the older group activation map were computed using 3dttest in AFNI. For all between-group comparisons,

the statistical cut-off was set at $p < 0.005$, uncorrected, with the additional criterion that the given contrast also was significant in at least one group (either younger or older) at $p < 0.005$, uncorrected. This resulted in an overall threshold value of $p < 0.000025$ (i.e., the product of the two p values).

2. Results

2.1. Behavioral results

2.1.1. Memory task

Recognition performance was calculated, for each block, as proportion of hits minus proportion of false alarms. The resulting recognition accuracy score was then averaged across all similar block types (FA recognition, DA animacy, DA digits; see Table 1 for means). Also shown (in Table 1) are the mean reaction times for correctly recognized words. Recognition accuracy data were analyzed using a within-participant (FA, DA digits, DA animacy) ANOVA, with Age group as a between participant factor. There was a main effect of Recognition condition, $F(2, 42) = 27.34$, $p < 0.001$. Planned contrasts showed that recognition during DA animacy was lower than that during both FA, $F(1, 21) = 57.25$, $p < 0.001$, and DA digits, $F(1, 21) = 34.31$, $p < 0.001$. Recognition during DA digits did not differ from that under FA, $F(1, 21) = 1.06$. There also was a significant age effect, $F(1, 21) = 12.82$, $p = 0.002$, with older adults recognizing fewer words than younger adults, but the Age × Recognition condition interaction was not significant.

To determine the degree of interference in the two DA conditions, we also analyzed the percentage decline in memory performance in the DA relative to FA condition for each participant (see Fig. 1A). On this measure, there was a significant effect of DA condition, $F(1, 21) = 19.15$, $p < 0.001$, indicating that memory interference was greater in the DA animacy compared to DA digits condition. However, neither the effect of age nor the interaction of age and condition was significant, indicating that younger and older had equivalent magnitudes of interference in both DA conditions.

In terms of reaction time (RT), there was a significant effect of Recognition condition, $F(2, 42) = 14.35$, $p < 0.001$ (Table 1). Planned contrasts showed that RTs during FA were faster than during either DA animacy or DA digits, $F(1, 21) = 21.32$ and 21.66, respectively ($p < 0.001$), though there was no difference in recognition RT across the DA conditions. There was a trend for older adults to be slower to respond, $F(1, 21) = 2.88$, $p = 0.10$. In addition, the interaction of Age group × Recognition condition was significant, $F(2, 42) = 3.40$, $p < 0.05$. Post hoc contrasts

Table 1
Recognition task performance in full and divided attention conditions

Measure	Full attention		DA animacy		DA digits	
	Young	Old	Young	Old	Young	Old
Hit rate	0.67 (0.13)	0.57 (0.16)	0.55 (0.11)	0.41 (0.17)	0.64 (0.18)	0.56 (0.14)
False alarm rate	0.10 (0.04)	0.19 (0.09)	0.17 (0.06)	0.20 (0.12)	0.10 (0.05)	0.21 (0.12)
Accuracy	0.57 (0.14)	0.38 (0.14)	0.38 (0.15)	0.21 (0.11)	0.55 (0.20)	0.35 (0.11)
RT	1114 (66)	1180 (120)	1271 (68)	1262 (145)	1182 (62)	1292 (125)

Note: DA, divided attention; RT, reaction time in milliseconds. Accuracy = hit rate – false alarm rate. Standard deviations are shown in parentheses.

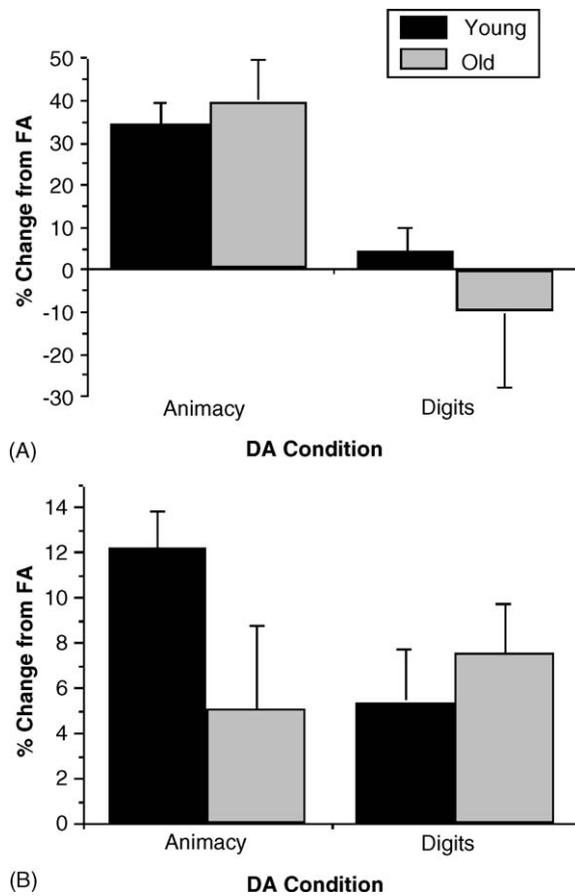


Fig. 1. Percent change in memory performance from FA during the DA digit and DA animacy conditions in younger and older adults is shown for accuracy (A) and RT (B). Error bars represent the standard error.

indicated that the older adults had significantly slower RTs only for the DA digits condition, $t(21) = -2.73, p < 0.05$.

Percentage increase in RT in the DA conditions relative to the FA condition was also calculated (Fig. 1B). For this measure, the main effects of age and condition were not significant, but the interaction was significant, $F(1, 21) = 6.91, p < 0.02$. Younger adults showed more RT interference in the DA animacy condition, $t(11) = 2.72, p < 0.05$ (Fig. 1B), whereas there was no difference between DA conditions in older adults.

These behavioral results replicate our earlier findings that greater interference with verbal retrieval is found using a word,

compared to a digit-based, distracting task, and that there are no age differences in the magnitude of interference, although older adults recognize fewer words overall than do younger adults. Further, the only significant interaction of age and task condition was found on RT and this indicated a greater influence of the DA animacy condition in the younger adults only.

2.1.2. Distracting task

Performance was calculated, for each block, as proportion of hits minus proportion of false alarms. The resulting distracting task accuracy score was then averaged across all similar block types (single-task for animacy and digit task, DA animacy, and DA digits; see Table 2 for means) using data across both short and long runs. Also shown (in Table 2) are the mean reaction times for correct responses. Accuracy data were analyzed using a 2 (Attention condition: single and divided) \times 2 (Task: animacy and digits) \times 2 (Age group: younger and older) ANOVA, with repeated measures on the Attention and Task factors. The main effect of attention was significant, $F(1, 21) = 24.23, p < 0.001$, as was the main effect of age, $F(1, 21) = 9.16, p < 0.01$. Performance on the distracting tasks was more accurate in the single-task conditions than in the DA conditions, and younger adults were more accurate overall than the older adults. The main effect of task also was significant, $F(1, 21) = 47.80, p < 0.001$, indicating that the animacy task was more difficult than the odd-digit monitoring task. The interaction of attention and task was significant, $F(1, 21) = 15.88, p = 0.001$, such that there was a greater effect of dividing attention on the animacy task. Finally, the interaction of attention and age was significant, $F(1, 21) = 7.52, p < 0.05$. This interaction was due to a larger effect of dividing attention on distracting task performance in older adults.

To examine this last interaction in more detail, we calculated the percentage change in performance from single to DA conditions for each distracting task and compared younger and older adults on these two measures. There was a significant difference between groups on the percentage decline in performance for the animacy task, $t(21) = -3.45, p < 0.01$, with younger adults showing less cost on the DA animacy task ($M = 7.7 \pm 10.2\%$) compared to the older adults ($M = 24.2 \pm 12.8\%$). There was no age difference on the digits task (younger, $M = 2.3 \pm 7.2\%$; older, $M = 9.8 \pm 16.2\%$). Thus, both younger and older adults showed larger costs of dividing attention on the animacy distracting task, compared to the digit task, and the older adults showed an additional cost, compared to the younger adults, only on this task.

Table 2
Performance on distracting tasks in full and divided attention conditions

Measure	Animacy		Digits	
	Young	Old	Young	Old
Single-task condition				
Accuracy	0.91 (0.07)	0.93 (0.08)	0.99 (0.02)	0.96 (0.05)
RT	742 (99)	830 (124)	623 (78)	673 (102)
Divided attention condition				
Accuracy	0.84 (0.10)	0.70 (0.10)	0.96 (0.07)	0.87 (0.13)
RT	1046 (95)	1127 (83)	914 (128)	1000 (127)

Note: RT, reaction time in milliseconds. Accuracy = hit rate – false alarm rate. Standard deviations are shown in parentheses.

For RT on the distracting tasks, the main effect of attention was significant, $F(1, 21) = 184.98, p < 0.001$, as was the effect of age, $F(1, 21) = 6.16, p < 0.05$. Thus, RTs on the distracting tasks were longer in the DA compared to the single-task conditions, and older adults responded somewhat more slowly than younger adults. The only other significant effect was that of task, $F(1, 21) = 45.99, p < 0.001$, such that RTs were faster in the digit task than the animacy task.

This distracting task analysis is in line with other work indicating greater distracting task costs in older compared to younger. However, this result applies only to performance on the animacy but not digits task.

2.2. Behavioural correlational analysis

We examined correlations between memory and distracting task interference, to look for trade-offs in performance. We found no indication that memory interference in either DA condition was related to interference on the respective distracting tasks. In younger adults, the correlation between memory interference and interference on the distracting tasks was $r = 0.28$ in the DA animacy, and $r = -0.01$ in the DA digits condition, and in older adults correlations were $r = 0.02$ and -0.07 (all $p > 0.05$), for each DA condition, respectively. We also considered correlations between single-task performance and memory interference. In younger, the correlation between single-task performance on the distracting task and memory interference was $r = -0.02$ in the DA animacy, and $r = -0.01$ in the DA digits con-

dition, and in older adults, correlations were $r = 0.01$ and -0.08 (all $p > 0.05$), for each DA condition, respectively.

2.3. fMRI results

2.3.1. Full attention

The first analysis of the fMRI data identified those areas with increased activity during word recognition in the FA condition, compared to the auditory control task. There were only a few regions that were activated in *both* younger and older adults during FA (Table 3). These were the dorsal anterior cingulate, the left middle frontal gyrus, and the left precentral gyrus. Many more regions were found that *differentiated* younger and older adults during FA recognition (Table 4). Younger adults had more activity in the left inferior frontal gyrus and cuneus. Older adults showed more activity in a number of areas including bilateral medial frontal gyri, right middle frontal gyrus, dorsal cingulate (posterior to the region active in both groups), and bilateral middle temporal gyri. In all of these regions there was significant activation in the older adults, and no change in activity in the younger adults during FA recognition. Fig. 2 shows these age differences in the left IFG where younger adults had more activity during FA, and in the right dorsolateral PFC and left medial frontal regions where older adults had more activity.

2.3.2. Divided attention

The second analysis identified those brain regions with increased activity during the DA conditions, compared to activ-

Table 3
Modulations of brain activity common to both young and old adults

Gyrus or region	Hem	BA	X	Y	Z	Group	Young	Old
Increases during full attention								
Cingulate	R	32	5	22	33	7.0	5.7***	6.9***
Inferior frontal	L	45	-38	19	21	4.1	4.3**	4.0**
Precentral	L	6	-40	2	29	5.7	3.6**	5.6***
Increases during DA digits								
Middle frontal	L	9	-40	24	35	11.7***	5.6**	9.0***
Fusiform gyrus	L	19	-36	-69	-19	17.8***	14.1***	9.4***
Precuneus	L	7	-22	-67	40	14.1***	8.2***	12.5***
Precuneus	R	7	24	-66	38	11.9***	5.1**	27.4***
Precentral	L	6	-31	-10	44	10.2***	6.8***	7.4***
Precentral	R	6	23	-6	50	12.2***	9.0***	10.7***
Increases during DA animacy								
Middle frontal	L	46	-36	40	29	12.9***	9.7***	10.2***
Middle frontal	L	9	-40	25	35	14.6***	6.4***	10.2***
Middle frontal	R	9	29	30	38	7.4**	5.4**	5.5**
Fusiform	L	37	-39	-53	-16	11.3***	8.1***	4.0*
Precentral	L	6	-29	-5	52	10.8***	8.2***	5.8**
Precentral	R	6	23	-4	50	12.0***	8.2***	8.8***
Precuneus	L	7	-9	-61	42	16.7***	11.7***	13.0***
Precuneus	R	7	28	-61	43	9.0***	5.9**	6.4***

Note: For DA conditions FA is the baseline, and for FA auditory control is the baseline. In this and subsequent tables, Hem: hemisphere; BA: Brodmann area; X: right/left coordinate; Y: anterior/posterior coordinate; Z: superior/inferior coordinate; group: t value for the between-group contrast; young: t value for the within-group contrast in young adults; old: t value for the within-group contrast in old adults.

* $p < 0.005$.

** $p < 0.001$.

*** $p < 0.0001$.

Table 4
Brain areas where activity differs with age during the full attention task

Gyrus or region	Hem	BA	X	Y	Z	Group	Young	Old
Young > old								
Inferior frontal	L	45	-48	14	20	-3.7*	4.1**	0.3
Cuneus	L	18	-11	-84	12	-3.8*	4.5**	-1.7
Old > young								
Medial frontal	L	8	-11	26	34	4.6**	2.0	5.6**
Superior frontal	L	6	-16	16	56	4.4**	-2.1	3.4*
Medial frontal	R	9	11	34	31	3.9**	-1.5	3.2*
Middle frontal	R	9	34	10	41	4.6**	0.9	6.7**
Precentral	R	4	35	-24	47	4.2**	-3.2*	3.4*
Cingulate	L	24	-13	-14	35	3.7*	-0.6	5.4**
Cingulate	R	24	2	7	34	4.5**	-2.1	4.9**
Middle temporal	L	22	-27	-54	21	4.3**	-0.5	3.6**
Middle temporal	R	39	39	-58	23	3.7*	-1.7	3.1*
Precuneus	R	18	25	-65	24	3.9**	-0.6	4.5**

* $p < 0.005$.

** $p < 0.001$.

ity seen during the FA condition. During DA digits, both younger and older adults had increased activity in the left middle frontal gyrus, bilateral precuneus, and bilateral precentral gyrus (Table 3). Increased activity also was found in the left fusiform, as would be expected from the addition of a visual distracting task to the verbal recognition task. Activity in left premotor cor-

tex increased, reflecting the use of the right hand to respond to the visual stimuli in the distracting task; interestingly, activity in right premotor cortex also increased during DA digits compared to FA.

During DA animacy increased activity in both younger and older adults was seen in bilateral dorsolateral PFC, in contrast

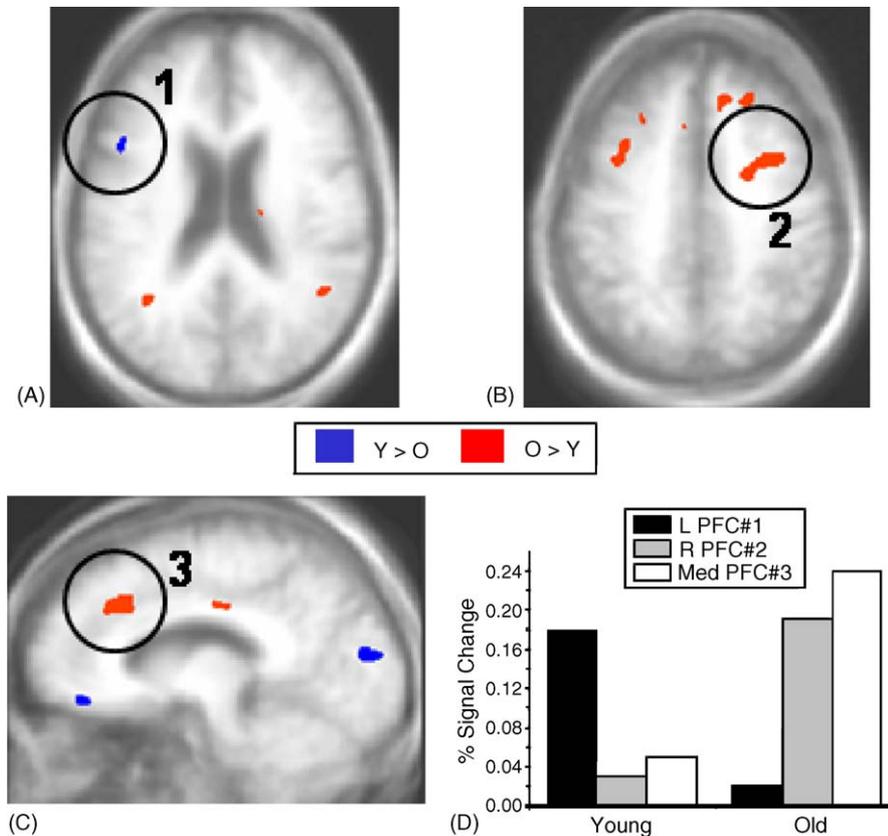


Fig. 2. Brain areas with age differences in activity during the FA condition are shown on representative slices of the average structural MRI from the older adults. (A) An axial slice at $Z = 20$ mm above the AC–PC line; (B) an axial slice at $Z = 40$ mm; (C) a sagittal slice at $X = -11$ mm from the AC (left hemisphere). The numbered circles in (A–C) indicate the regions whose mean activity is plotted in (D) (percent change from the auditory control task). The left PFC (#1) had greater activity in younger adults, and the right PFC (#2) and medial PFC (#3) showed greater activity during FA in older adults. Percent signal change is relative to the auditory baseline condition.

Table 5
Brain areas where activity differs with age during the divided attention tasks

Gyrus or region	Hem	BA	X	Y	Z	Group	Young	Old
Young > old DA digits								
None								
Old > young DA digits								
Inferior parietal	R	40	37	-49	29	5.2**	-0.1	4.7**
Middle temporal	L	21	-56	-34	-6	3.6*	-0.7	5.2**
Young > old DA animacy								
Inferior frontal	L	44	-33	10	23	-3.8*	5.6**	-0.1
Inferior frontal	L	45	-40	25	16	-3.7*	5.1**	-1.4
Old > young DA animacy								
Middle frontal	L	10	-24	44	1	3.5*	-5.6**	4.4*
Middle frontal	R	10	28	49	-3	3.7*	-1.8	6.3**
Inferior parietal	L	40	-50	-32	46	4.3**	-0.5	5.3**
Parahippocampus	L	35	-20	-42	-8	3.2*	-3.6*	1.6
Hippocampus	R		34	-28	-9	3.6*	-4.8**	1.6
Superior temporal	L	42	-62	-24	7	5.7**	-3.9*	1.7

* $p < 0.005$.

** $p < 0.001$.

to the left sided PFC activity seen during DA digits (Table 3). Bilateral precuneus also was more active in DA animacy, compared to FA, in regions similar to those seen during DA digits. Also similar to DA digits, DA animacy was accompanied by activation in bilateral premotor cortex and left fusiform gyrus.

Age differences in brain activity during DA digits were few (Table 5). There were no regions where younger adults had more activity than older adults. Older adults had more activity during DA digits in left temporal regions, and in a right inferior parietal region (Fig. 3). During DA animacy, younger adults had more

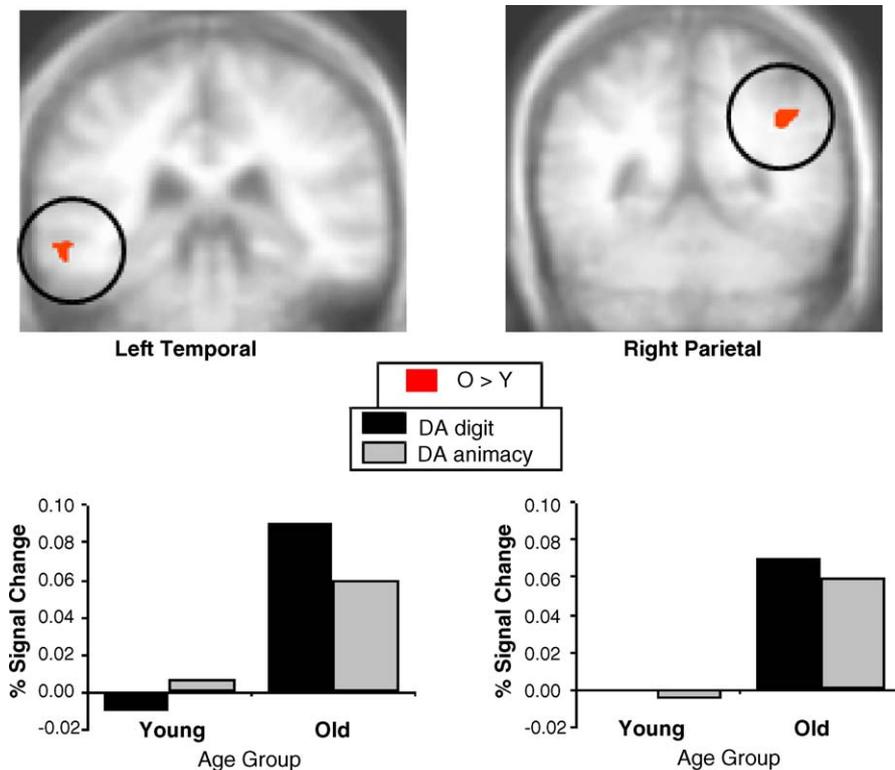


Fig. 3. Brain areas with age differences in activity during the DA digit condition are shown on representative slices of the average structural MRI from the older adults. The image on the left is a coronal slice at $Y = -34$ mm posterior to the AC, and the one on the right is a coronal slice at $Y = -50$ mm. Mean activity in the circled regions is plotted in the graphs below each image, which show significantly increased activity in the older adults in left temporal and right parietal regions during the DA digit condition (black bars) compared to the younger adults. Mean activity in DA animacy (grey bars) is also plotted for comparison. Percent signal change is relative to the FA condition.

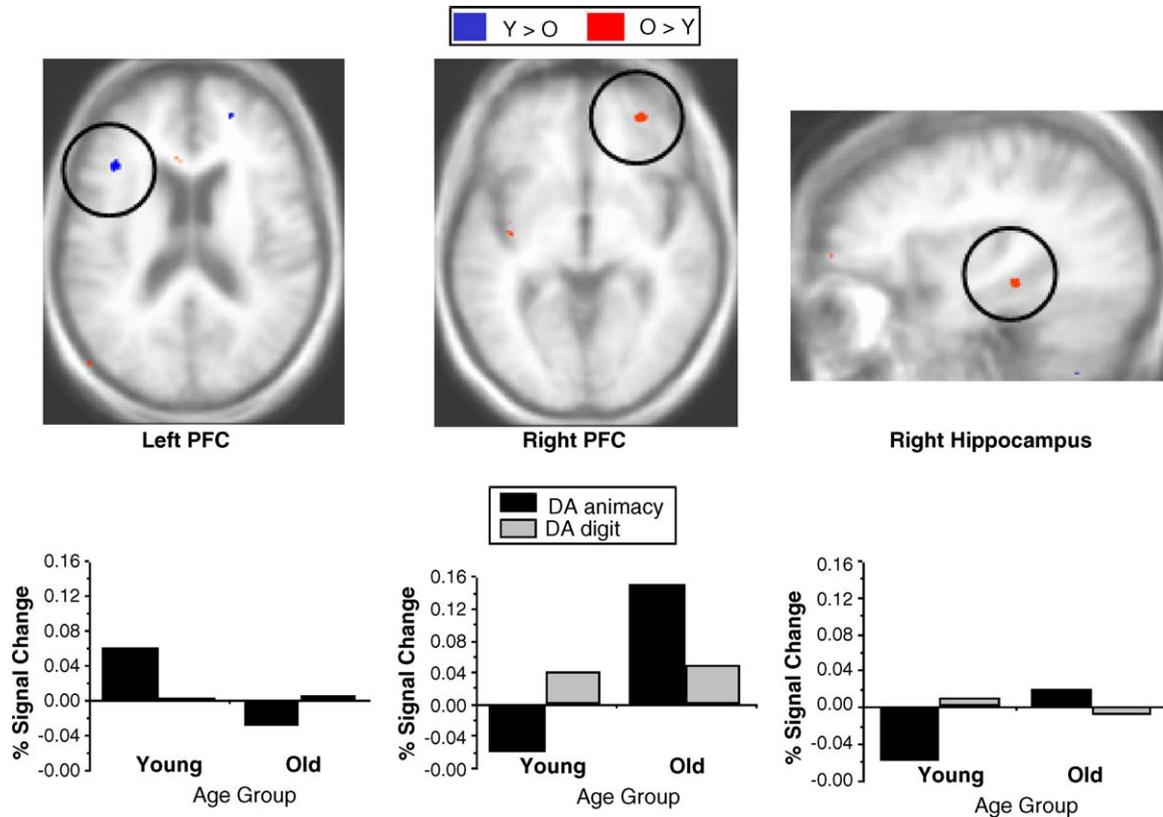


Fig. 4. Brain areas with age differences in activity during the DA animacy condition are shown on representative slices of the average structural MRI from the older adults. The images from left to right are: an axial slice at $Z = 16$ mm above the AC–PC line; an axial slice at $Z = -3$ mm; and a sagittal slice at $X = 34$ mm from the AC. Mean activity in the circled regions is plotted in the graphs below each image, which show significantly increased activity during DA animacy (black bars) in the left PFC of younger adults (compared to old), and significantly increased activity in the right PFC and hippocampus of older adults (compared to younger). Mean activity in DA digits (grey bars) is also plotted for comparison. Percent signal change is relative to the FA condition.

activity than older adults in two left PFC regions, both in the inferior frontal gyrus (Table 5 and Fig. 4). One of these regions was similar in location to the region of left IFG where younger adults had more activity than older adults during FA. Older adults had more activity during DA animacy in anterior regions of the middle frontal gyrus bilaterally, and in the left inferior parietal lobule. In addition, there were three regions where younger adults had reduced activity during DA animacy, compared to FA, and older adults showed no significant change. These were in the left parahippocampal gyrus, left lateral temporal cortex, and the right hippocampus (Fig. 4).

2.4. Brain–behaviour correlation analysis

In addition to examining group differences in brain activity across tasks, we conducted an additional analysis to examine whether there were any changes *within* key brain areas in younger and older adult groups that predicted memory interference in either of the DA conditions. To examine the direction of brain activation–behaviour relationships, we correlated the percent signal change during the DA animacy and DA digits condition (each relative to the FA condition), in key brain regions that differentiated younger and older adults, with memory interference scores in each DA condition, separately for the two groups.

We examined the correlation between signal change in right inferior parietal cortex and memory interference in the DA digits condition. We also examined the correlation between signal change in left inferior parietal, right hippocampus, left inferior frontal, and right and left middle frontal cortex and memory interference in the DA animacy condition. An outlier analysis excluded participants with either brain activation or memory interference scores greater or lesser than two units of standard deviation from the mean. This resulted in the exclusion of four younger participants in the DA digits correlation; for the DA animacy correlations this resulted in the following exclusions: one younger participant for the left inferior parietal cortex correlation, one younger and one older adult for the right hippocampus correlation, two younger adults for the left inferior frontal correlation, and two younger adults for the right and left middle frontal correlations.

The relationship between activity in right inferior parietal cortex and memory interference under DA digits was negative for the younger adults, indicating that memory interference decreased as brain activity here increased, and positive for the older adults, though both were non-significant.

Memory interference under DA animacy was significantly positively correlated with left inferior parietal activation in younger ($r = 0.63$, $p = 0.04$) but not in older adults ($r = 0.24$, $p = 0.48$). Thus, in younger adults, as activity in this region

increased, so did memory interference. In younger adults, activity in right hippocampus increased somewhat with increasing memory interference under DA animacy ($r = 0.51$, $p = 0.11$), but in older adults this correlation did not approach significance. In younger adults, memory interference under DA animacy was negatively correlated with activity in left inferior frontal cortex, and this correlation was in the opposite direction in older adults, though for both age groups these relationships were non-significant. Memory interference, in both younger and older adult groups under DA animacy, did not correlate significantly with activity in right or left middle frontal cortex.

3. Discussion

In this experiment, we examined the brain regions recruited during auditory recognition in younger compared to older adults under full and dual-task conditions at retrieval. We used a similar approach in examining the behavioral and brain changes resulting from dividing attention during recognition. For both behavioral and brain measures we contrasted each of the two DA conditions to recognition under FA to identify interference with memory performance and the brain regions mediating this interference. Replicating our earlier work we found that the animacy task interfered with memory more than did the digit-based distracting task, and there were no age differences in the magnitude of this interference, although older adults performed more poorly overall on the memory tests. The present data also suggest that the means of achieving memory performance, under dual-task conditions with the animacy task, differed across the age groups: younger adults showed an increase in recognition latency, compared to older adults, whereas older adults showed more costs to distracting task performance than did younger adults. This last finding is consistent with our previous work (Fernandes et al., 2004; Fernandes & Moscovitch, 2003), and that of others (Anderson et al., 1998; Naveh-Benjamin, Craik, Guez, & Kreuger, 2005) showing greater costs to distracting task performance under DA conditions.

Though we did find larger overall distracting task RT costs on the animacy compared to digit task, under dual-task conditions, this effect was common to both age groups. 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 et al., 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. We also note that all correlations between memory interference and distracting task interference in the current study were non-significant, which indicates there were no trade-offs in performance across dual-tasks. Similarly, the correlations between single-task performance and memory interference were

non-significant, indicating that task difficulty in the single-tasks does not affect dual-task performance.

Because the memory interference effects were equivalent in younger and older adults, any differences in brain activity during DA between groups, after taking into account activity during FA, reflects age differences in the way the brain copes with the distracting tasks and not differences in performance level per se. Because younger and older adults appear to use different strategies (i.e., increase in recognition latency in younger, and increase in distracting task costs in older adults) to protect memory in the DA animacy condition, neuroimaging data may also reflect the use of these strategies. The ability of older adults to perform as well as younger under DA conditions (equivalent memory interference was observed), particularly in the DA animacy condition, appears to be the result of several age-related differences in brain activity. The first of these is a dampening of the changes in brain activity that we previously noted in younger adults during DA animacy: young show more activity in the left inferior frontal gyrus (IFG) due to the phonological aspects of the animacy task, and a reduction in MTL structures involved in reactivating the memory trace (the hippocampus). The second is that older adults rely more heavily on activity in inferior parietal cortex during recognition under both DA conditions. Finally, older adults show more activation in PFC regions, outside of the IFG, during both FA and DA animacy. Each of these is discussed in turn in the following sections.

3.1. Dampening of brain activity in older adults

During recognition in the DA animacy condition, younger adults showed increased activity in left inferior frontal cortex (BA 44 and 45), together with a reduction in right hippocampal activity (Fernandes et al., 2005). The decrease in hippocampal activation was associated with poorer retrieval, consistent with similar observations by Anderson et al. (2004) who reported a reduction in right hippocampal activity under conditions in which participants suppressed unwanted memories, and in which such items are remembered poorly. Thus, in younger adults, increases in hippocampal activation, as seen in the FA and DA digits, were associated with better memory, and decreases in hippocampal activity, as seen in the DA animacy condition, were associated with poorer memory.

The increase in left IFG activity, during DA animacy compared to DA digits, likely reflects the phonological aspects of both the verbal recognition and animacy tasks. That is, the increase in left prefrontal cortex activation during the DA animacy condition in younger adults (see Fig. 4) overlaps with regions previously shown to be implicated in semantic retrieval (see Cabeza & Nyberg, 2000) and phonological working memory (WM) tasks (Crosson et al., 1999). Dobbins, Foley, Schacter, and Wagner (2002) suggest 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. In our study, it is likely that both semantic and phonological processing regions are involved during recognition of auditorily presented words, and also during the word-based

animacy distracting task. We believe that competition for word-processing resources needed for both verbal recognition and the word-based animacy distracting task (i.e., left IFG activation) interferes with memory trace reactivation (hippocampal deactivation).

Older adults, however, showed less inferior frontal activity and less diminution of hippocampal activity, compared to younger adults during DA animacy. Such a pattern indicates there may have been less competition between the two tasks, which could result in maintained recognition performance. Reduced left IFG activity in older adults during the DA animacy condition would also predict that they should have greater performance costs on the distracting task in that DA condition. That is, they would not be engaging the left IFG as much as do younger adults since older adults would not be maintaining distracting task performance under DA conditions. Indeed, this is precisely what we observed in the distracting task accuracy data: older adults had markedly higher distracting task costs than younger in the DA animacy condition, indicating that they could not maintain performance to a similar level as did the younger adults. Thus, the reduced modulation of left IFG and hippocampus in older adults appears to contribute to their ability to maintain DA memory performance, but only at a cost to performance on the distracting task.

Alternatively, one might suggest that the increase in activation in left IFG in young adults in the DA animacy condition may reflect interference resolution, or selection processes (between competing concurrent tasks). These processes have led to reduced activation in IFG in older adults, suggesting a disruption of interference resolution processes with increasing age (Persson et al., 2004). We favour the first account detailed above as there was no change in left IFG during the DA digits condition, in which participants are still required to handle two tasks concurrently, in either age group. If the interference resolution account were true then we should have observed an age difference in IFG activation in that DA condition as well, but we did not.

3.2. Increases in posterior neocortex activity in older adults

During both DA conditions, a significant increase in activity in older compared to younger adults was seen in posterior parietal cortex (BA 40; in the right during DA digits, and left during DA animacy), as well as in left middle temporal regions (BA 21) during DA digits. Roland and Gulyas (1995) and Krause et al. (1999) suggest that activity in posterior cortex during episodic memory retrieval represents reactivation of stored engrams. In line with this suggestion, Dobbins, Rice, Wagner, and Schacter (2003) and Wheeler and Buckner (2004) found that increased activity in the parietal cortex was associated with successful, compared to unsuccessful, memory performance. Increased activity in these areas in our study, in older adults, may indicate greater demand on these regions to recover stored representations by directing parietal-based attention towards them. This suggests that under DA conditions, another means of maintaining performance in older adults is via modulation of parietal regions. That is, older adults may rely more heavily on activity

in posterior regions to activate the memory trace during recognition under DA conditions.

In younger adults we also found that memory interference increased as left inferior parietal (−50, −32, 46) activation increased. In our previous work (Fernandes et al., 2005), activity in a slightly different region of left inferior parietal (−40, −30, 33) was increased in the DA digits condition, in which memory was preserved, relative to the DA animacy condition, in which memory was disrupted. This finding supported our claim that left inferior parietal activation is related to *retrieval success*. The correlational analysis presented here, however, suggests that increases in another region of left inferior parietal cortex are associated with greater memory interference, indicating modulation with *retrieval failure*. It may thus be the case that the greater the memory interference, the greater the activity in one region of left inferior parietal cortex and also, that despite this, activity is also higher in another region of left inferior parietal in the digits compared to animacy DA condition. We can thus conclude that, across conditions, one region of left inferior parietal cortex activity is associated with retrieval success, as we, and others, have suggested (Dobbins et al., 2003; Fernandes et al., 2005; Wheeler & Buckner, 2004). However, within a particular domain, activity in a slightly different region of left inferior parietal cortex may also be correlated with the amount of effort, or attention, needed in recovering the item. The greater the interference, the more attention is needed to recover the items.

3.3. Increases in PFC activity in older

A number of studies have shown that older adults have more PFC activation (in BA 9/44 and 46/10) than younger across numerous cognitive tasks, particularly those involving memory retrieval (Cabeza, Grady et al., 1997; Cabeza, McIntosh et al., 1997), with lateralization of this increased activity depending on the demands of the memory task (Cabeza et al., 2004). This additional activation is frequently associated with preserved memory performance in older adults, leading to the suggestion that it compensates for age-related changes elsewhere in the brain (Grady et al., 1994; Grady, McIntosh, & Craik, 2005; Madden et al., 1996, 1997; Rypma & D'Esposito, 2000). In the present study, as older adults show no more interference than younger adults during DA at retrieval, we hypothesized that this preservation would be accompanied by an increase in dorso-lateral PFC activity in the older group. Indeed this is what we found, mainly during DA animacy.

As others have reported, we found that older adults had more frontal activity than younger adults during FA recognition. During FA (contrasted to an auditory control task), younger adults had more activity in left IFG, whereas older adults had more activity in bilateral medial frontal gyri, and right middle frontal gyri, as well as in cingulate and temporal regions. During DA animacy there were further age differences in PFC activity after accounting for activity at FA. These consisted of greater activity in left IFG in younger adults, and more activity in bilateral middle frontal gyri in older adults.

Although additional PFC activation observed in older adults in memory retrieval tasks has sometimes been related to bet-

ter performance, as noted above, it also could reflect a task difficulty effect to some extent. That is, older adults may find recognition more difficult in general, and thus recruit PFC to a greater extent than do younger adults; similarly, increasing task difficulty in younger adults is associated with increased PFC activation (Barch et al., 1997; Szameitat, Schubert, Müller, & von Cramon, 2002). The increased PFC activity that we found in our older adults during retrieval under FA could be influenced by task difficulty, as the older adults performed more poorly than the younger group. However, more widespread PFC activity in older adults during the DA animacy condition is unlikely to reflect task difficulty or simple performance differences, as the interference effects are the same in younger and older groups. Thus, the additional recruitment of PFC in older adults during the DA animacy condition may reflect a compensatory function, as has been proposed in other experiments where task performance is equivalent between younger and older groups (Cabeza et al., 2002), or be related to better performance in those older adults who are better able to recruit PFC (Cabeza et al., 2002; Grady et al., 2003).

In conclusion, our work provides evidence that behaviourally, older adults are maintaining similar levels of memory interference compared to younger adults, but that the means of achieving performance vary greatly across age groups. The present work specifies the different ways in which older adults achieve performance under DA conditions. These include recruitment of both dorsolateral PFC and posterior neo-cortex to a greater extent than that seen in younger adults. Older adults also have less modulation of activity due to the distracting task in left inferior PFC and hippocampus. This latter change results in maintained performance on the memory task, but comes at a cost to performance on the distracting task. Put another way, increased activation in PFC, and possibly other regions in older adults, reflects their choice of strategy to emphasize memory at the expense of distracting task performance. This age-related alteration of brain activity may indicate that older adults modify their priorities for which aspects of the environment gain access to processing resources, in response to decrements in those resources with age.

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