

The functional roles of prefrontal cortex in episodic memory

II. Retrieval

P. C. Fletcher,¹ T. Shallice,² C. D. Frith,¹ R. S. J. Frackowiak¹ and R. J. Dolan^{1,3}

¹Wellcome Department of Cognitive Neurology, Institute of Neurology, ²Institute of Cognitive Neuroscience and Department of Psychology, University College London, ³Royal Free Hospital Medical School, London, UK

Correspondence to: Paul Fletcher, Wellcome Department of Cognitive Neurology, Institute of Neurology, 12 Queen Square, London WC1N 3BG, UK.
E-mail: p.fletch@fil.ion.ucl.ac.uk

Summary

Functional neuroimaging studies of memory retrieval show consistent activation of the right prefrontal and superior parietal cortex. We examined the specific role of the prefrontal cortex during retrieval with the hypothesis that this region mediates monitoring processes necessary for optimal recall. During functional neuroimaging with PET, subjects retrieved verbal material under two conditions. In the first, an organizational structure had been provided, prior to scanning, and this formed the basis for a monitored memory search while the scan took place. A comparison condition did not require a monitored search because recall was externally cued. In both conditions, when compared with baseline tasks prefrontal cortex and

medial parietal activation was observed. Within the right prefrontal cortex activation an anatomical dissociation was seen between the dorsal and ventral prefrontal cortex. The dorsal region showed greater activation when monitoring demands were emphasized, while the ventral region showed greater activation when external cueing was emphasized. An unpredicted dissociation within the superior parietal activation was also observed, a dorsal region showing activation during the monitored search task and a more ventral region showing activation under the externally cued condition. The results provide evidence for functional specialization of the right prefrontal cortex for discrete cognitive processes during episodic memory retrieval.

Keywords: functional neuroimaging; memory; organization; retrieval; prefrontal

Abbreviations: DLPFC = dorsolateral prefrontal cortex; PFC = prefrontal cortex; SPM = statistical parametric mapping

Introduction

Activation of the right prefrontal cortex (PFC) during memory retrieval is widely observed in functional neuroimaging studies employing a variety of psychological paradigms and test modalities (Fletcher *et al.*, 1997). The functional significance of these activations has not been explained. One suggestion is that the predominance of right PFC activation during retrieval experiments reflects the adoption of a 'retrieval mode' necessary for the initiation and maintenance of retrieval processes (Kapur *et al.*, 1995; Nyberg *et al.*, 1995). However, it has also been argued that right prefrontal activation is sensitive to the degree of retrieval success (Rugg *et al.*, 1996). Other evidence implicates this region in error-checking at retrieval (Fletcher *et al.*, 1996) or in processes necessary for retrieval of information regarding feature rather than location information (Nyberg *et al.*, 1996; Owen *et al.*, 1996).

It has been suggested that optimal recall involves

monitoring the products of a strategic retrieval search to check their accuracy (Norman and Bobrow, 1979; Burgess and Shallice, 1996). From the perspective of neuropsychology, one suggestion is that the PFC is particularly involved in such strategic control of memory retrieval (Shallice, 1988; Moscovitch, 1989). In this respect, a widely used neuropsychological task involves the retrieval of an organized list of words. This form of uncued retrieval, using an internally organized structure created from a single encoding trial, makes critical demands upon monitoring operations. Empirical evidence indicates that frontal lesions interfere with an organized and monitored memory search, in that frontally damaged patients retrieve material in a relatively haphazard way (Incisa della Rocchetta and Milner, 1993; Gershberg and Shimamura, 1995). One study (Incisa della Rocchetta and Milner, 1993) stressed the use of organization at encoding or retrieval by varying the amount

Table 1 Task requirements and measurements of retrieval performance

	Retrieval 1	Retrieval 2
Prescan list presentation	Blocked list	Unrelated category–exemplar pairs
Cueing at retrieval	'Next'	Category
Performance (per 16-item list)	11.2 (1.1)	14.2 (0.8)

Average number of correct items per pair (SD).

Table 2 Brain regions activated in association with retrieval

	Retrieval 1	Retrieval 2
Right DLPFC (BA 9/46)	36, 44, 24 (5.3)	38, 38, 24 (3.5)
Right VLPFC (BA 45)	52, 18, 12 (2.9)	38, 12, 0 (4.8)
Precuneus (left and right) (BA 7)	-24, -74, 36 (5.6) 28, -76, 36 (4.8)	-16, -70, 36 (4.3) 12, -72, 40 (3.2)
Right anterior cingulate cortex (BA 24)	–	6, 24, 16 (4.5)
Thalamus (bilateral)	–	0, -18, 8 (4.9)

Coordinates (Talairach and Tournoux, 1988) of voxels of maximal activation are given together with Z scores (in brackets). Activations produced by contrasting the Retrieval 1 and the Retrieval 2 tasks with their repetition control tasks are shown. Direct comparisons of the two types of retrieval are described in the text and in Fig. 1. Statistical thresholds were set at $P < 0.01$ ($Z = 2.33$) in view of the constrained analysis used. DLPFC = dorsolateral PFC; VLPFC = ventrolateral PFC; BA = Brodmann area.

Table 3 Brain regions activated when Retrieval 1 and Retrieval 2 were contrasted

Region	Coordinates	Z score
(A) Regions showing significantly greater activity in Retrieval 1 (Retrieval 1 vs Retrieval 2)		
Right DLPFC (BA 9/46)	36, 34, 32 42, 26, 32	3.6 3.5
Medial parietal region (BA 7)	24, -78, 36	3.3
No additional areas seen in unmasked contrast		
(B) Regions showing significantly greater activity in Retrieval 2 (Retrieval 2 vs Retrieval 1)		
Right insula/ventrolateral PFC	22, 8, 0 36, 18, 0 34, 24, 8	3.6 3.1 2.4
Posterior cingulate/medial parietal cortex	-2, -48, 28 8, -50, 24	3.2 2.6
Additional areas seen in unmasked contrast		
Left middle temporal gyrus	-54, -32, -4	4.6
Right superior temporal/ inferior parietal region	40, -14, 24 60, -32, 8	3.5 3.2
Medial ventral PFC	-10, 56, 4	4.4

Statistical thresholds were set at $P < 0.01$ ($Z = 2.33$).

of structure supplied to subjects at these stages, and found no significant difference between the left and right frontally damaged groups. However, the observation that repetition

errors in free recall occur most in patients with right dorsolateral frontal damage (Stuss *et al.*, 1994) is suggestive of a role for this region in monitoring/checking processes at

retrieval. The existence of a syndrome where confabulatory recognition difficulties occur in patients whose lesions principally affect the right PFC is also consistent with the suggestion of a critical role for this region in monitoring (Delbecq-Derouesne *et al.*, 1990; Schacter *et al.*, 1996b).

Functional neuroimaging is well suited to disaggregating and localizing the stages and processes of normal human memory. The current study addressed the hypothesis that the right PFC is important for a monitored memory search. We examined brain activity during verbal retrieval, using PET to differentiate between activity associated with the use of a prelearned structure to guide recall and that of a reference task in which recall was guided by the experimenter. From our earlier functional imaging study, we predicted that the right PFC activity would be greater in the task requiring a monitored search. To allow direct comparison with neuropsychological data, we used experimental paradigms based on the tests used on frontal lobe patients (Incisa della Rochetta and Milner, 1993; Gershberg and Shimamura, 1995). The paradigm also allowed a comparison with our study of the use of organization at encoding (Fletcher *et al.*, 1998).

Method

Subjects

Six healthy, male, right-handed subjects (mean age 29.5 years, age range 19–56 years) were scanned. Each subject underwent 12 separate scans. No subject had a history of past psychiatric or neurological illness, and all gave informed consent. The studies were approved by the combined ethics committee of the National Hospital for Neurology and Neurosurgery and the Institute of Neurology, London, and the Administration of Radiation Safety Advisory Committee (UK). Scans of the distribution of $H_2^{15}O$ were obtained using a Siemens/CPS ECAT EXACT HR+ (model 962) PET scanner operated in high sensitivity 3D mode. Subjects received a total of 350 MBq of $H_2^{15}O$ over 20 s through a forearm cannula. Data were acquired over 90 s for each scan. Attenuation-corrected data were reconstructed into 63 image planes, with a resulting resolution of 6 mm at full width at half maximum.

Retrieval tasks

Subjects performed two distinct episodic memory tasks (Table 1).

Retrieval 1: internally cued retrieval

Study lists were presented 5 min prior to scanning. Each list consisted of 16 words. Lists were structured, with an overall heading and four subheadings, each subheading containing four unique items. The list was presented in a blocked manner, the subjects already having been alerted to the heading and subheadings. During scanning, responses were

paced by prompting subjects with the word 'next' once every 4 s, and each time subjects were required to produce a word from the prescan study list. Prior to the study, subjects were instructed that using the list structure to guide retrieval would help their overall performance.

Retrieval 2: externally cued retrieval

Study lists were presented 5 min prior to scanning. Each list consisted of 16 paired associate words, each pair consisting of a category and an exemplar. During scanning, subjects were presented with categories at a rate of once per 4 s and were required to generate the relevant exemplar.

Control tasks

For the Retrieval 1 control, subjects repeatedly heard the word 'next' at an identical rate to the activation task, and they were simply required to repeat it each time. For the Retrieval 2 control, subjects were presented with items comparable to those heard in the experimental condition (i.e. categories and exemplars) at the same rate, and were required to repeat each one.

Thus, across the 12 scans, each task (Retrieval 1, Retrieval 2 and two baseline conditions) was presented three times.

Data analysis

Images were reconstructed into 63 planes, using a Hanning filter, resulting in a 6.4 mm transaxial and 5.7 mm axial resolution (full width at half maximum). The data were analysed by statistical parametric mapping (SPM) (Friston *et al.*, 1995a, 1995b) using SPM software from the Wellcome Department of Cognitive Neurology, London (<http://www.fil.ion.ucl.ac.uk>) implemented in Matlab (Mathworks, Sherborn, Mass., USA). After initial realignment, the scans were transformed into standard stereotaxic space (Talairach and Tournoux, 1988). The scans were smoothed using a Gaussian filter set at 12 mm full width at half maximum. The regional cerebral blood flow equivalent measurements were adjusted to a global mean of 50 ml/dl/min. A blocked (by subject) analysis of covariance model was fitted to the data at each voxel, with a condition effect for each of the two memory retrieval and the two repetition control conditions, using global CBF and retrieval performance data as a confounding covariate. Predetermined contrasts of the condition effects of each voxel were assessed using the t statistic, giving a statistic image $[SPM_{(t)}]$ transformed into an $[SPM_{(Z)}]$ for each contrast. The chosen threshold of significance for main effects of conditions was $P < 0.001$ (uncorrected for multiple comparisons). An uncorrected threshold was chosen because of our *a priori* hypothesis with regard to the prefrontal changes.

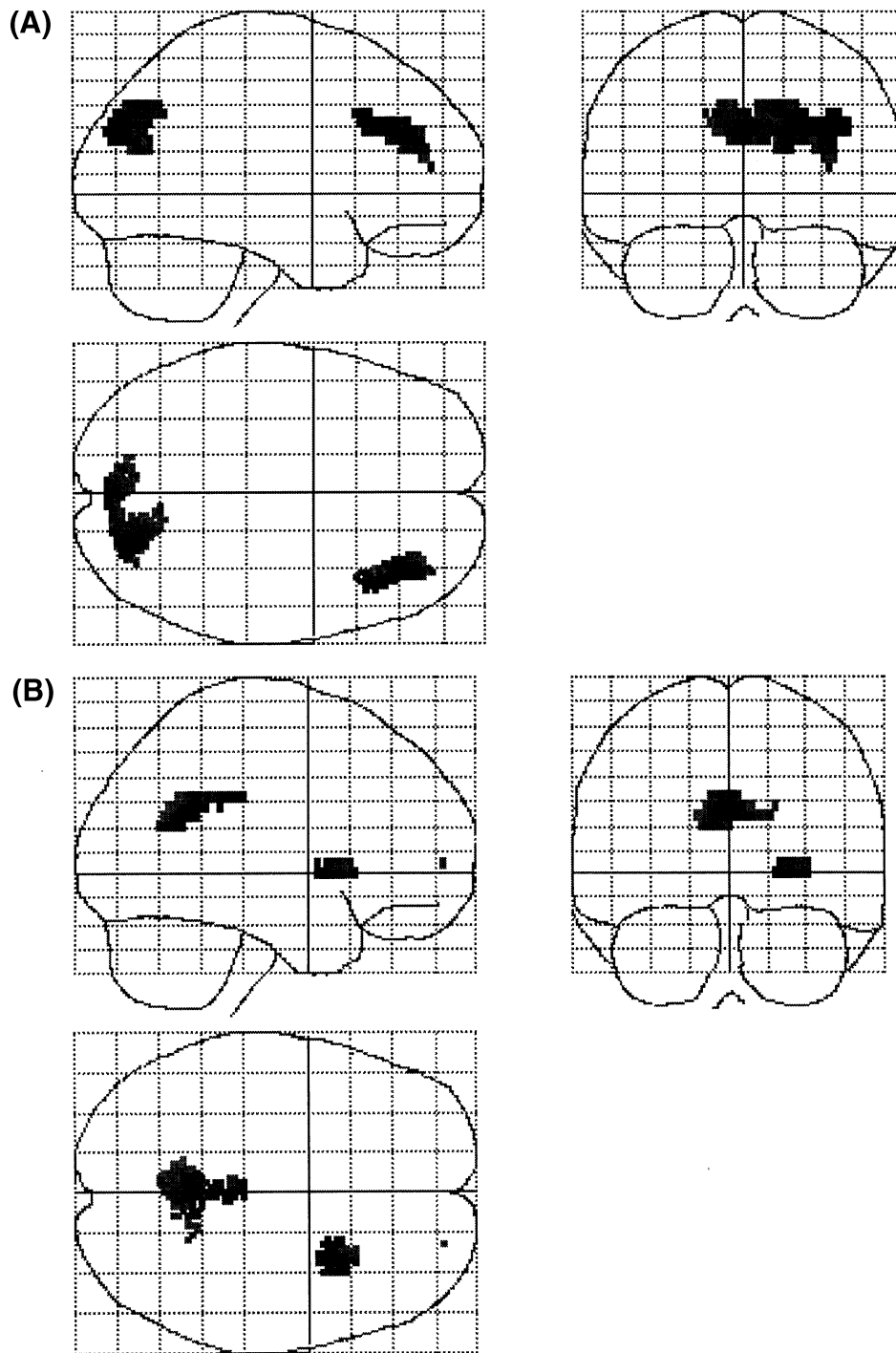


Fig. 1 Retrieval-related activations. SPMs showing direct comparisons between the Retrieval 1 and Retrieval 2 conditions. The activations are seen as orthogonally viewed 'glass brains', from the right (top left image), from behind (top right image) and from above (bottom left image). In both cases the analyses were constrained to the subset of voxels identifying a retrieval system identified by our previous study (Fletcher *et al.*, 1995). The contrast identifying this system was thresholded at $P < 0.001$ (uncorrected) and the contrasts between Retrieval 1 and Retrieval 2 were set at $P < 0.01$ (uncorrected). **A** shows regions significantly more active in the internally cued retrieval condition when it is compared directly with the externally cued condition. The right dorsolateral PFC and the posterior superior region of the medial parietal cortex are seen. **B** shows regions significantly more active in the externally cued retrieval condition when it is compared directly with the internally cued condition. Here the insula/ventral PFC and the posterior cingulate/anterio-inferior region of medial parietal cortex are seen to be active.

Results

Memory performance data

Retrieval performance during scanning is shown in Table 1. As can be seen, performance was significantly less in the internally cued retrieval condition ($P < 0.01$). A measure of the degree to which subjects utilized the semantic categorization within the internally cued retrieval list was provided by recording the number of unforced category shifts (since there were four categories covered in each list, at least three category shifts were required during recall). The high degree to which subjects used categorization as an aid to retrieval was evidenced by the low number of unforced category shifts (mean = 0.3). We performed simulations of random list generation from a similar 4×4 structure, and this indicated that, in all cases, subjects were producing far fewer category shifts than would be expected if they were failing to use the list structure.

Functional neuroimaging results

We initially performed a combined comparison of the two memory retrieval conditions with their respective repetition control tasks (i.e. all retrieval minus all baseline conditions). This showed activation of the right, but not the left, PFC and medial parietal cortex. This accords with our previous findings (Shallice *et al.*, 1994). In addition, the two types of retrieval were contrasted separately with their respective baseline, repetition conditions. Retrieval 1 minus its baseline showed no additional areas of activation to the right PFC and medial parietal cortex. Retrieval 2 minus its baseline was associated with additional activation of the anterior cingulate cortex and the thalamus. These results are shown in Table 2.

A second, and more crucial, comparison contrasted the two different types of retrieval directly, i.e. Retrieval 1 (internally cued) versus Retrieval 2 (externally cued). In order to do this, we selected the subset of voxels which our previous data (Shallice *et al.*, 1994) had shown to be associated more purely with the demands of an episodic memory retrieval task *per se*. The subset of voxels was defined using the 'masking' option in SPM such that one contrast defines the space within which another contrast is implemented. In other words, we used the brain system delineated by our previous work to constrain the analysis. Such an approach can improve the sensitivity of analysis while reducing the risk of false-positive results. This constraint enables us to address more specific questions about dissociations within this system in response to differing task demands. With regard to the prefrontal activation, this analysis revealed a significantly greater right dorsolateral PFC (DLPFC) (roughly corresponding to Brodmann's areas 9/46) activation associated with Retrieval 1. The reverse comparison showed that a more ventromedial region, lying in the region of Brodmann area 44 and the insula, was significantly more active during Retrieval 2 (these results are

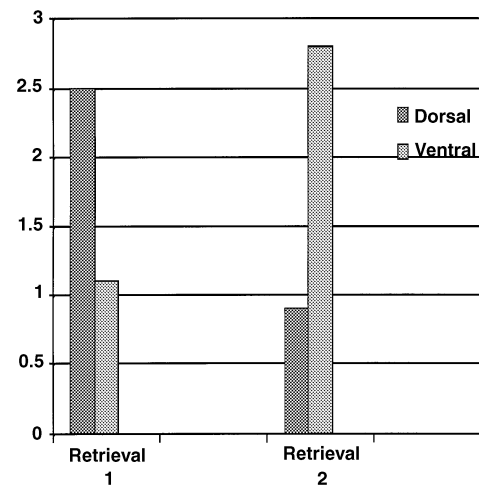


Fig. 2 A graphic representation of activation in these two frontal regions [coordinates (Talairach and Tournoux, 1988) $x, y, z = 36, 36, 32$ for the dorsolateral region; $30, 12, 0$ for insula/ventral PFC region] when the Retrieval 1 and Retrieval 2 conditions are compared separately with their respective control tasks. As can be seen, both are active to a significant extent when the retrieval conditions are compared with these baselines, the dorsal region showing relatively (and significantly) greater activation in Retrieval 1 and the insula/ventral regions showing greater activation in Retrieval 2.

shown in Fig. 1 and represented graphically in Fig. 2). This PFC dissociation was not the result of differential performance across the two conditions, as entering performance level as a covariate did not affect the observed activation in these regions.

In addition to the regional dissociation in right PFC activations, the other region widely implicated in memory retrieval, a medial posterior parietal region (Brodmann area 7/31), also showed activation differences as a function of whether retrieval was internally or externally cued. In association with Retrieval 1, there was significantly greater activity in a more dorsal and posterior region. The Retrieval 2 condition showed significantly greater activity in a more anteroventral region, at the transition between the part of the medial parietal area (referred to as the precuneus) and the posterior cingulate cortex. Results of the comparisons between Retrieval 1 and Retrieval 2 conditions are summarized in Table 3.

In view of the fact that, as Table 2 indicates, Retrieval 2, but not Retrieval 1, was associated with activation of the thalamus and the cingulate cortex, when compared with its baseline condition, and since neither of these regions fell within the area defined by the mask, we also performed the same analyses (Retrieval 1 minus Retrieval 2 and Retrieval 2 minus Retrieval 1) unmasked. All results which survived an uncorrected threshold of $P < 0.001$ are shown in Table 3. For the former contrast, no additional regions were identified. For the latter contrast (Retrieval 2 minus Retrieval 1) additional activations were seen in the medial and superior temporal gyri extending into the parietal lobes bilaterally, and in the medial ventral PFC. These regions have been

implicated in previous studies of memory (Grasby *et al.*, 1993, 1994; Fletcher *et al.*, 1995a), in which they have shown relative deactivations compared with the baseline condition. It may therefore be the case that, for this contrast, these additional activations reflect a greater deactivation in Retrieval 1 rather than an activation in Retrieval 2. Interpretation of the behavioural implications of these activations must be highly speculative since the functional significance of these relative deactivations is unclear. Our discussion will consequently focus on those regional activations constrained by the masking since, in these cases, we can be confident that, relative to baseline, there is significant activation.

Discussion

The findings support our hypothesis that the right prefrontal activation found at memory retrieval reflects executive processes that optimize memory function at this stage. The creation of the organizational structure at encoding emphasizes the abstraction of meaning of studied items. At retrieval, no such abstraction is necessary and the emphasis is on the use of this previously learned structure to internally control and monitor the retrieval process. The findings suggest that the dorsolateral region of the right PFC is sensitive to such a demand, whereas in the externally cued condition, when retrieval specifications for each item are provided by the experimenter, dorsolateral activity is reduced and ventrolateral activity augmented.

Activation of the right PFC (dorsolateral and ventrolateral) was seen when both retrieval conditions were compared with baseline, repetition tasks. There have been suggestions from the neuropsychological literature that retrieval emphasizing organizational processes makes more demands on the left than on the right frontal lobe (Incisa della Rochetta and Milner, 1993). However, this evidence is limited in that it is much more difficult to distinguish an effect operating at encoding from one operating at retrieval when neuropsychological, as opposed to functional neuroimaging, techniques are used. For the encoding of an organizational structure, the left frontal lateralization is strongly supported (Fletcher *et al.*, 1998). It is striking, with regard to the present experiment, that manipulating monitoring demands at retrieval results in differential activations only on the right, and that the left–right episodic memory PFC lateralization is therefore maintained.

The behavioural data strongly indicated that subjects were using the prelearned list structure during retrieval insofar as the number of category shifts was much less than would be expected if the subjects were not using such organizational structures. All subjects reported that they engaged in careful monitoring of their list recall, checking backwards and forwards to avoid omissions and repetitions. Evidence supporting this explanation—that the right PFC activity can be related to monitoring processes—comes from both

neuropsychology (Stuss *et al.*, 1994) and recent functional imaging work (Fletcher *et al.*, 1996).

An unexpected finding is the double dissociation between activation of the right dorsolateral and the insula/ventrolateral prefrontal regions. Previous PET studies of episodic memory retrieval have not described a ventral–dorsal dissociation, the majority of studies showing activation in both regions (Tulving *et al.*, 1994; Fletcher *et al.*, 1995a; Kapur *et al.*, 1995; Haxby *et al.*, 1996). This is unsurprising given that these studies did not seek to fractionate retrieval into subprocesses. A study of the influence of monitoring demands on a spatial working memory task, however, has shown evidence for regional specificity within the PFC (Owen *et al.*, 1996a), the greatest degree of monitoring being associated with a dorsal activation.

In our study, both areas showed significant activation when each of the memory tasks was compared with its control. However, in the direct comparison of the two types of retrieval, Retrieval 1 showed significantly greater right DLPFC activation and Retrieval 2 showed significantly greater ventral PFC activation. Retrieval 2, unlike Retrieval 1, did not require that subjects refer to items that had already been retrieved or were yet to be retrieved. However, Retrieval 2 showed significantly greater ventral/insula activity. One possible explanation is that retrieval specifications (determined by the cue which provides the subject with a memory search ‘description’) (Burgess and Shallice, 1996) change more frequently in Retrieval 2 than in Retrieval 1, and this may be reflected in greater ventral PFC activation.

While caution is necessary when comparing human verbal memory tasks with findings from animals, we suggest that this observation is consistent with theoretical perspectives derived from monkey experiments, where it has been suggested that the ventrolateral region is concerned with acting directly upon the products of memory retrieval, particularly in relation to contextual operations (e.g. salience, temporal sequence). It has been argued that the deficits in mnemonic tasks produced by ventrolateral lesions arises because of disruption of judgements on mnemonic information (Petrides, 1994, 1995). The dorsolateral region, on the other hand, is held to be required for ‘complex, high-level planning’ of intended acts and the monitoring of the retrieved information within working memory (Petrides, 1994). Thus, a lesion to the DLPFC in monkeys leads to profound deficits in tasks requiring that animals monitor their own responses in order to guide their next response, but does not affect the animals’ performance on delayed response and delayed alternation tasks (Petrides, 1995). With regard to functional imaging studies, the right prefrontal activation at retrieval has been discussed in terms of a non-specific retrieval attempt or ‘set’ (Kapur *et al.*, 1995; Nyberg *et al.*, 1995; Schacter *et al.*, 1996a). Our data, however, indicate that its role can be highly process-specific.

A further, retrieval-related dissociation was noted in the medial parietal/posterior cingulate region. Specifically, a posterior and more dorsal region showed significantly greater

activation during the internally cued (Retrieval 1) condition, whereas an anterior and inferior region showed greater activation during the externally cued (Retrieval 2) condition. The focus of maximal activity in the latter condition was actually located in the posterior cingulate cortex, spreading upwards into the medial parietal cortex. Although the medial parietal region has been implicated in a number of functional imaging studies of memory retrieval (Squire *et al.*, 1992; Shallice *et al.*, 1994; Tulving *et al.*, 1994; Fletcher *et al.*, 1996; Buckner *et al.*, 1996), its function has yet to be clarified. One suggestion is that it plays a role in the use of imagery as a memory retrieval strategy (Grasby *et al.*, 1993; Fletcher *et al.*, 1995). This is supported by the finding of a selective activation of this region during recall of imageable material, compared with abstract material (Fletcher *et al.*, 1996). However, a further study which also varied this component did not find differential activity (Buckner *et al.*, 1996). This latter study did, however, suggest that the region shows a functional dissociation, a posterior part being active in association with a recall task while an anterior part showed a relative deactivation. Our finding thus adds to the functional neuroimaging evidence that this region consists of functionally separable parts. However, the significance of this unpredicted observation can only be speculated upon. Moreover, it is worth restating that, as with the dorsolateral PFC and the insula/ventrolateral PFC, both parietal regions were found to be relatively activated when compared with their baseline control tasks (unlike the findings of Buckner *et al.*, 1996). It was only in response to the varying retrieval demands that activity in different parts of the system predominated. Such a finding highlights the need to devise ever more specific tasks in order to fractionate the components of memory retrieval systems.

The findings from this study and the complementary encoding experiment (Fletcher *et al.*, 1998) suggest that the prefrontal cortex has multiple roles in memory. The data directly address the widely reported encoding–retrieval lateralization between prefrontal cortices by providing evidence on the nature of the contrasting executive processes that predominate at encoding and retrieval stages. Our evidence addresses a highly consistent functional imaging finding, and we conclude that at encoding the production of an organizing structure is associated with left DLPFC activity, whereas at retrieval the use of such a structure to guide retrieval is associated with right DLPFC activity. Further, tasks which emphasize different types of retrieval processes are reflected in activation of different right prefrontal regions.

Acknowledgements

P.C.F., C.D.F., R.S.J.F. and R.J.D. are supported by the Wellcome Trust. We thank Andrew Holmes for statistical advice.

References

Buckner RL, Raichle ME, Miezin FM, Petersen SE. Functional anatomic studies of memory retrieval for auditory words and visual pictures. *J Neurosci* 1996; 16: 6219–35.

Burgess PW, Shallice T. Confabulation and the control of recollection. *Memory* 1996; 4: 359–411.

Delbecq-Derouesne J, Beauvois MF, Shallice T. Preserved recall versus impaired recognition: a case study. *Brain* 1990; 113: 1045–74.

Fletcher PC, Frith CD, Grasby PM, Shallice T, Frackowiak RS, Dolan RJ. Brain systems for encoding and retrieval of auditory–verbal memory: an in vivo study in humans. *Brain* 1995; 118: 401–16.

Fletcher PC, Shallice T, Frith CD, Frackowiak RS, Dolan RJ. Brain activity during memory retrieval: the influence of imagery and semantic cueing. *Brain* 1996; 119: 1587–96.

Fletcher PC, Frith CD, Rugg MD. The functional neuroanatomy of episodic memory. *Trends Neurosci* 1997; 20: 213–8.

Fletcher PC, Shallice T, Dolan RJ. The functional roles of prefrontal cortex in episodic memory. I. Encoding. *Brain* 1998; 122: 000–000.

Friston KJ, Ashburner J, Frith CD, Poline J-B, Heather JD, Frackowiak RS. Spatial registration and normalization of images. *Hum Brain Mapp* 1995a; 3: 165–89.

Friston KJ, Holmes AP, Worsley KJ, Poline JB, Frith CD, Frackowiak RS. Statistical parametric maps in functional imaging: a general linear approach. *Hum Brain Mapp* 1995b; 2: 189–210.

Gershberg FB, Shimamura AP. Impaired use of organizational strategies in free recall following frontal lobe damage. *Neuropsychologia* 1995; 13: 1305–33.

Grasby PM, Frith CD, Friston KJ, Bench C, Frackowiak RS, Dolan RJ. Functional mapping of brain areas implicated in auditory–memory function. *Brain* 1993; 116: 1–20.

Grasby PM, Frith CD, Friston KJ, Simpson J, Fletcher PC, Frackowiak RS, et al. A graded task approach to the functional mapping of brain areas implicated in auditory–verbal memory. *Brain* 1994; 117: 1271–82.

Haxby JV, Ungerleider LG, Horwitz B, Maisog JM, Rapoport SI, Grady CL. Face encoding and recognition in the human brain. *Proc Natl Acad Sci USA* 1996; 93: 922–7.

Incisa della Rocchetta A, Milner B. Strategic search and retrieval inhibition: the role of the frontal lobes. *Neuropsychologia* 1993; 31: 503–24.

Kapur S, Craik FI, Jones C, Brown GM, Houle S, Tulving E. Functional role of the prefrontal cortex in retrieval of memory: a PET study. *Neuroreport* 1995; 6: 1880–4.

Moscovitch M. Confabulation and the frontal systems: strategic versus associative retrieval in neuropsychological theories of memory. In: Roediger HL, Craik FIM, editors. *Varieties of memory and consciousness: essays in honor of Endel Tulving*. Hillsdale (NJ): Lawrence Erlbaum; 1989. p. 133–60.

Norman DA, Bobrow DG. Descriptions: an intermediate stage in memory retrieval. *Cognit Psychol* 1979; 11: 107–23.

Nyberg L, Tulving E, Habib R, Nilsson LG, Kapur S, Cabeza R, et al. Functional brain maps of retrieval mode and recovery of episodic information. *Neuroreport* 1995; 7: 249–252.

Nyberg L, McIntosh AR, Cabeza R, Habib R, Houle S, Tulving E. General and specific brain regions involved in encoding and retrieval

- of events: what, where, and when. *Proc Natl Acad Sci USA* 1996; 93: 11280–5.
- Owen AM, Evans AC, Petrides M. Evidence for a two stage model of spatial working memory processing within the lateral frontal cortex: a positron emission tomography study. *Cereb Cortex* 1996a; 6: 31–8.
- Owen AM, Milner B, Petrides M, Evans AC. Memory for object features versus memory for object location: a positron emission tomography study of encoding and retrieval processes. *Proc Natl Acad Sci USA* 1996b; 93: 9212–7.
- Petrides M. Frontal lobes and working memory: evidence from investigations of the effects of cortical excisions in non-human primates. In: Boller F, Grafman J, editors. *Handbook of neuropsychology*, Vol. 9. Amsterdam: Elsevier; 1994. p. 59–82.
- Petrides M. Impairments on non-spatial self-ordered and externally ordered working memory tasks after lesions to the mid-dorsal part of the lateral frontal cortex in the monkey. *J Neurosci* 1995; 15: 359–75.
- Rugg MD, Fletcher PC, Frith CD, Frackowiak RS, Dolan RJ. Differential activation of the prefrontal cortex in successful and unsuccessful memory retrieval. *Brain* 1996; 119: 2073–83.
- Schacter DL, Alpert NM, Savage CR, Rauch SL, Albert MS. Conscious recollection and the human hippocampal formation: evidence from positron emission tomography. *Proc Natl Acad Sci USA* 1996a; 93: 321–5.
- Schacter DL, Curran T, Galluccio L, Milberg WP, Bates JF. False recognition and the right frontal lobe: a case study. *Neuropsychologia* 1996b; 34: 793–808.
- Shallice T. *From neuropsychology to mental structure*. Cambridge: Cambridge University Press, 1988.
- Shallice T, Fletcher P, Frith CD, Grasby P, Frackowiak RS, Dolan RJ. Brain regions associated with acquisition and retrieval of verbal episodic memory. *Nature* 1994; 368: 633–5.
- Squire LR, Ojemann JG, Miezin FM, Petersen SE, Videen TO, Raichle ME. Activation of the hippocampus in normal humans: a functional anatomical study of memory. *Proc Natl Acad Sci USA* 1992; 89: 1837–41.
- Stuss DT, Alexander MP, Palumbo CL, Buckle L, Sayer L, Pogue J. Organizational strategies of patients with unilateral or bilateral frontal lobe injury in word list learning tasks. *Neuropsychologia* 1994; 8: 355–73.
- Talairach J, Tournoux P. *Co-planar stereotaxic atlas of the human brain*. Stuttgart: Thieme; 1988. p. 1–122.
- Tulving E, Kapur S, Markowitsch HJ, Craik FI, Habib R, Houle S. Neuroanatomical correlates of retrieval in episodic memory: auditory sentence recognition [see comments]. *Proc Natl Acad Sci USA* 1994; 91: 2012–5. Comment in: *Proc Natl Acad Sci USA* 1994; 91: 1989–91.

Received December 16, 1997. Accepted March 10, 1998