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Anterior prefrontal cortex and the recollection of contextual information

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Abstract

Recollective memory can involve the retrieval of many different kinds of contextual information, including where and when an event took place, as well as our thoughts and feelings at the time. The brain regions associated with this ability were examined in an event-related fMRI experiment, where participants made decisions about words or famous faces which were presented either on the left or right of a monitor screen. Subsequently, the studied words and faces were again presented and participants underwent fMRI brain scanning while recollecting either which of the decisions they had made on each item ("task memory"), or whether it had been presented on the left or right of the screen ("position memory"). A functional dissociation was observed within anterior prefrontal cortex (principally Brodmann's area 10), with activation in lateral regions associated with remembering either type of information (relative to baseline), and a medial anterior PFC region showing significantly greater activation during the "task memory" conditions. These results suggest different roles for lateral and medial anterior prefrontal cortex in recollection.

Keywords: Functional magnetic resonance imaging (fMRI); Episodic memory; Executive function; Cognitive control; Rostral prefrontal cortex; Hippocampus

According to a number of prominent theories of memory, recollection of previously experienced events involves not only an ability to remember the events themselves (e.g., where and when an event took place, and who was involved) but also our personal reactions to those events (e.g., our thoughts and feelings at the time) (Burgess & Shallice, 1996; Johnson & Raye, 1981; Johnson, Hashtroudi, & Lindsay, 1993; Schacter, Norman, & Koutstaal, 1998; Tulving, 1983). The integration of these different aspects of the "context" in which an event occurred enables the recollection of the event in such rich detail that we can feel as if we are 're-living' the experience. Cognitive neuroscience has provided extensive evidence that the prefrontal cortex (PFC) and medial temporal lobe (MTL) play central roles in recollective memory function (Aggleton & Brown, 1999; Fletcher & Henson, 2001; Simons & Spiers, 2003), and event-related potential recordings suggest PFC involvement in memory for thought processes as well as perceptual details relating to a past event (Johnson, Kounios, & Nolde, 1996). Recently, functional neuroimaging has begun to elucidate more precisely the prefrontal brain regions involved in recollecting this kind of context information (Dobbins, Foley, Schacter, & Wagner, 2002; Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Henson, Shallice, & Dolan, 1999; Nyberg et al., 1996; Ranganath, Johnson, & D'Esposito, 2000; Rugg, Fletcher, Chua, & Dolan, 1999), but the issue of whether different brain regions are associated with memory for previous thought processes versus perceptual details has yet to be examined.

Anterior PFC (approximating Brodmann's area 10) is one candidate prefrontal area that might be involved in the recollection of context details. Previously, it has not been clear how to account for the anomaly that some functional imaging experiments investigating recollection of context have found activation in anterior PFC (e.g., Rugg et al., 1999)

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whereas others have not (e.g., Nyberg et al., 1996). One possible explanation may relate to the different types of context that were tested in the different experiments. In all previous studies that have examined brain regions associated with recollecting which of two study tasks had previously been undertaken, anterior PFC activation was observed (Burgess, Maguire, Spiers, & O'Keefe, 2001; Dobbins et al., 2002; Kahn, Davachi, & Wagner, 2004; Rugg et al., 1999). By contrast, studies that have used ostensibly very similar paradigms, but focused on perceptual features of context derived more directly from the external environment (e.g., recollecting the position on a monitor screen target items had been presented), have given less clear-cut results. While some reported activation in anterior PFC (Cansino, Maquet, Dolan, & Rugg, 2002; Ranganath et al., 2000), others implicated different regions (Henson, Shallice, et al., 1999; Nyberg et al., 1996).

Recollecting which of two study tasks were undertaken is likely to primarily involve memory for aspects of context that might be thought of as "internally generated" (Johnson et al., 1993), such as the processing operations engaged in thinking about study task goals, considering the judgements required, and making appropriate responses. It is generally considered that brain regions active during different kinds of information processing are reactivated during memory for such information (e.g., visual processing areas during retrieval of visual information; Wheeler, Petersen, & Buckner, 2000). The possibility that anterior PFC may be differentially involved in recollecting previous thought processes is, therefore, given support by recent findings that anterior PFC may contribute to evaluating one's own *current* thought processes (Burgess, Scott, & Frith, 2003; Christoff & Gabrieli, 2000; Frith & Frith, 2003; Gusnard, Akbudak, Shulman, & Raichle, 2001; Koechlin, Basso, Pietrini, Panzer, & Grafman, 1999). In the present event-related fMRI study, we sought to explore this possibility directly by characterising anterior PFC responses during a recollection task in which subjects were required to recollect the way in which they had processed a study item as opposed to recollecting the item's spatial position. Furthermore, we identified the extent to which activation was specific to different stimulus types by examining recollection of task and position for both word and face stimuli (Fig. 1).

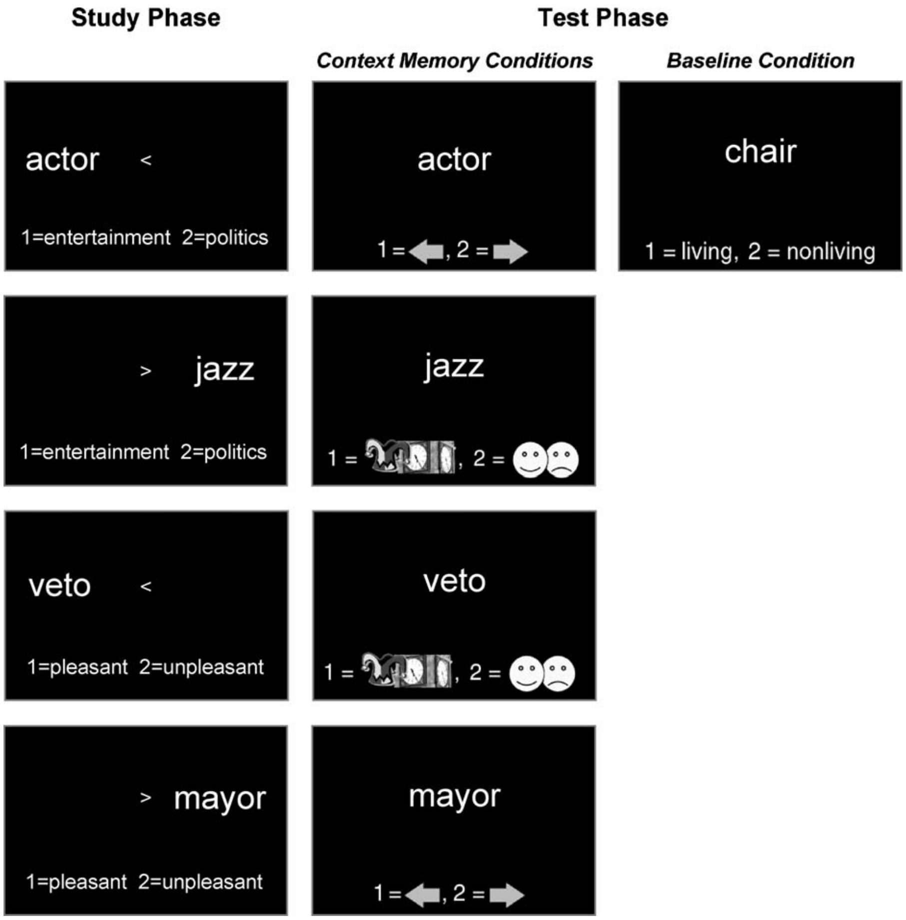

Fig. 1. Examples of the cues and stimuli used during the study and test phases. Study phase: task cues indicated whether entertainment/politics or pleasant/unpleasant judgements were to be made on stimuli that were presented either on the left or right of the screen. Task and position were crossed in the study phase design. Test phase: context memory conditions involved recollecting whether stimulus had been presented on left or right of the screen (e.g., top example) or whether entertainment/politics or pleasant/unpleasant task had been undertaken with stimulus (e.g., second example). Note that study and test trials also involved identical judgements with famous faces (entertainers and politicians) to determine stimulus-specificity of results.

1. Methods

1.1. Participants

Sixteen right-handed native speakers of English (6 male, 10 female), with normal or corrected-to-normal vision, took part in the experiment. The volunteers (mean age = 22.8 years, range 19–28) were screened using a comprehensive medical questionnaire and informed consent was obtained in a manner approved by the Addenbrooke's NHS Trust Local Research Ethics Committee.

1.2. Design and materials

Participants were administered a study phase and a test phase. The study phase was undertaken prior to going into the MRI scanner, on a laptop computer in another room, and the test phase was administered in the scanner.

The stimuli consisted of 120 words and 120 greyscale photographs of famous faces (Fig. 1). Forty-eight of each stimulus type related to entertainment and 48 to politics. These 96 words and 96 faces were used as target items in the study and test phases, in addition to 12 living and 12 nonliving concrete words and 12 male and 12 female famous faces drawn from fields other than entertainment or politics, which were used as baseline items in the test phase. The words assigned to each condition were matched as closely as possible for Kucera-Francis frequency (Wilson, 1988), and the famous faces for gender and approximate time-period of fame. Four different versions of each paradigm were created, which systematically counterbalanced the task undertaken in the study phase (entertainment/politics or pleasant/unpleasant; see below) and the position of the item on the monitor in the study phase (left or right). Items were also counterbalanced in terms of the type of recollection that was cued during the test phase (memory for task or position; see below). Additionally, to control for study-test delay time, items appeared in the same quarter of both the study and test lists, with the particular quarter to which each item was assigned rotated over versions of the task. Within each quarter of the lists, item order was pseudo-randomised such that no more than three consecutive trials were of the same condition.

1.3. Procedure

During the non-scanned study phase, participants were instructed to fixate on an arrow in the centre of the monitor screen, which indicated whether the stimulus item in the upcoming trial would be presented on the left or the right of the screen (Fig. 1). After 500 ms of fixation, a cue appeared at the bottom of the specified side of the screen, indicating the task that was to be carried out on the stimulus item when it was presented. After a further 500 ms, the stimulus item (either a word or famous face) was presented on the specified side of the screen. If the cue was "1 = entertainment, 2 = politics", participants were instructed to decide whether the stimulus item related more to entertainment or to politics, and press the appropriate key on the keyboard. If the cue was "1 = pleasant, 2 = unpleasant", participants made a judgement as to whether the stimulus item seemed pleasant or unpleasant to them. They were given 3.5 s to make their judgement, and were instructed to remember the position of the stimulus item, and the task they carried out on it, for a later memory test in the scanner.

Following the study phase, participants entered the scanner and undertook the test phase, trials of which involved the presentation of a cue at the bottom of the display, indicating the judgement participants were to make on the stimulus item when it was presented. After 500 ms, the stimulus item (either a word or famous face presented during the study phase, or a non-studied baseline word or famous face) appeared in the centre of the display. In order to reduce possible encoding specificity influences, the cues consisted of graphical icons (Fig. 1). If the task memory cue was presented, participants tried to remember whether they had carried out the entertainment/politics task or the pleasant/unpleasant task on the stimulus item during the study phase. If the position memory cue appeared, participants tried to remember whether the stimulus item had been presented on the left or the right of the screen. In the baseline conditions, participants were presented with a non-studied word or famous face. They were cued to decide whether the word specified a living or nonliving object, or whether the famous person was male or female. Participants had 3.5 s to make their judgement, which they indicated by pressing one of two buttons on a button-box. To increase the efficiency of the event-related fMRI design, the inter-trial interval was jittered according to an exponential distribution (Henson, 2003) between 480 and 1080 ms.

1.4. Imaging acquisition and data analysis

A 3T Bruker system was used to acquire 991 echo-planar functional images per subject (TR = 1100 ms, TE = 27.5 ms, 21 interleaved axial slices oriented ∼10° from the AC–PC transverse plane, 4 mm thickness, 1 mm inter-slice skip, 200 mm FOV, 64 × 64 matrix). Fifteen additional volumes were collected and discarded at the beginning of each run to allow for T1 equilibration. In addition, two magnetic field maps were acquired for each subject, which were used in the field map undistortion stage of preprocessing (see below).

Data were preprocessed and analysed using SPM2 (Wellcome Department of Imaging Neuroscience, London). Because anterior prefrontal cortex can be subject to susceptibility distortion in fMRI due to its proximity to the sinus area, efforts were taken to minimise the effects of this distortion. Images were first corrected for differences in slice acquisition timing by resampling all slices in time to match the middle slice, followed by motion correction by realigning all images with respect to the first (using 4th-degree B-spline interpolation). The realigned images then underwent an undistortion procedure using the acquired magnetic field maps (Cusack, Brett, & Osswald, 2003), and a mean undistorted image was created. A mask image was specified using MRIcro software (Rorden & Brett, 2000), which identified regions of residual signal dropout in the undistorted mean image. This mask image was used to weight the spatial normalisation of the undistorted data (Brett, Leff, Rorden, & Ashburner, 2001) to an EPI template in MNI stereotactic space (Cocosco, Kollokian, Kwan, & Evans, 1997). Normalised images were resampled into 3 mm cubic voxels and then spatially smoothed with an 8 mm FWHM isotropic Gaussian kernel. The time series in each voxel was highpass-filtered to 1/128 Hz to remove low-frequency noise, corrected for temporal autocorrelation using an AR(1) + white noise model, and scaled to a grand mean of 100 across voxels and scans within the session.

Statistical analysis was undertaken twice, once using all trials, and once using RT-matched trials (see Section 2.1 for more details). Each analysis was conducted in two stages of a mixed effects model. In the first stage, 11 event types were defined, consisting of 5 regressors for words (correct and incorrect responses in the task and position recollection conditions plus the baseline condition responses, which were all correct) and 5 for faces, plus the few trials for which participants made no behavioural response (in the RT-matched analysis, excluded trials were modelled along with the missed responses). Events for each of the 11 conditions were modelled by convolving onset times with a canonical haemodynamic response function and its second- and third-order temporal derivatives. The temporal derivatives were used to capture possible delayed responses (delayed by 2 and 3 s, respectively) in anterior prefrontal cortex, which have been observed in some previous studies (Henson, Rugg, & Shallice, 2000; Schacter, Buckner, Koutstaal, Dale, & Rosen, 1997). Parameters for each covariate were estimated using a subject-specific fixed-effects model, with movement parameters in the three directions of motion and three degrees of rotation included as confounds, and a single covariate representing the mean session effect.

Linear contrasts were used to obtain subject-specific estimates for each of the effects of interest which, apart from where specified, involved correct response regressors only. These estimates were entered into the second stage of analysis treating subjects as a random effect, using a one-sample *t*-test across subjects. Separate analyses were undertaken for the canonical and the two delayed response functions. Because the primary experimental hypotheses concerned central context memory processes that could be expected to be engaged significantly irrespective of the type of stimuli involved, contrasts of interest involved inclusive masking across stimulus type. Statistical parametric maps of the independent word and face contrasts were constructed using uncorrected height thresholds of $p < 0.001$. The inclusive mask between these contrasts was then calculated to identify brain regions significantly activated for both words and faces. Given the orthogonality of the independent words and faces pairwise contrasts, the conjoint probability threshold of the inclusive mask can be calculated to be $p < 1.5 \times 10^{-5}$ (see Fisher, 1990, for more details). The anatomical locations of significant cluster maxima of at least five contiguous voxels were localised on the mean structural scan across subjects, with approximate Brodmann areas estimated from the Talairach and Tournoux (1988) atlas, after adjusting coordinates to allow for differences between the MNI and Talairach templates (Brett, Christoff, Cusack, & Lancaster, 2001). To further explore the nature of the activation associated with task and position recollection, mean percentage signal change magnitude relative to the baseline conditions was extracted from the subject-specific parameter estimates of cluster maxima and subjected to repeated-measures analyses that included condition and, where specified, region, as repeated factors.

2. Results

2.1. Behavioural results

Recollection accuracy and reaction time data are displayed in Table 1. Importantly, given that the primary hypothesis in the present experiment concerns the contrast between task and position memory, there was no effect of the type of contextual detail on recollection accuracy, $F(1, 15) = 0.03$, n.s. There was a significant effect of stimulus type with context information related to faces recollected to a greater extent than that for words, $F(1, 15) = 26.1$, $p < 0.001$, and a significant interaction between the two factors, $F(1, 15) = 7.49$, $p < 0.05$, which indicated that stimulus type differences were more apparent in position memory (mean difference between words and faces was 0.06 for task recollection and 0.14 for position recollection). Accuracy was significantly above chance in all memory conditions, all $t(15) > 3.0$, $p < 0.01$. In terms of reaction time, there was a significant main effect of context type, $F(1, 15) = 20.0$, $p < 0.001$, with recollection of task associated with longer reaction times than position. There was no effect of stimulus type, $F(1, 15) = 0.9$, n.s., but a significant interaction, $F(1, 15) = 7.63$, $p < 0.05$, which occurred because the

Table 1
Accuracy and reaction time (ms) data

	Recollection of task		Recollection of position	
	Words	Faces	Words	Faces
	Full data set			
Accuracy				
Mean	0.62	0.68	0.58	0.72
S.D.	0.11	0.12	0.08	0.11
Reaction time				
Mean	1803	1907	1636	1602
S.D.	357	313	298	277
	Reaction time matched data set			
Accuracy				
Mean	0.58	0.60	0.54	0.64
S.D.	0.11	0.12	0.08	0.11
Reaction time				
Mean	1740	1780	1687	1678
S.D.	357	319	308	292

Table 2
Regions of significant activation in the contrast between correct context recollection and baseline conditions, averaging over context type (memory for task and position)

Brain region	Coordinates			Z	Voxels
	x	y	z		
Left anterior PFC (BA 10)	−30	63	0	4.6	134
Right anterior PFC (BA 10)	33	60	12	3.6	34
Left ventrolateral PFC (BA 47)	−42	45	−9	3.5	9
Left dorsomedial PFC/anterior cingulate (BA 9/32)	−6	33	36	4.5	126
Left ventrolateral PFC/insula (BA 47)	−30	24	−9	5.5	41
Right ventrolateral PFC/insula (BA 47)	33	24	−9	3.9	17
Right dorsolateral PFC (BA 9)	48	24	36	3.4	25
Left dorsolateral PFC (BA 9)	−54	18	33	4.0	94
Left caudate (BA 25)	−12	18	3	3.7	8
Left superior PFC (BA 8)	−30	12	51	4.0	32
Right precuneus (BA 23)	15	−63	27	3.6	10
Right lateral parietal cortex (BA 7)	39	−69	45	4.3	143
Left lateral parietal cortex (BA 7)	−27	−75	51	5.7	684

Coordinates are in MNI atlas space (Cocosco et al., 1997), with brain regions and Brodmann areas (BA) estimated from the Talairach and Tournoux (1988) atlas. PFC = prefrontal cortex.

context type difference was greater for faces (mean difference 305 ms) than words (mean difference 167 ms).

To rule out an explanation for any significant fMRI activations in terms of reaction time differences, the fMRI analysis was undertaken with data that were matched for reaction time, as well as with the full data set. The matching was achieved by progressively removing from the analysis outlying trials from each condition equally for all participants until the context memory conditions did not differ from one another in reaction time. The matched data set (Table 1) was similar to the full data set in terms of recollection accuracy, with no difference in terms of context type, $F(1, 15) = 0.03$, n.s., a significant main effect of stimulus type, $F(1, 15) = 9.46$, $p < 0.01$, and a significant interaction, $F(1, 15) = 7.56$, $p < 0.05$. The fMRI analysis included correct recollection trials only, apart from where specified. Importantly, in the matched data set there was no longer any difference in reaction time, either in terms of context type, $F(1, 15) = 2.07$, n.s., stimulus type, $F(1, 15) = 0.16$, n.s., or the interaction, $F(1, 15) = 0.95$, n.s.

2.2. Neuroimaging results

Brain regions implicated in putatively central stimulus-independent recollection processes were characterised using group contrasts that involved inclusive masking (identifying common regions showing significant activation in both word and face pairwise comparisons at a conjoint probability threshold of approximately $p < 1.5 \times 10^{-5}$; see Section 1.4 for further details). Analysis involving both the full data set and those where the conditions were matched for reaction time yielded virtually identical results. For the sake of brevity, we report the results from the RT-matched data set here; the full results are available from the first author on request. The significant activations were all found when a model based on the canonical haemodynamic response function was applied; no further significant activations were observed with two delayed response functions (see Section 1). To identify the regions involved in recollection regardless of the type of detail being remembered, we contrasted first the correct context memory and baseline conditions, while averaging over context type (recollection of task and position). Significant activation was seen (Table 2; Fig. 2A) in bilateral anterior PFC, ventrolateral PFC/insula, dorsolateral PFC, and lateral parietal cortex. This network of regions was recruited to a similar extent in both task and position conditions (Fig. 2B and C) with, for example, no significant effect of context type on activation in lateral anterior PFC, $F(1, 15) = 1.93$, n.s. Moreover, activation in this lateral anterior PFC region did not differ according to stimulus type, with recollection of words and faces associated with similar levels of activation, $F(1, 15) < 1$, n.s.

Thus, activation in lateral regions of anterior PFC occurred irrespective of the kind of contextual detail that was recol-

Table 3
Regions exhibiting significantly greater activation for correct recollection of task than position

Brain region	Coordinates			Z	Voxels
	x	y	z		
Left anterior PFC (BA 10)	−9	63	21	4.7	31
Left ventrolateral PFC (BA 47/11)	−48	39	−18	3.6	7
Left superior PFC (BA 8)	−3	33	54	3.8	45
Left ventrolateral PFC (BA 45)	−51	27	15	4.0	221
Right ventrolateral PFC (BA 45)	48	27	24	3.2	9
Left premotor cortex (BA 6)	−9	15	60	3.7	11
Left thalamus	−9	−15	3	3.2	7
Left medial temporal lobe (BA 20)	−21	−30	−9	3.5	10
Left fusiform cortex (BA 19)	−27	−72	−15	4.8	479
Right cuneus (BA 18)	12	−72	6	3.6	20
Left cuneus (BA 17)	−6	−81	9	3.7	7
Right occipital cortex (BA 18)	30	−84	9	5.6	768

Coordinates are in MNI atlas space (Cocosco et al., 1997), with brain regions and Brodmann areas (BA) estimated from the Talairach and Tournoux (1988) atlas. PFC = prefrontal cortex.

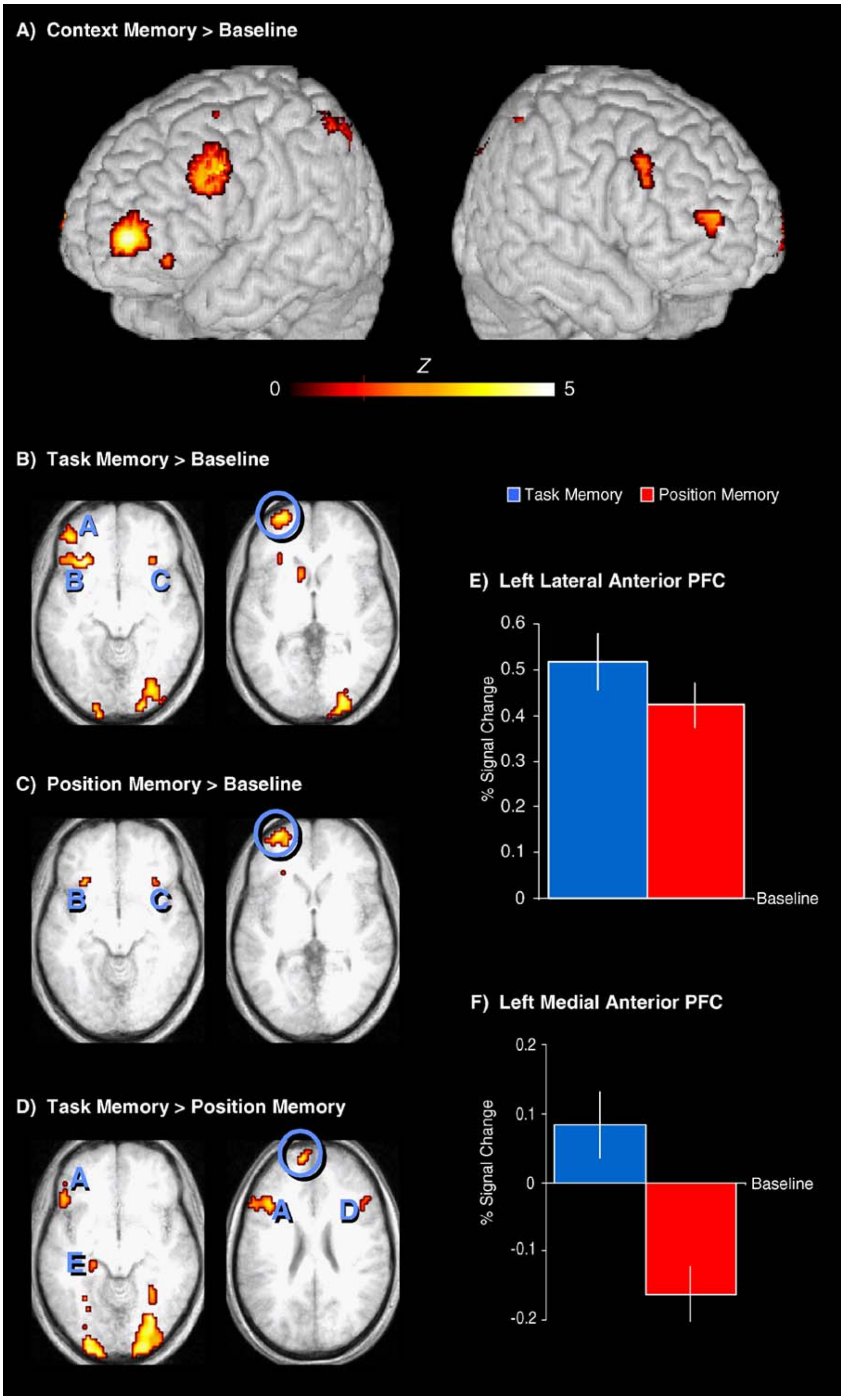

Fig. 2. Group functional activation maps and plots of percentage signal change relative to the baseline conditions, inclusively masked across stimulus type (words and faces). (A) In the general correct context memory > baseline contrast, averaging over context type (recollection of task and position), regions of significant activation, rendered onto a 3D template structural image, included bilateral anterior PFC (BA 10), ventrolateral PFC/insula (BA 47), dorsolateral PFC (BA 9), and lateral parietal cortex (BA 7). Very similar networks of activation, displayed on axial slices of an averaged structural image, were observed in recollection of task > baseline (B) and recollection of position > baseline (C), including left lateral anterior PFC (circled; BA 10), left ventrolateral PFC (A; BA 47/10), and bilateral ventrolateral PFC/insula (B and C; BA 47). (D) Regions showing significant activation in the correct task > position contrast included left medial anterior PFC (circled; BA 10), bilateral ventrolateral PFC (A and D; BA 45/47 on left and BA 45 on right), and left medial temporal lobe (E; BA 20). Plots of signal change for each context condition relative to the baseline conditions (error bars represent standard errors of the mean) indicate that recruitment of the left lateral anterior PFC was significantly greater during both context memory conditions than the baseline conditions but did not differentiate between recollection of task and position (E), whereas there was significantly greater response in left medial anterior PFC during task than position memory (with position associated with reduced activation relative to the baseline conditions) (F).

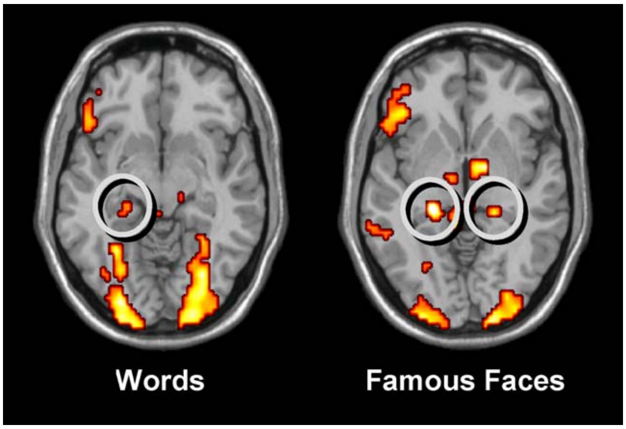

Fig. 3. Stimulus-specific lateralisation in the medial temporal lobe in the correct task > position contrast. Activation was significant only on the left for words, but was bilateral for famous faces.

lected. However, direct contrast between correct task and position memory conditions (Table 3; Fig. 2D) revealed a more medial region of left anterior PFC in which signal differentiated significantly between context type, $F(1, 15) = 54.23$, $p < 0.0001$. A direct test using repeated measures ANOVA confirmed that there was a statistically significant dissociation between these two areas, as reflected in a region by condition interaction, $F(1, 15) = 9.59$, $p < 0.01$. It is important to ensure that this interaction could not be confounded by possible differences in overall signal magnitude between regions. When analysis was repeated using signal change values that were z-transformed within each region, the interaction was still significant, $F(1, 15) = 10.31$, $p < 0.01$. As a final verification, the potential confound of signal variance differences between regions was addressed with the use of the non-parametric Friedman test. The region by condition interaction remained significant even using this conservative statistical analysis, $\chi^2(3) = 12.15$, $p < 0.01$.

Other brain regions activated in the contrast between correct task and position memory included bilateral ventrolateral PFC and an area of the left MTL. Closer examination revealed that MTL involvement in the task was lateralised according to stimulus type (Fig. 3), with individual pairwise contrasts showing that words were associated with relatively higher left MTL (−21, −30, −9; $Z = 3.46$) and faces with bilateral MTL (left: −21, −30, −3; $Z = 5.34$; right: 21, −33, −3; $Z = 4.19$) activation, respectively. The inclusive mask between these contrasts therefore implicated left MTL only. Regions showing greater activation for correct position than task recollection included right lateral parietal (60, −45, 27; $Z = 4.48$; 15, −60, 60; $Z = 4.25$) and temporal (54, −60, 6; $Z = 4.79$; 60, −63, 0; $Z = 4.38$) cortices and the posterior cingulate (12, −36, 39; $Z = 3.94$), consistent with the results of a number of previous studies (Cansino et al., 2002; Fujii et al., 2004; Henson, Shallice, et al., 1999; Wheeler & Buckner, 2004).

To examine in further detail the left medial anterior PFC region that was more engaged by task than position recollection, a subsequent analysis sought to address whether its differential recruitment could be attributed to variations in task difficulty. Inspection of the behavioural data suggests this to be an unlikely explanation: greater activation was observed for task than position memory despite the conditions being matched behaviourally for recollection accuracy and reaction time. Consistent with this, correlation analysis revealed no correspondence between reaction time and fMRI signal change in this region across subjects, $r(16) = 0.16$, n.s. A second analysis examined whether the observed activation results could be reflecting recollection success by contrasting signal associated with correct and incorrect context attributions. The PFC and left MTL regions all showed virtually identical patterns of activation for both successful and unsuccessful recollection. This is in contrast to the left and right lateral parietal regions identified in the basic recollection contrast that averaged over context type (Table 2; Fig. 2A). These two regions exhibited significant effects of recollection success on signal change, responding more for successful than unsuccessful remembering, both $F(1, 15) > 7.5$, $p < 0.015$. Thus, an account of the anterior PFC results in terms of task difficulty or retrieval success can be rejected.

3. Discussion

The principal finding of the present experiment is that the recollection of different kinds of contextual information is associated with differential recruitment of anterior PFC. This result provides empirical confirmation of a hypothesis that emerged qualitatively on the basis of discrepant results in a series of functional neuroimaging studies (Burgess et al., 2001; Cansino et al., 2002; Dobbins et al., 2002; Henson, Shallice, et al., 1999; Kahn et al., 2004; Nyberg et al., 1996; Ranganath et al., 2000; Rugg et al., 1999). Moreover, we have demonstrated a functional dissociation within anterior PFC, with the processes supported by lateral regions apparently playing an important but non-specific role in recollection of context details and a medial region supporting processes recruited specifically when an individual is shown a stimulus and asked to recollect which task was previously associated with it. While context-specific, however, the pattern of activity in this region indicates that it is not material-specific since it was recruited regardless of whether words or faces were being recollected. Furthermore, it is implausible on the basis of current findings to attribute anterior PFC activation to task difficulty, as estimated by accuracy and reaction time. This is consistent with previous studies of recollection and prospective memory that have ruled out task difficulty as an adequate explanation (Burgess et al., 2003; Dobbins et al., 2002).

The differential involvement of anterior PFC in recollection of details about the context in which a task was carried out suggests that this region contributes to the processing of “internally generated” information such as, for example, the thought processes involved in study task performance (Burgess et al., 2003; Christoff & Gabrieli, 2000; Frith & Frith, 2003; Gusnard et al., 2001; Koechlin et al., 1999;

Shimamura, 2000). This hypothesis can explain observations of activation in this area associated with seemingly diverse cognitive functions such as the attribution of mental states to others (Frith & Frith, 2003), self-referential cognitive processing (Gusnard et al., 2001), remembering to carry out intentions after a delay (Burgess et al., 2003), and mediating between goals and sub-goals (Koechlin et al., 1999), all of which require coordinated control of internally generated thoughts and externally derived perceptions (see also Christoff & Gabrieli, 2000).

The present data indicate that lateral anterior PFC may play a general role in the processing of contextual information, associated with similar levels of activation during recollection of both task and position. We can be less sure of the precise role played by processes supported by the medial region. It may be preferentially involved when the retrieval cue requires the recollection of contextual details that were internally generated such as, for example, the processing operations engaged in making semantic or pleasantness decisions about stimuli and responding appropriately during study phase trials – operations not present in the position memory condition. However a function of this kind must involve a wide range of processing, and theories about the mechanisms of recollection of context details that occur when presented with a previously seen stimulus do not exist at the level of detail that would enable us to specify precisely which processes the medial regions are supporting. For instance, it is possible that the medial BOLD response may reflect initial stages of stimulus inspection rather than the instantiation of the context details themselves. This view would explain why medial anterior PFC was not significantly activated in comparisons with the baseline conditions, $t(15) = 1.72$, $p = 0.1$, and would be congruent with recent findings by this group of medial anterior PFC increases in simple RT conditions (e.g. Gilbert, Simons, Frith, & Burgess, submitted). We prefer at this stage therefore to take a conservative approach to the characterization of the processing which the medial anterior PFC activations reported here represent.

This raises the important question of which stage of the retrieval process anterior PFC might be recruited in. A number of theories of episodic retrieval (Burgess & Shallice, 1996; Fletcher & Henson, 2001; Rugg & Wilding, 2000; Simons & Spiers, 2003) have differentiated between two main stages (among others): the specification of retrieval strategies and the monitoring of retrieved information. Previous studies have proposed roles for anterior PFC in one or other of these stages. For example, one study of working memory observed activation in anterior PFC that occurred when the task cue was presented, before stimulus items appeared (Sakai & Passingham, 2003), suggesting a role in the transformation of the cue into the specification of task parameters, or what is termed, retrieval ‘orientation’. The possibility that this region may be involved at an early stage of the recollection process is supported by data from event-related potential studies which found recollection effects over frontal sites that occurred as early as 200 ms following stimulus onset (Ranganath & Paller, 2000). It is of interest that in the present fMRI data, like the other study of recollection to model different haemodynamic response latencies (Rugg, Henson, & Robb, 2003), significant anterior PFC effects were seen with the canonical response function rather than with delayed functions (see Section 1.4 for more details), consistent with the idea of early involvement of this region in recollection. In contrast, two studies of recognition memory observed anterior PFC effects that were modelled best by delayed functions (Henson et al., 2000; Schacter et al., 1997), interpreting their results by suggesting that in recognition memory (which may be supported by recollection and/or a sense of familiarity with target items), anterior PFC may play a role in post-retrieval processes.

An additional question, on which there is conflicting evidence from previous studies (Cansino et al., 2002; Dobbins, Rice, Wagner, & Schacter, 2003; Kahn et al., 2004; Rugg et al., 1999), is whether anterior PFC could be differentially engaged depending on the success or failure of retrieval. Greater activation during successful than unsuccessful recollection could be interpreted as evidence that a region is involved in processes occurring following the retrieval of sought-after information from memory (Konishi, Wheeler, Donaldson, & Buckner, 2000). In keeping with the results of Dobbins et al. (2003) and Kahn et al. (2004), recruitment of anterior and other regions of PFC in the present data was not contingent on retrieval success, with virtually identical levels of activation for successful and unsuccessful recollection. The retrieval success data are thus consistent with the haemodynamic response results in suggesting a pre-retrieval role for these regions. This is in contrast to left and right lateral parietal cortex, which were observed to be differentially modulated by retrieval success, consistent with a number of previous studies (Henson, Shallice, et al., 1999; Konishi et al., 2000; Wheeler & Buckner, 2003).

Other regions to show greater activation for recollection of task than position included ventrolateral PFC, consistent with the idea that this region is involved in processing retrieval cues and specifying retrieval strategies (Dobbins et al., 2002; Fletcher, Shallice, Frith, Frackowiak, & Dolan, 1998). Differential activation was also observed in left MTL, confirming that in demanding retrieval situations such as contextual recollection, interactions between PFC and MTL regions are particularly important (Simons & Spiers, 2003). Although the fMRI protocol employed lacks the spatial resolution to enable definitive specification between particular MTL regions, the present activation appeared to be centred on the left hippocampus, consistent with the suggested role for this structure in recollective memory (Aggleton & Brown, 1999). Pairwise contrasts established that involvement of this region was lateralised according to the type of stimuli involved, with significant activation on the left for words, and bilateral involvement for famous faces. These results echo previous findings from both neuropsychological and functional imaging studies of recognition memory, which have suggested lateralisation according to the verbal/nonverbal nature of the stimuli involved (Kelley et al., 1998; McDermott, Buckner, Petersen, Kelley, & Sanders, 1999; Milner, 1972; Simons, Graham, Galton, Patterson, & Hodges, 2001; Simons, Graham, Owen, Patterson, & Hodges, 2001; Warrington, 1984). Consistent with this formulation, famous faces, which are processed using both verbal and nonverbal (i.e., perceptual) information, were associated with bilateral recruitment of MTL regions.

In conclusion, the present results advance our understanding of the role of anterior PFC in human cognition by revealing that this region may be responsible for the experience of recollecting different kinds of contextual information relating to previous events. Future studies are required to establish how well these results generalize to other instances of context retrieval, such as for example distinguishing between recollection of events that were experienced as opposed to those that were imagined, or recollecting our emotional reactions to events when they occurred.

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