

# Brain Activity Underlying Encoding and Retrieval of Source Memory

Selene Cansino, Pierre Maquet<sup>1,2</sup>, Raymond J. Dolan<sup>2</sup> and Michael D. Rugg<sup>3</sup>

Laboratory of NeuroCognition, Faculty of Psychology, National Autonomous University of Mexico, Mexico City, Mexico, <sup>1</sup>Cyclotron Research Center, University of Liege, Liege, Belgium, <sup>2</sup>Wellcome Department of Cognitive Neurology, Institute of Neurology and <sup>3</sup>Institute of Cognitive Neuroscience and Department of Psychology, University College London, UK

**Neural activity elicited during the encoding and retrieval of source information was investigated with event-related functional magnetic resonance imaging (efMRI). During encoding, 17 subjects performed a natural/artificial judgement on pictures of common objects which were presented randomly in one of the four quadrants of the display. At retrieval, old pictures were mixed with new ones and subjects judged whether each picture was new or old and, if old, indicated in which quadrant it was presented at encoding. During encoding, study items that were later recognized and assigned a correct source judgement elicited greater activity than recognized items given incorrect judgements in a variety of regions, including right lateral occipital and left prefrontal cortex. At retrieval, regions showing greater activity for recognized items given correct versus incorrect source judgements included the right hippocampal formation and the left prefrontal cortex. These findings indicate a role for these regions in the encoding and retrieval of episodic information beyond that required for simple item recognition.**

## Introduction

Episodic memory can be operationalized as memory for an item along with the spatio-temporal context in which the item was studied. According to some authors, there is a qualitative distinction between the forms of memory that support recognition of an item that is accompanied as opposed to unaccompanied by contextual information. Whereas the former is truly episodic, the latter can rely upon an acontextual sense of familiarity that is mediated by neurally and functionally distinct processes (Mandler, 1980; Jacoby and Kelley, 1992; Gardiner and Java, 1993; Brown and Aggleton, 2001). These two forms of memory are referred to as 'recollection' and 'familiarity', respectively. By contrast, other authors have proposed that the difference between recognition with and without retrieval of study context is merely quantitative and depends on the amount of contextual information retrieved (Haist *et al.*, 1992; Johnson *et al.*, 1993; Hirshman and Master, 1997; Donaldson, 1996). While not denying that memory with and without contextual retrieval may be phenomenologically distinct and have different behavioural consequences, this 'single process' view holds that the two forms of memory are better conceived as lying along a continuum rather representing dichotomous processes.

Regardless of whether one adopts a dual- or single-process framework, the nature and amount of contextual information that is encoded along with item information are important variables in determining patterns of performance on episodic memory tests. For example, in the 'remember/know' procedure (Tulving, 1985), subjects are required to endorse recognized study items according to whether, on the basis of introspection, recognition was ('remember' response) or was not ('know' response) associated with retrieval of information about the item's encoding context. Presumably, it is items belonging to those study episodes where relatively rich contextual information was encoded that are most likely subsequently to be

endorsed as 'remembered'. More pertinent to the present study, in tests of source memory subjects are required not only to discriminate studied from nonstudied items, but also to judge in which of two or more encoding contexts (sources) the item was studied. Clearly, source judgements will fail if insufficient or inappropriate contextual information is encoded at the time of study.

One aim of the present experiment was to address the question of whether it is possible to identify neural activity at the time of study that is associated with the encoding of contextual information. The question was addressed by using event-related functional magnetic resonance imaging (efMRI) to search for so-called 'subsequent memory effects' in a source memory task. In the subsequent memory procedure, event-related responses are obtained for each of a series of study items and subsequently segregated according to whether items are 'remembered' or 'forgotten' on a subsequent memory test. Previous studies using this approach have demonstrated that a number of brain regions, notably in the prefrontal cortex and medial temporal lobe, show greater activity for items that are subsequently remembered as opposed to forgotten (Brewer *et al.*, 1998; Wagner *et al.*, 1998; Kirchoff *et al.*, 2000; Baker *et al.*, 2001; Buckner *et al.*, 2001; Otten *et al.*, 2001; Otten and Rugg, 2001). In the present context, two of these studies are of particular relevance. Brewer *et al.* (Brewer *et al.*, 1998) required subjects to study complex scenes and subsequently tested memory for these items with a remember/know procedure. Relative to items subsequently forgotten and those that attracted a 'know' response, they reported that items receiving 'remember' judgements elicited greater activity in bilateral parahippocampal and right prefrontal cortex. The finding of greater activity for 'remembered' versus 'known' items suggests that these regions participated in the encoding of more than mere item information. Since Brewer *et al.* restricted their image acquisition to only four slices, it was not possible to determine whether other regions, notably posterior areas likely involved in the perceptual analysis of the study items, also showed subsequent memory effects.

Henson *et al.* (Henson *et al.*, 1999b) also employed a remember/know procedure at test, but used words as items. They reported that study items attracting subsequent remember responses elicited greater activity in left ventral and dorsolateral prefrontal cortex and left medial parietal cortex than did words given a know response.

Together, these studies (Brewer *et al.*, 1998; Henson *et al.*, 1999b) suggest that the encoding of item plus contextual information, as opposed to item information alone, is associated with increased activity in a variety of regions, notably the prefrontal cortex. One difficulty with this interpretation, however, arises from the employment in these studies of the remember/know procedure, which relies on introspective report to separate trials with and without contextual retrieval. A second difficulty

concerns the degree to which the subsequent memory contrast between remembered and know responses confounded contextual retrieval with item memory. In the case of Henson *et al.* (Henson *et al.*, 1999b), ~50% of old items received remember responses, whereas ~25% received know responses. The rates of remember and know responding for false alarms were 2 and 14%, respectively. Viewed from the perspective of either of the two most commonly employed approaches to the interpretation of remember/know data – the single process signal detection model (Donaldson, 1996) and the independence model (Yonelinas and Jacoby, 1995) – these data indicate that item memory was weaker for those items attracting a know response than for those endorsed as remembered and that recognition accompanied by a know response was more likely to be based on a ‘lucky guess’ than on veridical memory. The subsequent memory contrast between remembered and known items was therefore confounded with strength of item memory. The same problem may or may not have afflicted the study of Brewer *et al.* (Brewer *et al.*, 1998), but as false alarm rates were not reported this cannot be determined.

The present study builds on these previous findings by employing an objective method for determining whether recognition memory was or was not accompanied by retrieval of contextual information and by employing a task designed to minimize the confound between unsuccessful contextual retrieval and unsuccessful item memory discussed above. We achieved these goals by employing as test items perceptually rich and distinctive pictorial images (see Fig. 1), thereby ensuring a high level of item memory. To segregate items according to the amount of contextual information retrieved at test we employed a source memory procedure. In the study phase, subjects were presented with items in one of four spatial locations. At test, they were required to determine whether each item presented was new or old and, if old, in which location it had been presented at study. Items which were correctly recognized, but for which source memory failed, were considered to have been associated with the retrieval of less contextual information than items for which source memory was accurate. At issue was whether, as previously (Brewer *et al.*, 1998; Henson *et al.*, 1999b), it would be possible to find brain regions in which activity was greater for correctly recognized test items subsequently accorded accurate, as opposed to inaccurate source judgements. By using a four-choice source memory task rather than the more conventional two-choice procedure, we attempted to ensure adequate power for this contrast by reducing the probability that a correct source judgement could arise by chance ( $P = 0.25$  rather than  $P = 0.5$ ).

A second aim of this experiment was to investigate the neural correlates of successful versus unsuccessful contextual retrieval. Other studies (Henson *et al.*, 1999a; Nolde *et al.*, 1998; Ranganath *et al.*, 2000; Rugg *et al.*, 1999) have investigated the neural correlates of source memory by task-wise contrasts that identified differences in activity during performance of source versus yes/no recognition judgements. The findings from these studies do not speak to the question addressed here; namely, where does item-evoked activity elicited in a source memory task differ according to the accuracy of the associated source judgement? However, two previous studies (Henson *et al.*, 1999b; Eldridge *et al.*, 2000) addressed this question by contrasting activity elicited by old words accorded remember as opposed to know responses. In both studies, greater activity was found for remembered items in bilateral prefrontal and left lateral parietal cortex, as well as in medial parietal/posterior cingulate regions. In addition, in the Eldridge study greater activity was also

reported in the hippocampal region. For the reverse contrast, both studies reported increased activity in anterior cingulate and right prefrontal cortex. As noted already, in the Henson *et al.* study these contrasts likely confounded recognition with and without contextual retrieval with strength of recognition memory. This problem is present to an even greater degree in the case of Eldridge *et al.*; whereas rates of remember responding to old and new items were ~42 and 0.01%, respectively, some 31% of old items were endorsed as ‘known’, along with 33% of new items.

In the present study, we were able to perform contrasts analogous to those reported previously (Henson *et al.*, 1999b; Eldridge *et al.*, 2000), but using a procedure providing an objective measure of contextual retrieval and a high level of item recognition. At issue is whether the effects reported in these previous studies reflect, as the authors assumed, differences between recognition with and without retrieval of context, or whether instead they are more likely to reflect the neural correlates of relatively strong versus weak recognition memory [see Rugg and Henson (Rugg and Henson, 2002) for a review and discussion of these correlates].

## Materials and Methods

### Subjects

Twenty-two healthy right-handed subjects were paid for participating in the study after providing informed consent. The experiment was approved by the joint Medical Ethics Committee of the Institute of Neurology and the National Hospital of Neurology and Neurosurgery. The data from five subjects were excluded from the analysis: two of them because their performance was too high to allow a comparison of activity associated with incorrect and correct responses, and three because their source accuracy was near-chance. Mean age of the 17 remaining subjects (two males) was 24.6 years (range 20–37) and mean schooling was 14.6 years of education (range 13–18).

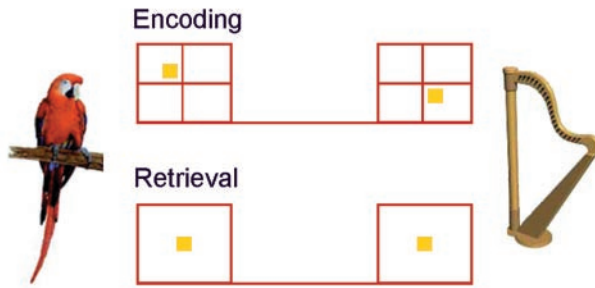
### Stimuli

A total of 150 colour images of common objects were employed, 15 of which were used during a training session. Half of the images represented natural objects and the rest artificial objects. From the pool of 135 images, different sets of 90 images were selected for each subject to be used during the encoding session, while during the retrieval session the complete pool of 135 images was employed. Each stimulus subtended horizontal and vertical angles ranging between 2.9 and 4.3°.

### Procedure

The experiment consisted of an encoding and a retrieval session. Scanning took place in both sessions. Before entering the scanner, subjects participated in a training session when they performed brief versions of the encoding and retrieval tasks. During the training session, subjects were familiarized with the response panel that was used during scanning; this consisted of five push-buttons: one of the buttons was located in the lower part of the panel to be pressed by the thumb and the other four buttons were arranged in two rows of two keys each. The left keys of each row were accessed by the index finger while the right keys were pressed by the middle finger. This four-button array represented the four screen locations where images were presented during encoding. During the encoding task only the two keys of the lower row were employed, while in the retrieval task all the keys in the panel were used (see below).

The encoding and retrieval tasks lasted ~6 and 9 min, respectively. The interval between the tasks was ~4 min. During encoding, 90 stimuli were presented, while during the retrieval task the same 90 stimuli were presented randomly intermixed with 45 new images. In both tasks the stimuli were randomly mixed with 45 null events. During the null events, the fixation point remained on the screen and subjects merely experienced a delay before the next trial. These events permitted the comparison of the blood oxygenation level dependent (BOLD) responses elicited by each class of experimental event against a no-stimulus baseline. After the two scanning sessions, a structural scan was acquired.



**Figure 1.** Two examples of the stimuli employed in the task. The red squares represent the screen and the small yellow squares represent the position of the stimuli. During encoding the display was divided in four quadrants and the stimuli were presented randomly in one of the quadrants, while during retrieval they were presented at the centre of the display.

### Source Memory Paradigm

During the encoding task, a cross was continuously displayed which divided the screen into four quadrants (Fig. 1). The centre of the cross was in the middle of the screen and indicated the fixation point. Each trial began with the presentation of a stimulus in one quadrant. Across a run, the four positions of the screen were selected randomly and with the same probability. The images were presented near the centre of the cross at a distance which ranged between 0.5 and 1.25° from the vertical or horizontal axes of the cross. Each stimulus was displayed for 1000 ms and the interval between successive stimulus onsets varied between 2.6 and 10.4 s, depending on the number of intervening null events. After the onset of each stimulus, subjects pressed one of two buttons on the response panel to signal whether the image represented an artificial or natural object. As it was described, subjects participated in a training session before entering the scanner where they had knowledge of the following retrieval task. Therefore, during encoding, subjects were instructed to concentrate on the artificial versus natural judgement.

For the retrieval session, a small cross, subtending an 0.5° horizontal and vertical angle, was displayed at the centre of the screen and indicated the fixation point. A trial began with the presentation of the stimulus at the centre of the screen for 1000 ms, after which the cross was again displayed. The interval between successive stimulus onsets was between 3 and 12 s, depending on the number of intervening null events. In this session, subjects were instructed to judge whether the image was new or old (presented in the encoding session). If the image was new, subjects pressed the lower key on the response panel and if it was old, subjects indicated at which position on the screen the stimulus was presented during the encoding session, by pressing one of the four keys, which represented each of the four screen quadrants. Subjects were instructed to guess if they were unable to remember the position of the stimulus at the time of encoding.

### fMRI Scanning

Anatomical and functional data were acquired on a 2 T Siemens Vision system (Siemens, Erlangen, Germany). Structural data were obtained using a  $T_1$ -weighted MPRAGE sequence with anatomical volume images of  $1 \times 2 \times 1.5$  mm voxels; functional images, sensitive to BOLD contrast, were acquired using a  $T_2^*$ -weighted echoplanar (EPI) sequence ( $64 \times 64$ ,  $3 \times 3$  mm pixels,  $T_E = 40$ ). Each functional volume consisted of 36 axial slices, 2 mm thick and separated by 1 mm. Functional sessions were acquired continuously with a repetition time ( $T_R$ ) of 2.74 s per volume. For each subject, 145 and 210 volumes were recorded during the encoding and retrieval sessions, respectively. To permit  $T_1$  equilibration, the first five volumes of each session were discarded.

### Image Processing

Data were processed and analysed using statistical parametric mapping (SPM99; Wellcome Department of Cognitive Neurology, London, UK) (Friston *et al.*, 1995). The volumes of each session were realigned to the first volume and resliced using a sinc interpolation in space. The  $T_1$  structural volume was coregistered and normalized with the mean realigned EPI volume. The signal measured in each slice was shifted

relative to the acquisition of the middle slice using a sinc interpolation in time, to correct signal differences over time acquisition. Each volume was normalized using nonlinear basis functions to a standard EPI template volume, based on the Montreal Neurological Institute Reference Brain (Cocosco *et al.*, 1997), of  $2 \times 2 \times 2$  mm voxels in the space of Talairach and Tournoux (Talairach and Tournoux, 1988). The volumes were smoothed with an 8 mm full-width half-maximum isotropic Gaussian kernel.

### Image Analysis

The volumes acquired during each session were treated as a time series. The haemodynamic responses to the stimulus onset of each event-type were modelled with a canonical haemodynamic response function (HRF) (Friston *et al.*, 1998) and a delayed HRF (Henson *et al.*, 2000). The delayed response was modelled one  $T_R$  (2.74 s) later than the canonical HRF. This procedure allows analysis of brain regions where activity occurs relatively late (Wilding and Rugg, 1996; Schacter *et al.*, 1997; Buckner *et al.*, 1998b). The covariates for the late HRF were orthogonalized with respect to those of the early HRF in order to give priority to the early covariate (Andrade *et al.*, 1999). Therefore, the orthogonalized late covariate accounted for the residual variance in the data not explained by the early covariate. These functions were included in a general linear model. The data were high-pass filtered to a maximum of 1/100 Hz. Parameter estimates for each event-type covariate were calculated from the least mean squares fit of the model to the data and stored as separated images for each subject.

Contrasts for data acquired during encoding and retrieval were computed separately. Items attracting an incorrect response during the encoding task were excluded from the analysis of both the encoding and retrieval data. The parameter estimates for the pre-experimentally planned contrasts were obtained in each subject's data for the early and late covariates. For encoding, the contrast tested for voxels where activity was greater for subsequently recognized items attracting correct as opposed to incorrect source judgements. For retrieval, two contrasts were performed on the responses elicited by correctly recognized items; one tested for voxels where the signal was greater for correct as opposed to incorrect source judgements and the other tested for the reverse effect. Contrasts with activity elicited by new items were not performed because of the marked differences between old and new items with respect to the response- and decision-related processes engaged in each case. The contrast images were subjected to repeated-measures  $t$ -tests to test whether, across-subjects, the mean of the parameter estimates of the contrasts differed from zero. The results of these tests were transformed into statistical parametric maps of the unit normal  $Z$ -distribution. The regional differences reported consist of at least five contiguous voxels that surpassed a threshold of  $P < 0.001$  ( $Z > 3.09$ ) uncorrected for multiple comparisons. The maxima of these regions were labelled using the nomenclature of Talairach and Tournoux (Talairach and Tournoux, 1988) and Brodmann (Brodmann, 1909) and they were localized on the across-subjects' mean normalized structural images.

### Results

#### Behavioural Data

Response accuracy during the encoding task was high (94%,  $SD = 3.1$ ), and RTs at encoding did not vary according to subsequent memory performance (1017 ms,  $SD = 212$  versus 1024 ms,  $SD = 239$  for correct and incorrect source, respectively;  $F < 1$ ). Behavioural data for the test task are shown in Table 1. Recognition hit and false alarm rates were 87 and 6.3%, respectively. Assuming that the false alarm rate provides a rough estimate of the guessing rate for hits (Snodgrass and Corwin, 1988), these data indicate that <10% of hits were based on a 'lucky guess'. Hit rate did not vary according to the quadrant in which items had been presented at study.

As shown in Table 1, subjects correctly judged the source of 61% of studied items, significantly exceeding the chance level of 25% [ $F(1,16) = 246.60$ ,  $P < 0.001$ ]. Corrected for guessing (Rugg *et al.*, 1998), this translates to veridical source memory for ~55%

**Table 1**Performance during the retrieval session for old and new items<sup>a</sup>

		Mean %	SD	RT	SD
Old items	Correct source responses	60.7	9.4	1156	183
	Incorrect source responses	26.3	8.1	1332	287
	Items judged as new	8.4	4.9	1212	251
New items	Correct responses	93.2	6.5	1024	184
	Incorrect responses	6.3	6.5	1354	354

<sup>a</sup>For old items, trials on which an incorrect judgement was made during encoding were excluded, as were trials on which no response was made (total exclusions = 4.6%). New item trials on which no response was made were also excluded (0.5%).

of all correctly recognized old items and to ~90% of the items that attracted a correct source judgement. There were no significant differences in accuracy of source memory according to spatial position at study. Crucially, the above pattern of performance meant that there were sufficient trials to estimate reliably the brain responses elicited by recognized items associated with both correct and incorrect source judgements (mean trial numbers of 55, SD = 8 and 24, SD = 7 for correct and incorrect judgements respectively; ranges 40–72 and 12–36).

As is evident from Table 1, correct source judgements were made more quickly than incorrect judgements [ $F(1,16) = 14.43$ ,  $P = 0.002$ ]. The consistent mapping between different fingers and the five response keys employed during the test phase makes it impossible to interpret any differences between the RTs associated with the different source locations.

### fMRI Data

We focus on the results of the analyses employing the early canonical haemodynamic response function. Results from the analyses employing the late covariate are reported only if they inform the experimental questions in a theoretically relevant way. The full results are available from the corresponding author on request.

### Encoding

Regions showing significant signal differences according to accuracy of the subsequent source judgement are listed in Table 2. The most prominent region to display a subsequent memory effect was the right lateral occipital cortex. Figure 2 shows the activity of this region for subsequently correct and incorrect source responses. Both responses are characterized by signal enhancement relative to null events, but these responses were greater for correct responses. Left superior and left inferior frontal cortex were also activated to a greater extent for items attracting a correct judgement. The activity in these brain regions is also displayed in Figure 2. In both regions, the subsequent memory effect took the form of a relative deactivation for incorrect source trials.

### Retrieval

The maxima of brain regions showing differential responses for correct versus incorrect source responses during retrieval are depicted in Table 3. For correct source responses, the most prominent activation relative to incorrect responses was in the medial frontal cortex (BA 10). The responses relative to null events are presented for this region in Figure 3. Responses for both classes of item were associated with reduced activity relative to the baseline, which was greater for the incorrect judgements. Greater activity for correct than incorrect judgements was also observed in a small region of left lateral anterior prefrontal cortex (BA 9), along with right parietal and temporal

**Table 2**Brain regions showing significant BOLD signal differences ( $P < 0.001$ ) for correct versus incorrect source memory during encoding<sup>a</sup>

Region	Location	BA	Peak Z	No. of voxels
Left superior frontal gyrus	-20 42 48	8/9	4.07	25
	-4 30 62	8	3.56	9
Left inferior frontal gyrus	-38 4 18	44/6	3.55	18
Right precentral gyrus	52 -6 54	6	3.45	8
Left precentral gyrus	-48 -4 54	6	3.85	6
	-38 -10 60	6	3.62	24
Paracentral lobule	0 -36 62	4	3.70	9
Left lateral parietal cortex	-44 -42 32	40	3.81	6
	-58 -54 4	40	3.22	7
Left superior temporal sulcus	-42 -52 2	37	3.72	11
Right lateral occipital cortex	50 -70 0	19/37	4.32	128
Right fusiform gyrus	28 -74 -10	19	4.09	17
	38 -46 -12	19	4.11	13
Left fusiform gyrus	-38 -54 -24	19	3.57	13
Left nucleus accumbens	-14 16 -12	—	3.91	20
Left cerebellum	-10 -56 -18	—	3.72	12

<sup>a</sup>Locations (x, y, z) correspond to Talairach and Tournoux (Talairach and Tournoux, 1988); BA, Brodmann's areas; Z values correspond to the maxima within activated clusters, which number of voxels are indicated.

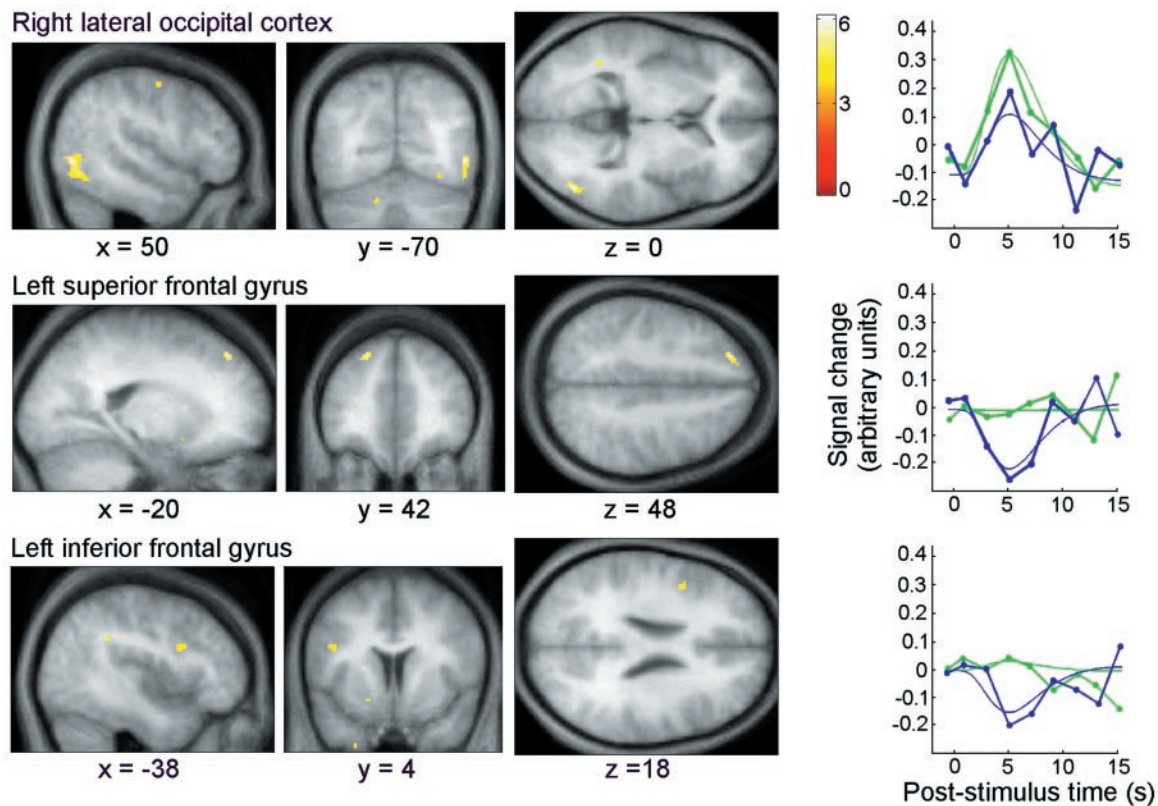
cortex. Significant signal differences were also observed in the right hippocampal formation and amygdala, as illustrated in Figure 3.

Items attracting incorrect source judgements elicited greater activity than those given correct judgements in a wide variety of regions (see Table 4 and Fig. 4), of which the most prominent was medial premotor cortex (BA 6). In addition, differential activity for incorrect judgements was observed bilaterally in the middle and inferior frontal gyri, and lateral parietal cortex. Analyses with the late covariate revealed a further bilateral ventral frontal region in which activity was greater for items attracting incorrect judgements (left x, y, z = -46, 42, -10, Z = 3.88, 12 voxels; right x, y, z = 48, 48, -2, Z = 4.21, 30 voxels).

### Discussion

The pattern of behavioural performance permits three important conclusions to be drawn. First, the equivalent RTs observed during the study task for items subsequently accorded correct versus incorrect source judgements mean that the differential neural activity elicited by these items is unlikely merely to reflect differences in how difficult or time-consuming they were to classify. Second, the high level of item memory demonstrated at test means that relatively few items (<10%) were given a positive recognition judgement on the basis of a guess. Thus, contrasts between recognized items accompanied or unaccompanied by retrieval of study context were likely confounded with accuracy of item memory to a lesser extent than was the case in earlier studies (Henson *et al.*, 1999b; Eldridge *et al.*, 2000). Third, the level of performance on the four-choice source procedure permitted a reasonable balance to be achieved between obtaining a sufficient proportion of correct source trials based on veridical judgements rather than guesses (only ~10% of correct judgements were guesses) and having a sufficient number of incorrect trials (>20 on average) to permit the BOLD responses elicited on these trials to be adequately estimated.

Turning to the fMRI data, in the following discussion we do not attempt to offer an interpretation for every effect documented in Tables 1–3. We focus instead on those that are of most relevance in light of previous research. One general conclusion, however, is that these data offer strong evidence that regional



**Figure 2.** Regions showing significantly different fMRI signals ( $P < 0.001$ ) during encoding of items attracting correct versus incorrect subsequent source memory judgements. The activations here and in the following figures are shown on the mean normalized structural MR image of the 17 experimental subjects. Adjacent to each image are estimates of the time-courses of the evoked signals elicited by items given correct (green) and incorrect (blue) judgements. Also shown are the best fitting haemodynamic responses, obtained by adding the two basic functions employed to model the responses after their multiplication by the appropriate parameter estimates.

**Table 3**  
Brain regions showing significant BOLD signal differences ( $P < 0.001$ ) for correct versus incorrect source memory during retrieval<sup>a</sup>

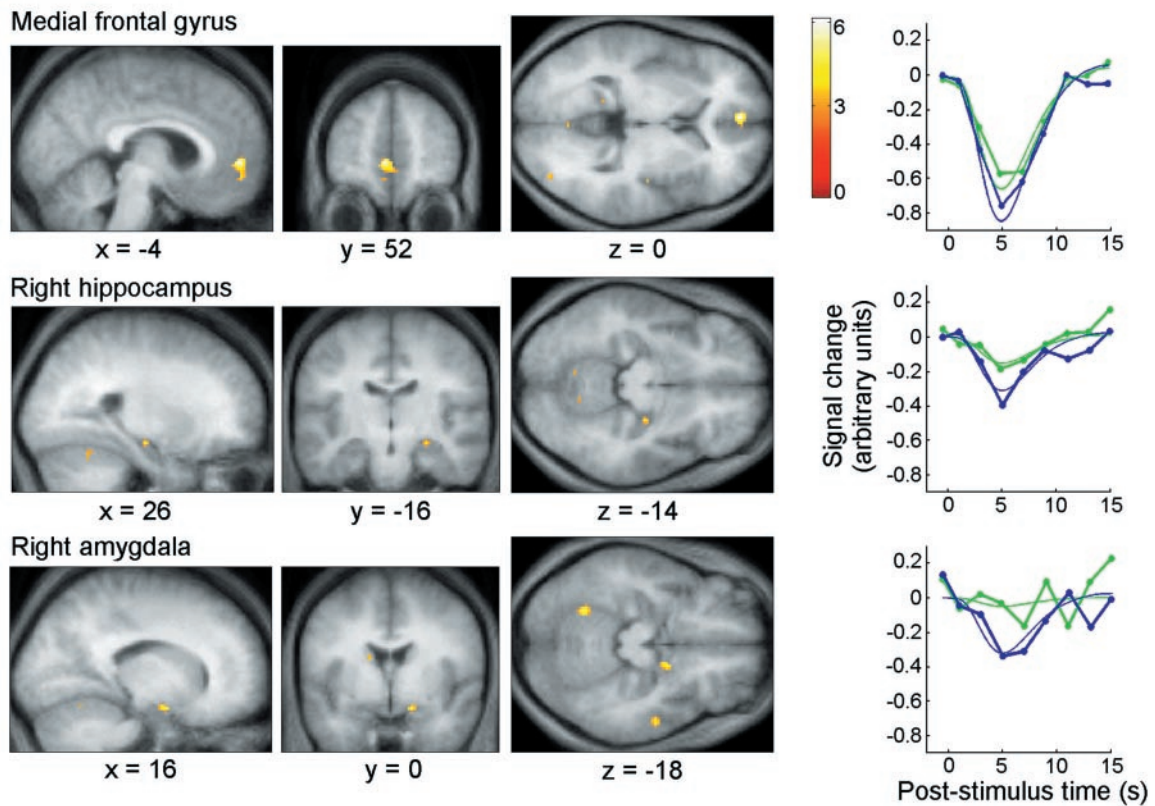
Region	Location	BA	Peak Z	No. of voxels
Left medial frontal gyrus	-4 52 0	10/32	4.70	114
Left superior frontal gyrus	-10 58 32	9	3.49	7
Right posterior insula	46 -10 4	41	4.40	29
Right middle temporal gyrus	56 -8 -18	20/21	3.69	17
Right middle/inferior temporal gyrus	48 -26 -12	20/21	3.66	6
Right lateral parietal cortex	62 -34 24	40	3.62	31
	60 -42 26	40	3.35	7
Medial occipital cortex	-14 -82 44	19	3.64	8
Left middle occipital gyrus	-30 -80 22	19	3.85	35
Right inferior occipital gyrus	38 -86 0	18	3.43	7
Right lingual gyrus	4 -74 -6	18	3.52	25
Left parahippocampal gyrus	-14 -44 -4	19/31	4.18	18
Right hippocampal formation	26 -16 -14	—	3.51	7
Right amygdala	16 0 -18	—	4.03	18
Left caudate nucleus	-14 -2 20	—	3.66	9
Right cerebellum	20 -84 -32	—	3.41	8
Left cerebellum	-24 -60 -20	—	4.46	66

<sup>a</sup>Locations (x, y, z) correspond to Talairach and Tournoux (Talairach and Tournoux, 1988); BA refers to Brodmann's areas; Z values correspond to the maxima within activated clusters, which number of voxels are indicated.

neural activity is sensitive to the amount of contextual information, additional to that necessary to support item memory, that is encoded during study and retrieved at test. In drawing this conclusion we are not implying that there is necessarily a

qualitative difference between item memory with and without memory for the encoding context. As was noted in the Introduction, the distinction between item and source memory can be viewed as quantitative rather than qualitative. In the present experiment, for example, it possible that on those trials where source memory was inaccurate, item memory was none the less accompanied by retrieval of some contextual information, albeit insufficient to support an accurate source judgement – so called 'non-criterial' or 'non-diagnostic' recollection (Yonelinas and Jacoby, 1996; Mulligan and Hirshman, 1997). The finding that 'depth of processing' manipulations have parallel effects on item memory and memory for incidentally encoded contextual information – presentation modality in the study of Hayman and Rickards (Hayman and Rickards, 1995), speaker voice in Naveh-Benjamin and Craik (Naveh-Benjamin and Craik, 1996) – adds further weight to the view that the encoding of item and contextual information depends upon a common set of processes. In light of these considerations, we view the present findings as agnostic with respect to the debate as to whether recognition memory is supported by one or more than one process.

A final general point relates to the nature of the source memory task employed here, which required retrieval of information about the (incidentally encoded) spatial location of the study objects. The task closely resembles those used in previous electrophysiological and neuroimaging studies of source memory, where source information takes the form of some task-irrelevant, physical attribute of the study items, such as voice (Wilding and Rugg, 1996), colour (Cycowicz *et al.*, 2001),



**Figure 3.** Regions showing significantly different haemodynamic response differences ( $P < 0.001$ ) during retrieval of items receiving correct versus incorrect source judgements. Time-course details as for Figure 2.

location (Henson *et al.*, 1999a), or modality (Wilding *et al.*, 1995). The general assumption underlying such manipulations (see Introduction) is that more episodic or contextual information was retrieved on trials where the source judgement was successful than on trials where it was not. The extent to which the present and previous findings depend upon the nature of the contextual information probed for in the source task remains an open question. In the present case, for example, it would be of interest to determine which of the effects observed during encoding and retrieval differ according to the requirement to recover spatial versus non-spatial source information.

### Encoding

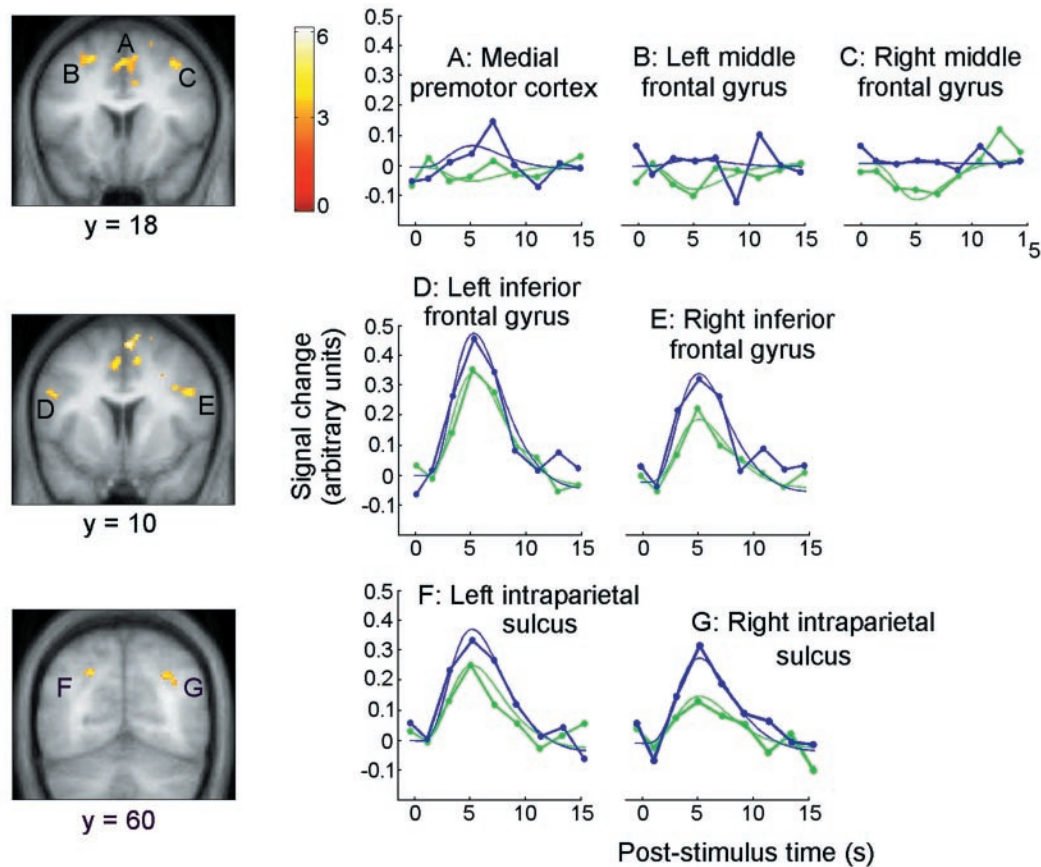
The most prominent region manifesting a subsequent memory effect was right lateral occipital cortex, a region overlapping an area that has been termed the 'lateral occipital complex' (Malach *et al.*, 1995; Grill-Spector *et al.*, 2001). This area in both hemispheres is thought to play a role in the relatively early stages of object recognition. The implication of the present findings is that objects (and their contexts) which engage these perceptual processes to a relatively greater extent are more likely to be effectively encoded into episodic memory.

The lateral occipital subsequent memory effect described here is in keeping with the conclusions of earlier workers (Otten and Rugg, 2001). They found that the loci of subsequent memory effects for words varied according to the type of encoding task undertaken (semantic versus phonological) and, in each case, the effects were found primarily in a subset of the regions selectively engaged by the respective task. Otten and Rugg argued that episodic encoding is based upon the products of whatever processes are engaged by a given combination of study

item and task. Thus, subsequent memory effects should vary in location according to which regions supported these processes in any particular encoding situation. In the present case, it is reasonable to assume that the item/task combination that was employed would have strongly engaged regions, such as the lateral occipital complex, necessary for object recognition. Therefore, the subsequent memory effects found in these regions are in accordance with Otten and Rugg's (Otten and Rugg, 2001) proposal.

Among other regions demonstrating a subsequent memory effect were three in the left frontal cortex, a small area in the dorsal inferior frontal gyrus (BA 6/44) and two regions in the anterior superior frontal gyrus (BA 8/9). The first of these regions is very near, if not overlapping with, one of the frontal regions found to demonstrate subsequent memory effects for words subjected to semantic processing (Otten *et al.*, 2001; Otten and Rugg, 2001; Wagner *et al.*, 1998). The more medial of the two anterior regions is near, though superior to, a medial frontal region also found to show subsequent memory effects for semantically encoded words (Otten *et al.*, 2001; Otten and Rugg, 2001). Given that the study task employed in the present experiment required a semantic judgement (natural versus artificial) it is possible that both of the left prefrontal subsequent memory effects found here reflect the benefit to episodic memory of additional semantic processing, as proposed previously for the analogous effects found for words (Wagner *et al.* 1998; Buckner *et al.*, 1999; Otten *et al.*, 2001).

We have suggested above that study items (and their contexts) which were effectively encoded received relatively greater perceptual and conceptual (semantic) processing than did items that were encoded less well. An interesting question is whether



**Figure 4.** Regions showing significantly different haemodynamic response differences ( $P < 0.001$ ) at retrieval for items given incorrect versus correct source judgements. Time-course details as for Figure 2.

**Table 4**

Brain regions showing significant BOLD signal differences ( $P < 0.001$ ) for incorrect versus correct source memory during retrieval<sup>a</sup>

Region	Location			BA	Peak Z	No. of voxels
Medial premotor cortex	4	10	64	6	4.71	300
Right superior frontal gyrus	4	42	42	8	3.67	18
Right middle frontal gyrus	36	18	50	9	3.85	19
	44	30	40	8	3.68	21
	42	46	18	46	3.70	26
Left middle frontal gyrus	-22	18	54	9	3.92	47
	-36	36	36	9	3.45	20
	-38	54	14	46	3.81	14
Right inferior frontal gyrus	48	8	28	44	4.07	114
	42	28	10	45	3.71	26
Left inferior frontal gyrus	-52	12	30	44	3.64	37
Right precentral gyrus	26	-14	54	6	3.40	22
Left precentral gyrus	-20	-8	48	6	4.54	127
Right intraparietal sulcus	28	-56	46	40	4.54	112
Left intraparietal sulcus	-24	-66	40	40	4.17	23
Left inferior temporal gyrus	-52	-8	-14	20	3.73	10
Left cerebellum	-32	-72	-38	—	3.60	7

<sup>a</sup>Locations (x, y, z) correspond to Talairach and Tournoux (Talairach and Tournoux, 1988); BA refers to Brodmann's areas; Z values correspond to the maxima within activated clusters, which number of voxels are indicated.

these two classes of processing give rise to representations that are encoded into memory independently, or whether instead they interact in some way. According to the first scenario, it may be that the occipital and frontal subsequent

memory effects reflect encoding based on two distinct forms of information – visual and lexical/semantic – an idea dating back at least to Paivio (Paivio, 1971). At the other extreme, it could be that the occipital subsequent memory effects reflect the benefit to memory of earlier or greater availability of object/location information to the prefrontal cortex, allowing more opportunity for the formation of durable, semantically elaborated episodic representations. These possibilities could perhaps be teased apart by the employment of objects which differ in the ease with which they can be semantically encoded.

In contrast to some previous studies (Brewer *et al.*, 1998; Wagner *et al.*, 1998; Kirchhoff *et al.*, 2000; Otten *et al.*, 2001), there was no evidence in the present experiment for subsequent memory effects, either in the hippocampal formation or in medial temporal cortex more generally. This negative finding is not without precedent; for example Otten and Rugg (Otten and Rugg, 2001) were unable to replicate their previous finding (Otten *et al.*, 2001) of a left hippocampal subsequent memory effect for semantically encoded words. In light of previous negative findings, it is possible that the present failure to observe medial temporal subsequent memory effects reflects nothing more than a lack of power. Another possibility, however, arises out of the fact that, unlike in previous studies, the present subsequent memory comparison was not between subsequently remembered and forgotten items, but between two classes of remembered items. It is possible, therefore, that relatively high levels of encoding-related hippocampal activity were elicited even for those items attracting an inaccurate subsequent source judgement.

## Retrieval

The contrast between recognized items according to the accuracy of source memory identified a number of regions where activity was greater for accurate judgements. Several of these regions, notably lateral parietal cortex and left anterior prefrontal cortex, have been described in previous event-related studies of recognition memory (Rugg and Henson, 2002) and were found to be more active for items attracting remember than know judgements in other studies (Henson *et al.*, 1999b; Eldridge *et al.*, 2000). The present findings strengthen the proposal that these regions may play a role in either the representation or the further processing of retrieved episodic information (Rugg and Henson, 2002).

Perhaps the most notable of the regions demonstrating increased activity in association with successful source memory was the right hippocampal formation. Reports of increased hippocampal activity in association with successful recognition memory are quite sparse in the functional imaging literature and the present finding represents one of only a handful of fMRI studies to have reported this effect (Cabeza *et al.*, 2001; Donaldson *et al.*, 2001; Eldridge *et al.*, 2000; Maratos *et al.*, 2001). Since the contrast yielding the effect in the present case was largely unconfounded with successful versus unsuccessful item memory, this finding provides strong support for the proposal of Eldridge *et al.* (Eldridge *et al.*, 2000) that activity in the hippocampal formation differs according to the amount of episodic (contextual) information retrieved. Our findings further support those of Eldridge *et al.* (Eldridge *et al.*, 2000) in respect of the nature of the hippocampal responses elicited by the items receiving incorrect source judgements. As was reported for items attracting know judgements (Eldridge *et al.*, 2000), items given incorrect source judgements elicited a transient hippocampal deactivation relative to baseline (see Fig. 3). Unlike in the previous study, however, we did not find robust hippocampal activation for items associated with successful contextual retrieval.

In addition to the hippocampal formation, we also observed differential responses in a more anterior right medial temporal region, which was tentatively identified as the amygdala. This finding was unexpected and does not lend itself to any obvious interpretation. We note, however, an earlier report (Henson *et al.*, 1999b) of an effect bilaterally in a nearby region, which the authors also identified as amygdala. In their case, however, the effect took the form of greater activity for new items relative to old items given a know response.

Another region demonstrating robustly greater activity in association with correct source judgements was anterior medial frontal cortex (BA 10/32). This region was not identified in the analogous contrasts of earlier workers (Henson *et al.*, 1999b; Eldridge *et al.*, 2000) and, while medial frontal activations have been reported in some recent fMRI studies of simple recognition memory (Konishi *et al.*, 2000; McDermott *et al.* 2000), these were dorsal and caudal to the peak of the effect identified here. However, in one such study (Maratos *et al.*, 2001), greater activity was reported for successfully recognized old words relative to new items in the same medial frontal region as that identified here. Together with the current findings, this suggests that this medial frontal area can be sensitive to whether recognition test items elicit successful episodic retrieval. The functional significance of this is, however, unclear, as are the reasons why it is reported so infrequently.

Finally, we turn to the results of the contrast identifying regions where activity was greater for test items associated with unsuccessful as opposed to successful source memory. The

interpretation of these data is complicated by the fact that RTs were almost 200 ms longer for incorrect judgements, raising the possibility that at least some of these effects may merely reflect the consequences of such factors as increased response uncertainty. Indeed, differences in response-related factors seem the most likely explanation for the most prominent of the activations identified by this contrast – a medial frontal region just anterior to the supplementary motor area (preSMA). Among the other regions revealed by this contrast, two stand out. The first is bilateral dorsolateral prefrontal cortex (BA 9/46). This is near (on the right) to the right dorsolateral region identified by Henson *et al.* (Henson *et al.*, 1999b) in their 'know-remember' contrast and argued by them (Henson *et al.*, 1999b, 2000) to support post-retrieval 'monitoring' (Burgess and Shallice, 1996). By this argument, relatively weak evidence about an item's study status requires more monitoring prior to a memory judgement than does stronger evidence and is reflected in greater dorsolateral prefrontal activation. This account sits well with the present findings; presumably, when only limited information is available to support item or source judgements, monitoring operations would be engaged to a greater extent than when more information is retrieved.

A second bilateral prefrontal region to show greater activity for items given incorrect source judgements was a dorsal region of the inferior frontal gyrus (BA 44). Intriguingly, this region in the left hemisphere is very near to a left prefrontal region earlier reported (Buckner *et al.*, 1998a) to show reduced activity for repeated versus unrepeated objects presented in a 'semantic' classification task (does it move or not?). The authors interpreted this effect as a correlate of 'conceptual priming', one manifestation of which is the more efficient or fluent semantic processing of repeated objects and a resulting reduction in neural activity elicited in regions supporting such processing. The present findings may reflect a similar phenomenon. By this account, there was either overlap or correlation between the processing engaged at study that was conducive to effective episodic encoding of an item and processing that facilitated its subsequent conceptual analysis at test. Whether this facilitation contributed in any way to the superior memory performance shown for these items is an interesting issue (Donaldson *et al.*, 2001).

## Notes

We are grateful to L. Otten, R. Henson, J. Armony and D. Tsivilis for their advice on data analysis. R. Dolan and M. Rugg are supported by the Wellcome Trust. S. Cansino was supported by a sabbatical and research grant (IN300700) from DGAPA, National Autonomous University of Mexico.

Address correspondence to Selene Cansino, Laboratory of Neuro-Cognition, Faculty of Psychology, National Autonomous University of Mexico, Apartado Postal 25-308, Mexico DF, 03421 Mexico. Email: selene@servidor.unam.mx.

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