Title: The neural correlates of everyday recognition memory.

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Shortened title: fMRI during everyday image recognition

Abstract

We used a novel automatic camera, SenseCam, to create a recognition memory test for real-life events. Adapting a 'Remember/Know' paradigm, we asked healthy undergraduates, who wore SenseCam for two days, in their everyday environments, to classify images as strongly or weakly remembered, strongly or weakly familiar or novel, while brain activation was recorded with functional MRI. Overlapping, widely distributed sets of brain regions were activated by recollected and familiar stimuli. Within the medial temporal lobes, 'Remember' responses specifically elicited greater activity in the right anterior and posterior parahippocampal gyrus than 'Know' responses. 'New' responses activated anterior parahippocampal regions. A parametric analysis, across correctly recognised items, revealed increasing activation in the right hippocampus and posterior parahippocampal gyrus (pPHG). This may reflect modulation of these regions by the degree of recollection or, alternatively, by increasing memory strength. Strong recollection elicited greater activity in the left posterior hippocampus/pPHG than weak recollection indicating that this region is specifically modulated by the degree of recollection.

Keywords: fMRI; Recognition memory; SenseCam; Recollection; Familiarity.

1. Introduction

Recognition memory enables us to judge that a current stimulus has been encountered previously. It is widely thought to be facilitated by two distinct processes: *recollection*, the process by which items are recognized on the basis of the retrieval of contextual details; and *familiarity*, the process by which items are recognized on the basis of perceived memory strength (Mandler, 1980). An alternative view proposes that, rather than reflecting distinct underlying processes, familiarity and recollection differ in the strength of a common memory signal (e.g., Dunn, 2004).

The neural correlates of recognition memory have recently been subject to intense investigation using functional imaging techniques. The majority of these imaging studies have used laboratory stimuli. Thus, such studies have examined the ability to recognize words (Eldridge et al., 2000), faces (Gonsalves et al., 2005), objects (Vilberg & Rugg, 2007), and visual scenes (Montaldi, Spencer, Roberts, & Mayes, 2006).

Several approaches have been taken to distinguish the processes of recollection and familiarity. These include the use of confidence ratings, associative recognition, source memory, and the remember-know (R-K) paradigm (for a review, see Yonelinas, 2002). We adopted the last of these here. The R-K paradigm (Tulving, 1985) requires participants to specify whether an item is recognized on the basis of familiarity alone ('know' judgment) or whether they can recollect contextual details from their original encounter with the item ('remember' judgment). While the underlying conceptual

distinction between familiarity and recollection is clear, it is likely that everyday recognition commonly engages both processes to some degree.

Studies using the R-K paradigm have often found increased hippocampal and posterior parahippocampal gyrus (pPHG) activity for remember compared with know responses (Eldridge et al., 2000; Wais, 2008; Woodruff, Johnson, Uncapher, & Rugg, 2005). By contrast, familiarity is typically linked to perirhinal and anterior parahippocampal (aPHG) regions (Henson, Cansino, Herron, Robb, & Rugg, 2003; Strange, Hurlemann, Duggins, Heinze, & Dolan, 2005). These regional activations broadly support *dual-process* accounts of recognition memory (Aggleton & Brown, 1999; Diana, Yonelinas, & Ranganath, 2007), which propose that recollection is supported by the hippocampus and pPHG, whereas familiarity is supported by aPHG, and in particular the perirhinal cortex.

Recent evidence has suggested that brain activation during recollection and familiarity may be modulated by the strength of these processes. For example, Vilberg and Rugg (2007) found that the extent of neural activation during recollection varied with the amount of detail recollected. Specifically, Vilberg and Rugg identified regions activated by recollection which were sensitive to the amount of information recalled in the right precentral gyrus, left fusiform gyrus and left inferior lateral parietal cortex. Medial temporal lobe (MTL) activation was not modulated by memory strength or amount of information recalled. In contrast, Staresina and Davachi (2008) found that left hippocampal activity increased relative to the number of pieces of contextual information retrieved. In a study investigating levels of familiarity, increasing familiarity resulted in

linearly decreasing activation in the perirhinal cortex, insula and left superior temporal cortex (Montaldi et al., 2006). However, the level of familiarity had no effect on hippocampus activation. These findings are broadly in line with dual-process accounts of recognition memory.

Some studies, however, have failed to support the distinction between recollection and familiarity processes. For instance, Gonsalves et al. (2005) found a graded decrease in activation in the parahippocampal and perirhinal cortices corresponding to the distinctions between remembered items, which elicited maximal suppression, known items and new items, which elicited the least suppression. This suggests that memory strength is signalled by levels of activity in both perirhinal and parahippocampal cortices.

The majority of previous recognition memory studies have used lab-based stimuli. However, some recent work has examined the neural substrates of more naturalistic forms of recognition memory (Cabeza et al., 2004; Epstein & Higgins, 2007; St. Jacques, Rubin, LaBar, & Cabeza, 2008). For instance, Cabeza et al. (2004), asked participants to take photos in specified campus locations, and subsequently scanned them whilst they distinguished between pictures they had taken and pictures of the same places taken by other participants. Results showed greater activation for their own pictures in the medial prefrontal cortex, pPHG, and in the hippocampus. Nevertheless, this study was not specifically designed to explore the neural basis of recollection and familiarity memory. Furthermore, the method of stimulus acquisition (i.e., participants actively taking photos) encouraged greater intentional encoding of the scenes than is typically the case for real-

life memory encoding. Investigating the neural processes underlying different types of recognition memory in less artificial circumstances is a natural next step.

The current study used automatically captured everyday images and a modified R-K technique, assessing the strength of recollection and familiarity, to examine the functional imaging correlates of human recognition memory. Images of everyday scenes were captured by a novel wearable camera, SenseCam (Hodges et al., 2006), which is activated by a range of environmental sensors and takes on average one image every 30 seconds (Berry et al., 2007). The resulting photographic diary of the day's activities allowed assessment of memory for everyday scenes taken without user involvement.

The use of SenseCam has a number of advantages in the study of everyday recognition memory. First, the automatic capture of images reduces the intentional encoding of the items that will be tested later. Second, SenseCam provides an opportunity to study recognition of everyday scenes and events which differ in several ways from laboratory stimuli: they are typically of greater perceptual complexity, are likely to encourage more extensive processing of spatial information and are more personally relevant. Third, the richness of stimuli from an everyday environment and the potential wealth of associations are likely to result in the retrieval of varying levels of contextual information, facilitating comparisons between memories which vary in their strength of recollection. This final opportunity is linked to a potential disadvantage of these stimuli in the study of the contrast between recollection and familiarity: in everyday surroundings, processes of familiarity and recollection are intertwined. In particular, images which are classified as

'familiar' in our study depict scenes which may have supplied the context for recollection of pre-experimental memories: this potentially complicates interpretation of some of our results.

SenseCam images were presented during functional magnetic resonance imaging to participants who indicated whether the photos were strongly or weakly recollected, strongly or weakly familiar, or novel. Using this approach, we address the following questions: i) Which brain regions support recognition memory for everyday events? ii) Is activity in these brain regions modulated across memory types (Weak Know, Strong Know, Weak Remember, Strong Remember)? iii) Is there evidence for a dissociable pattern of activation within different regions of the MTL? iv) How does the pattern of activity for everyday recognition memory relate to theories developed on the basis of standard laboratory-based experiments?

2. Method

2.1. Participants

15 right-handed, healthy, participants who were students at the University of Exeter (8 male, 7 female), ranging in age from 18-25 years, took part in the study. Participants were paid £15 for their participation. All participants gave informed consent.

2.2. fMRI data acquisition

Images were collected using a 1.5-T Phillips Gyroscan magnet, with a Sense coil. A T2*-weighted echo planar sequence was used (Tr = 3000ms, Te = 45ms, flip angle = 90˚, 32

transverse slices, 3.5 x 2.5 x 2.5mm). 280 volumes were acquired in each of the two runs per subject. An additional 5 "dummy" scans were performed before each run prior to the start of the stimulus sequence. Standard volumetric anatomical MRI was performed after functional scanning by using a 3-D T1-weighted pulse sequence (Tr = 25ms, Te = 4.1ms, flip angle = 30˚, 160 axial slices, 1.6 x 0.9 x 0.9mm).

2.3. Equipment

The SenseCam (sized 6.5cm wide x 7cm high x 1.5cm long; see Fig. 1a) is built around a PIC 18F8722 6 MIPS microcontroller with 128KB of flash memory (Hodges et al., 2006). SenseCam is worn round the neck, with pictures captured using a fish eye lens. This maximizes the field-of-view and ensures that objects at head height were photographed. Images were captured automatically approximately every 30 seconds.

2.4. Procedure

Participants wore a SenseCam for two days whilst undertaking their everyday activities. Participants were encouraged to participate on days when they would be active and this instruction was repeated on collection of the camera. All participants complied with this request and experienced a number of unique events which took place in diverse locations. The camera was returned the following day and the images processed. Approximately 36 hours after wearing the camera, participants completed the scanning session.

The events recorded by participants were all characteristic of everyday experiences. In other words, the personal significance of events was low and generally consistent across

participants. Images were excluded from the selection process if they were of poor quality (usually induced by excessive movement), of ambiguous locations (e.g., ceilings, floors, non-distinct buildings), if they showed the identical event to a previous image, or if they were likely to be of high personal significance or emotionality (no images were excluded for this reason). Images were then selected so that distinct events were presented which were evenly distributed throughout the acquisition period.

Participants were told that a series of images would be shown, some of which would be theirs (old), and the rest images acquired by other participants (new). There were perceptual differences between images across participants (e.g., in the amount of time spent outdoors and variations in the weather) but this was controlled for by using 'new' images that possessed the same general characteristics as each individual's 'old' images (e.g., similar types of event, locations, weather, level of brightness). New images frequently, but not always, showed the same location from a different viewpoint.

Before entering the scanner, participants were trained to distinguish between different types of recognition memory. For pictures that they recognized, participants had to distinguish between images for which they could "Remember" specific contextual details associated with the event, and images which they "knew" were familiar but for which they were unable to retrieve any specific contextual details. The instructions outlining the Remember/Know distinction were modelled on those of Rotello, Macmillan and Reeder (2004) and Rajaram (1993). In addition, participants were asked to respond that the images were familiar only when they knew the photo was one of theirs, regardless of

whether the location itself was familiar (this approach has some resemblance to the recognition of word lists where the lures have typically been encountered previously by participants). Participants readily understood this distinction. Furthermore, participants had to divide the "Remember" images into those for which they could remember a high level of detail and those for which they could remember a low level of detail. For "Know" responses, participants were asked to distinguish between images of high familiarity and those of low familiarity. Participants were all able to explain the differences between these four memory types. They then completed a training session to further familiarize them with these distinctions. 15 trials were presented in a random order; ten were "old" and five were "new" images.

Inside the scanner, visual stimuli were presented on a back-projection screen positioned at the foot end of the MRI scanner and viewed via a mirror mounted on a head coil. Responses were measured using two fibre-optic button boxes held in the participants' right and left hands. E-Prime (Psychological Software Tools, 2002) was used for the presentation and timing of stimuli and collection of response data.

The current study employed an event-related design. During scanning, eighty "old" images and forty "new" images were presented, making 120 trials in total. The trial-by-trial procedure is displayed in Figure 1b. Trials began with a blank screen lasting between 250-3750ms (rapid ITIs have been shown to be very sensitive in detecting effects in randomized, event-related, designs, c.f., Josephs & Henson, 1999) followed by a fixation cross for 150ms. An image was then presented for 4000ms during which time participants

were asked not to respond. This was followed by instructions, which remained on the screen for 3000ms, asking participants to classify the image as “Remember”, “Know”, or “New”. If no response was made, a message appeared saying, “Time out!!” “Remember” and “Know” responses were made using the response box in one hand, “New” responses using the response box in the other hand. The hand corresponding to these judgments was approximately counterbalanced.

Following this, another message appeared which varied depending on participants’ responses. For “Remember” judgments, participants had to distinguish between a high and a low level of detail. “Know” images were to be divided into high and low familiarity. Responses indicating a high level of detail and high familiarity were made using the same hand, as were responses indicating a low level of detail and low familiarity (the hand corresponding to these judgments was again counterbalanced). For “New” images, participants had to press any button. If participants made no response for the initial judgment then the “Time out!!” message remained on the screen throughout this period and no further response was required. Participants had 3000ms to make a response; if no response was made in this time, the “Time out!!” message appeared.

There were six blocks of 20 images and presentation order was randomized. After each block, a message appeared for 13 seconds saying, “That is the end of the block. Please take a short break”. A message lasting 1500ms instructing participants to “Get ready to start the next block” followed this. The session was divided into two runs, each lasting 14 minutes, with three blocks presented in each run.

In a post-scan interview, participants were presented two images from each of the four categories of recognised items (Strong Remember, Weak Remember, Strong Know and Weak Know). Images were presented in a random order; no information was given about the classifications previously assigned to these images. With no time constraint, participants described their memory for the events, which were scored by the experimenter on a scale from 0 (no information) to 3 (lots of information). Participants also rated events for memory strength on a scale of 1 (weak memory) to 6 (strong memory).

2.5. Analysis of fMRI data

Analyses were carried out using SPM5 software (www.fil.ion.ucl.ac.uk/spm). Functional images were corrected for acquisition order, realigned to the first volume and resliced to correct for motion artifacts. The realigned images were coregistered with the structural T1 volume and the structural volumes were spatially normalized. The spatial transformation was applied to the realigned T2* volumes which were spatially smoothed using a Gaussian kernel of 8mm full-width half maximum. Data were high-pass filtered (128s) to account for low frequency drifts. The BOLD response was modelled by a canonical hemodynamic response function together with the temporal and dispersion derivatives. The six head movement parameters were included as confounds. Onset of the image was considered the beginning of the trial. A random effects analysis was performed on the first-level linear contrasts of parameter estimates for each voxel.

Pairwise contrasts for memory types were conducted using repeated-measures t-tests with a significance threshold of $p < .001$ (uncorrected) and a voxel cluster size threshold of 10 (c.f., Forman et al., 1995). Two participants who produced less than 8 Weak Know responses and one with less than 8 Weak Remember responses were removed from the relevant analyses (this exclusion criterion is generally comparable with related studies, e.g., Montaldi et al., 2006; Vilberg & Rugg, 2007; Wheeler & Buckner, 2004). An additional participant who failed to use the appropriate response buttons for the confidence ratings was also excluded from the relevant analyses. In addition, we used the first-order (linear) parametric analysis option integrated in SPM5 to identify regions that were associated with increasing activation across memory types (Weak Know, Strong Know, Weak Remember, Strong Remember). To complement these whole brain analyses, region of interest (ROI) analyses were conducted in bilateral MTL based on *a priori* hypothesis that this region is active during recognition memory. The ROI mask was applied using the WFU Pickatlas (for further details on using this ROI tool, see Maldjian, Laurienti, Burdette, & Kraft, 2003) with a threshold of $p < .005$ (cf., Montaldi et al., 2006) and 10 contiguously active voxels.

3. Results

3.1. Behavioural analyses

Participants correctly recognized 94% of the "old" pictures, and correctly rejected 87% of the "new" items. 2% of trials were excluded because participants failed to respond in time. The proportions for the different memory types are displayed in Table 1. The

distribution of response types for old images was evenly spread; however the relatively low number of incorrectly rejected old items (6%) and incorrectly accepted new items (12%) precluded further analyses of these classification types.

Table 1 shows the post-scan ratings for the level of detail and memory strength for the four memory types (two images sampled per classification). Strong Remember responses produced greater detail than Weak Remember ($p<.01$), Strong Know ($p<.001$), and Weak Know ($p<.001$) responses; Weak Remember responses more detail than Strong Know ($p<.01$), and Weak Know ($p<.001$) responses; and Strong Know responses more detail than Weak Know responses ($p<.01$). Overall, there was a significant linear trend with level of details increasing from Weak Know through Strong Remember responses, $F(1,14) = 124.653$, $p < .001$. Example responses for each of the different memory types are shown in the Appendix.

Perceived memory strength did not differ significantly between Strong Remember and Weak Remember responses ($p=.505$), but Strong Remember responses were rated as stronger than Strong Know ($p=.001$) and Weak Know responses ($p<.001$). Weak Remember responses were stronger than Strong Know ($p=.001$) and Weak Know responses ($p=.001$). Strong Know responses were not significantly stronger than Weak Know responses ($p=.343$). Overall, there was a significant linear trend with perceived memory strength rising from Weak Know through Strong Remember responses, $F(1,14) = 49.648$, $p < .001$.

3.2. Imaging analyses

3.3. MTL Region of Interest (ROI) analyses

3.4. Remember/Know/New analyses

The following analyses used a significance threshold of $p<.005$ and a cluster threshold of 10 contiguous voxels. Remember responses recruited greater right hippocampus and bilateral pPHG activation than New responses (Fig. 2a). A contrast comparing Remember to Know responses produced clusters in right aPHG and right pPHG (Fig. 2b; Table 2). Strong Remember responses recruited greater activation in the left hippocampus/ pPHG than Weak Remember responses (Fig. 2c; Table 2).

There was increased activity in right pPHG for Know compared with New responses (Fig. 3a). The New – Know contrast elicited greater activation in left aPHG and two aPHG clusters located in or near right perirhinal cortex and right entorhinal cortex respectively (Fig. 3b). Fig.3b also displays the percent signal change across all conditions for the highest activating voxel in the right aPHG for this contrast (calculated using the SPM Anatomy toolbox; Eickhoff et al., 2005). There was no significant activation when comparing Strong to Weak Familiarity or Weak to Strong Familiarity.

3.5. MTL areas parametrically modulated across Weak Know through Strong Remember responses

A first-order parametric analysis, using the four "old" memory types (Weak Know, Strong Know, Weak Remember, and Strong Remember), revealed activation in right hippocampus, right pPHG and a region of right amygdala (Fig. 4a, Table 3). The percent

signal change across memory types for the peak right hippocampus (Fig. 4b), right pPHG (Fig. 4c), and right amygdala (Fig. 4d) voxels was calculated. No regions were associated with decreasing memory strength.

Using analyses similar to those conducted by Vilberg and Rugg (2007), we assessed whether any regions had significant increases in activation when inclusively masking the outcomes of sequential contrasts (i.e, Strong Remember > Weak Remember, Weak Remember > Strong Know, Strong Know > Weak Know). No regions were identified in this analysis, even when a threshold of $p<.01$ (uncorrected) was used.

We then assessed whether there were dissociations in activation in regions linked with increased activity across familiarity and recollection responses (right hippocampus, right pPHG, and right amygdala) and novelty-responsive (right aPHG, Fig. 2b) regions. To do this, using the parametric estimates, we conducted 2 (region) x 5 (memory type) ANOVAs (for related analyses, see Daselaar et al., 2006). There was a significant region x memory type interaction between right hippocampus and right aPHG ($p = .002$). T-tests, investigating this interaction, revealed that the mean parameter estimates for Strong Remember stimuli were higher in the hippocampus than in the aPHG ($p<.05$) while the parameter estimates were higher for New stimuli in the aPHG than in the hippocampus ($p<.05$). Additionally, there was a significant region x memory type interaction between right pPHG and right aPHG ($p < .001$). Comparisons indicated that the parameter estimates were higher for Strong Remember stimuli in the right pPHG than in the aPHG ($p<.05$) but higher for New stimuli in the aPHG than in the pPHG ($p<.05$). These

analyses, therefore, indicate dissociable activation within different regions of the MTL. No such interaction emerged between the right hippocampus and right pPHG ($p = .48$). There was also no region x memory type interaction between the right amygdala and right aPHG ($p = .09$), right pPHG ($p = .37$), and right hippocampus ($p = .22$).

3.6 Extra-MTL analyses

3.7 Remember/Know/New analyses

These analyses used significance thresholds of $p<.001$ and 10 contiguous voxels. The Remember – New and Know – New contrasts both activated a wide-range of extra-MTL regions (Tables 4 and 5; Figure 5). A conjunction analysis, assessing regions that were commonly activated in both the Remember- New and the Know – New contrasts, was conducted using the masking function of SPM5 with both contrasts thresholded at $p<.001$ and 10 contiguous voxels. This conjunction analysis revealed extensive common activation including right inferior parietal lobe, posterior cingulate, and right dorsolateral prefrontal cortex (Figure 6). There was greater activation in the medial prefrontal cortex for Remember responses than Know responses (Table 2) but no activation for Strong Remember compared to Weak Remember responses. The Know – Remember contrast (Table 2) revealed activation of the cingulate gyrus and right ventrolateral frontal cortex (VLFC). Comparing Strong Know with Weak Know responses revealed no significant activation.

3.8. Extra-MTL areas parametrically modulated across Weak Know through Strong Remember responses

A first-order (linear) parametric analysis revealed that medial prefrontal cortex, right postcentral gyrus, and left cingulate gyrus increased in activation from Weak Know through Strong Remember (Table 3). Regions of left medial prefrontal cortex, right middle frontal gyrus and left middle frontal gyrus were associated with decreasing activation across memory types (Table 3).

4. Discussion

The present study combined the use of a novel automatic camera with fMRI to identify the neural systems supporting recognition of everyday events. Our key findings are that: i) compared with novel stimuli, remembered and familiar items are associated with activation of overlapping, widely distributed sets of brain regions; ii) novel stimuli, compared with familiar stimuli, activate the aPHG; iii) activation of the *right* hippocampus and bilateral regions of the pPHG increased linearly from weakly familiar through to strongly recollected items; iv) strong recollection is distinguished from weak recollection by the degree of activation of the *left* posterior hippocampus/pPHG; v) there is dissociable activation in the MTL between regions associated with novelty and regions which increase in activation across memory types. We discuss each of these findings in turn.

4.1 Recollected and familiar stimuli are associated with widespread brain activation.

Both recollected and familiar stimuli activated a common range of extratemporal regions when compared to novel events, including right inferior parietal lobe, posterior cingulate and right dorsolateral prefrontal cortex (DLFC). The left inferior parietal lobe is typically

implicated in recollection memory (e.g., McDermott et al., 2000; Wheeler & Buckner, 2003, 2004). The right-sided activation we observed may reflect the complex, visual nature of our stimuli. The posterior cingulate is associated with the retrieval of autobiographical memories (Svoboda, McKinnon & Levine, 2006) and activates more for old than new items (e.g., Eldridge et al., 2000). Right DLFC is also involved in the recollection of previously seen items (Hayes, Ryan, Schnyer, & Nadel, 2004; Henson et al., 2000); this may reflect post-retrieval monitoring processes (Burgess & Shallice, 1996; Henson et al., 1999), as well as temporal-order memory (St. Jacques et al., 2008).

There was greater activation in the medial prefrontal cortex (mPFC) for recollection than familiarity. This region is known to be active during recollection (Yonelinas et al., 2005), and is thought to support self-referential mental activity (Gusnard, Akbudak, Schulman, & Raichle, 2001). For familiarity compared with recollection, extra-MTL activations were observed in the cingulate gyrus and right VLFC. The cingulate gyrus has been associated with familiarity (Yonelinas et al., 2005), and right VLFC with active retrieval processes (Henson, Shallice & Dolan, 1998), and increasing activity as familiarity rises (Montaldi et al., 2006). In summary, the differences between brain activation associated with familiarity and with recollection suggest that while these processes have much in common their neural signatures are somewhat distinctive.

In broad terms, the regions of activation elicited by recollected and familiar items compared to new ones resemble those of the ‘autobiographical memory network’ (Maguire, 2001; Svoboda et al., 2006) identified by recent functional imaging studies,

suggesting a close relationship between real-life recognition memory and autobiographical memory. In particular our results are closely comparable to those of Levine, Turner, Tisserand, Hevenor, Graham, and McIntosh (2004) and Maguire, Vargha-Khadem and Mishkin (2001) who investigated recognition for autobiographical memories using markedly different techniques. Specifically, in Levine et al. (2004), participants documented personal episodic events using a microcassette recorder over the course of 6-8 months. Levine et al. found that when listening to these recordings inside the scanner, participants activated a number of regions that we also identified in our study including the DLPFC, VLPFC, the medial temporal lobes, the inferior parietal lobes, and the posterior cingulate. Similarly, in Maguire et al. (2001) participants were asked to generate events from their past and in a latter scanning session had to determine whether the autobiographical events presented were accurate or not. Maguire et al. (2001) found that a group of control participants engaged the medial frontal cortex, the medial temporal lobes, the cerebellum, and the lateral temporal lobes, regions similar to those we identified.

4.2 Recollected compared to familiar stimuli activate the aPHG and pPHG.

Comparing Remember to Know responses revealed stronger activation in regions of the right aPHG and pPHG (Fig. 2b). The pPHG activation is in line with previous work (e.g., Davachi et al., 2003; Eldridge et al., 2000) and supports the idea that this region is involved in the retrieval of contextual information. Activity in the aPHG has previously been observed (Eldridge, Engel, Zeineh, Bookheimer, & Knowlton, 2005), but is nevertheless surprising given that activation near this region is often assumed to decrease

with increasing familiarity (Diana et al., 2007; Montaldi et al., 2006). This activation may reflect greater re-encoding of remembered than known stimuli.

4.3 Novel stimuli activate the aPHG

The greater activation of the left aPHG and two regions of right aPHG by novel than by familiar stimuli (Fig. 3b) is in line with existing models (e.g., Aggleton & Brown, 1999) and in keeping with previous work (e.g., Hayama & Rugg, 2009; Montaldi et al., 2006). This activation may reflect a novelty signal (Daselaar et al., 2006) or less efficient item representation (Diana et al., 2007).

4.4 MTL activation increases linearly from Weak Know throug Strong Remember responses.

Activation of the right hippocampus/ pPHG, together with a small region of right amygdala, increased linearly from weakly familiar through strongly recollected items. Outside the MTL, the medial frontal gyrus showed a similar pattern of activation, possibly due to greater self-referential processing across memory types (Gusnard et al., 2001).

One caveat to these findings is that no regions were activated when inclusively masking the outcomes of sequential contrasts (i.e., Strong Remember > Weak Remember, Weak Remember > Strong Know, Strong Know > Weak Know). This analysis, is however, far more conservative than the linear parametric analysis traditionally used to investigate this issue (e.g., Daselaar et al., 2006; Gonsalves et al., 2005; Yonelinas et al., 2005) and was

adopted by Vilberg and Rugg (2007) to guard against misleading linear trends which contain markedly non-linear patterns of activation (as in their Fig. 5, p. 2223). This may be a concern with our right amygdala activation (Fig. 4d): specifically there is a non-significant decrease in activation between Weak Remember and Strong Remember responses. Consequently we do not discuss this finding further. However, both the right hippocampus (Fig 4b) and right pPHG (Fig. 4c) activations show a clear monotonic trend with no evidence for any marked non-linearities in the data, suggesting that the parametric analysis detected a genuine graded increase of activation within these regions.

There appear to be two plausible explanations for the findings from the parametric analysis. The first is that this activation is associated with increased memory strength. This explanation would be consistent with the finding that hippocampal activation predicts memory strength (Kirwan, Wixted, & Squire, 2008; Wais, 2008) but appear inconsistent with standard dual-process accounts. Relatedly, Gonsalves et al. (2005), in a parametric analysis, also found MTL activation is associated with memory strength; however, in their study they found *decreased* pPHG and perirhinal cortex activation. The reason for this discrepancy between our findings and those of Gonsalves et al. is unclear but may relate to differences between the types of stimuli employed, the categories of memories included, and the approach to the parametric analysis. In particular, the everyday scenes we used as stimuli may activate the pPHG, a region involved in spatial processing (e.g., Epstein & Kanwisher, 1998), to a greater extent than the face stimuli Gonsalves et al. (2005) used.

The second explanation is that activation of the MTL is modulated by graded levels of recollection. In particular, the 'familiar' items in this study were complex images of places that participants visited, often or occasionally, in the course of their everyday activities. It is possible that images of these familiar scenes may have cued incidental recollection of other, irrelevant, episodes linked with that location, or have activated associated spatial contextual information. Thus, in a study using rich, 'ecologically valid', stimuli like photographs of familiar scenes, 'familiarity' responses may be associated with a penumbra of recollection and spatial memory which contaminate the 'process purity' of the response. This explanation of our results is consistent with previous findings that the hippocampus/pPHG are involved in recollection processes (e.g., Davachi, 2006; Eichenbaum, Yonelinas, & Ranganath, 2007). Further support for the idea that the parametric modulation reflects recollection based processes comes from the post-hoc ratings which indicated that there was a significant linear trend in the level of detail provided across Weak Know through to Strong Remember memories (as well as significant differences for each of the sequential analyses, i.e., Strong Remember > Weak Remember, Weak Remember > Strong Know, and Strong Know > Weak Know which were not all significant for the memory strength post-hoc ratings, see Section 3.1).

The possibility that measures of recollection and familiarity may not be process pure is a common concern in recognition studies and is not restricted to our novel approach. For instance, there is substantial evidence that process impurity affects standard lab based procedures when recollection and familiarity are measured using the Remember-Know procedure (e.g., Conway & Dewhurst, 1995; Eldridge et al., 2005; Wais et al., 2008) or

confidence ratings (e.g., Slotnick & Dodson, 2005; Slotnick, Klein, Dodson, & Shimamura, 2000; Wixted, 2007a). A full discussion of how this is a problem inherent in all standard lab-based recognition tests hoping to discriminate between recollection and familiarity based processes can be found in Wixted, Mickes, and Squire (2010; see also Wixted & Mickes, 2010). Nevertheless, process impurity may be particularly apparent in our study, given the complexity of the stimuli. Thus, while our findings provide clear evidence for an increase in neural activity in the MTL across memory types, it is unclear whether it is due to increasing memory strength, graded recollection, or a combination of these two explanations.

4.5 Increasing strength of recollection is associated with increasing activation of the left posterior hippocampus/pPHG.

Strong recollection gave rise to greater left hippocampal/ pPHG activation than weak recollection. Interestingly, this comparison highlights a left-sided difference, while the other related comparisons (Remember-Know, Remember-New, Know-New, the parametric analysis) identify either right-lateralised or bilateral differences. This may reflect the frequent occurrence of memories of verbalised inner thought associated with Strong Remember judgements, as revealed by the post-scan interviews (see Appendix).

The graded activation in the left hippocampus/pPHG provides further evidence that recollection is a continuous process (Wixted, 2007a, 2007b, Mickes, Wais, & Wixted, 2009). The neural substrates that underlie this continuous recollection signal have, however, rarely been studied due to the fact that recollection is typically measured

categorically. The limited number of studies that have directly investigated this issue have, to date, provided discrepant results. For instance, Vilberg and Rugg (2007), found no relationship between strength of recollection and MTL activation, whilst Uncapher and Rugg (2009) found greater hippocampal activation at encoding when one rather than two pieces of information were recalled in a subsequent test session. In contrast, Staresina and Davachi (2008) found that left hippocampal activity increases relative to the amount of contextual information retrieved. Our results, using a very different procedure, appear more in line with the findings of Staresina and Davachi (2008). We note, however, that whereas previous studies (Staresina & Davachi, 2008; Uncapher, Otten, & Rugg, 2006; Uncapher & Rugg, 2009; Vilberg & Rugg, 2007) used objective measures to record the level of recollection, we relied on the subjective ratings of the participants to distinguish between 'high' and 'low' levels of recollection. Our post-hoc ratings indicated participants were able to accurately distinguish between strong and weak recollection, but these relied on only two memories of each type per participant. Our findings would have been stronger if we had quantified the level of recollection on a trial by trial basis. Nevertheless, our results add to the evidence that MTL activation reflects the strength of recollection. This implies that techniques that use a single discrete measurement of recollection memory may be unable to detect important modulations of recollection-based activity.

4.6 Dissociable activation with the MTL.

Analysis of activation across all memory types (Strong Remember, Weak Remember, Strong Know, Weak Know, and New) revealed that different regions of the MTL had a

distinct neural profile of activation. Specifically, a region of the aPHG, linked to novel stimuli, had a dissociable pattern of activation compared to regions of the right hippocampus and right pPHG that were associated with increased activity across familiarity and recollection. The statistically distinct patterns of activation in regions of the aPHG and the hippocampus are similar to results obtained by Daselaar et al. (2006), although they also obtained a dissociation between the hippocampus (linked to recollection) and pPHG (linked to familiarity). Our findings are also in keeping with dual process theories (e.g., Aggleton & Brown, 1999; Diana et al., 2007) which propose that different regions of the MTL are involved in different processes.

4.7 Relationship to laboratory based recognition studies.

In general, the pattern of activation was broadly consistent with previous lab-based studies, suggesting that the findings from such studies generalise to everyday recognition memory processes. This conclusion is somewhat different from that of McDermott, Szpunar, and Christ (2009) who found that laboratory recognition studies have little neural overlap with the recall of pre-experiment autobiographical memories. This likely reflects the considerable procedural differences between recognition and autobiographical memory studies which principally examine recollection. Having said this, our results resemble previous autobiographical memory studies that used a recognition based procedure (e.g., Levine et al., 2004; Maguire et al., 2001). The fact that our study produced common activation both with lab-based recognition studies and previous studies of autobiographical memory suggests that the study of everyday recognition memory may be a useful bridge between these two paradigms.

4.8 Future work

Future research with SenseCam should investigate recognition performance in a completely novel environment to reduce the retrieval of memories from outside the experimental context. This could be accomplished with the help of structured days out, such as visits to local attractions (c.f., Muhlert, Milton, Butler, Kapur, & Zeman, 2010). Performance was also generally high across participants, which precluded analyses of forgotten images. Testing recognition memory over longer retrieval delays (e.g., 3 months or longer as in for example, Dolcos, LaBar, & Cabeza, 2005; Milton, Muhlert, Butler, Smith, Benattayallah, & Zeman, in press) would likely result in more misses, and perhaps more importantly, reduce the reliance on recollection-based processes. It is an open question whether the graded right hippocampus/pPHG activation across recollection and familiarity judgments would still emerge under such conditions.

4.9 Conclusions

This study is the first to use automatically captured everyday images to explore the neural correlates of everyday recognition memory. Both recollection and familiarity judgements for everyday scenes were associated with activation of diverse temporal and extratemporal brain regions, substantially resembling those previously identified in studies of autobiographical memory. Activation of the right hippocampus/pPHG increased linearly from weakly familiar stimuli through to strongly recollected items. This may reflect either graded recollection, increased memory strength, or a combination of these two processes. Strong recollection, specifically, by comparison with weak recollection, was associated with activation of the left hippocampus/ pPHG suggesting

this region plays an important role in the continuous recollection signal. Novel items, by comparison with familiar ones, caused activation of anterior regions of the MTLs. There was dissociable activation between regions linked to novelty responses (aPHG) and those linked to the processing of old stimuli (right hippocampus/pPHG). In summary, the use of automatically captured images appears a promising approach to investigate the neural processes that underlie everyday recognition memory.

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Table 1.

Mean Proportions, Level of Detail and Memory Strength Ratings for Each Response Category.

	Proportion of trials (SD)	*Mean trials modelled (SD)*	*Details (SD)*	*Memory strength (SD)*
Strong Remember	0.27 (0.16)	24.23 (11.26)	2.59 (0.6)	4.28 (1.3)
Weak Remember	0.22 (0.11)	14.85 (5.99)	2.00 (0.9)	3.96 (1.3)
Strong Know	0.22 (0.07)	17.08 (4.85)	1.23 (0.8)	2.93 (1.3)
Weak Know	0.23 (0.11)	17.25 (6.63)	0.58 (0.9)	2.61 (1.5)

Note. Details (0 = No details, 3 = Many details); Memory strength (1 = vague memory, 6 = vivid memory).

Table 2.

Regions Showing Significant Activation for Remember Compared with Know, Strong Remember Compared to Weak Remember and for Know Compared with Remember Responses.

			Talairach Coordinates			
Region	*Cluster size*	*BA*	*x*	*y*	*z*	*z-score*
Remember – Know						
Right anterior parahippocampal gyrus	16 (46)	34	24	5	-17	3.48**
Medial prefrontal cortex	42	10	-2	55	3	3.40**
Right posterior parahippocampal gyrus	16 (72)	30	20	-31	-7	3.40**
Strong Remember – Weak Remember						
Left posterior parahippocampal gyrus	2(27)	36	-30	-35	-10	3.39**
Left hippocampus		-	-30	-35	-2	2.90*
Know – Remember						
Right cingulate gyrus	15	24	12	2	40	4.03**
Right paracentral lobule	16	5	20	-36	50	3.93**
Right ventrolateral frontal cortex	14	47	32	29	-1	3.83**
Left cingulate gyrus	11	24	-18	-2	42	3.38**

Note. BA = brodmann's area; ** = p< .001. Figures in parentheses indicate cluster size at p < .005. Indented rows indicate voxels in the same cluster as the non-indented row above them.

Table 3.

Regions Showing Increased Activation from Weak Know through to Strong Remember Responses and Decreased Activation from Weak Know through to Strong Remember Responses .

			Talairach Coordinates			
Region	*Cluster size*	*BA*	*x*	*y*	*z*	*z-score*
Regions associated with increasing memory strength						
Right parahippocampal gyrus	69 (133)	27	26	-28	-7	4.27**
Right hippocampus		-	30	-26	-7	3.72**
Right postcentral gyrus	22	3	40	-28	53	3.71**
Left medial frontal gyrus	66	10	-4	58	3	3.57**
Left cingulate gyrus	19	31	0	-41	3	3.37**
Right amygdala	(16)	-	26	1	-12	2.91*
Regions associated with decreasing memory strength						
Left medial frontal gyrus	13	6	-8	-15	58	3.71**
Right medial frontal gyrus	10	9	12	42	20	3.60**
Left middle frontal gyrus	30	10	-28	50	-1	3.44**

Note. BA = brodmann's area; ** = p<.001; * = p<.005. Figures in parentheses indicate cluster size at p < .005. Indented rows indicate voxels in the same cluster as the non-indented row above them.

Table 4.

Regions Showing Significant Activation for Remember Compared to New Responses.

			Talairach Coordinates			
Region	*Cluster size*	*BA*	*x*	*y*	*z*	*z-score*
Right frontal lobe	874	6	22	1	57	4.61
Right frontal lobe		6	38	1	53	4.47
Left thalamus, pulvinar	1807	-	-8	-27	11	4.43
Posterior cingulate		23	6	-30	24	4.41
Left posterior parahippocampal gyrus		34	-6	-37	6	3.59
Cingulate gyrus	1062	32	4	27	28	4.20
Cingulate gyrus		32	6	20	40	3.83
Right anterior cerebellum	185	-	8	-43	-15	4.18
Right anterior cerebellum		-	2	-49	-4	3.60
Right ventrolateral frontal cortex	156	47	48	14	-1	4.16
Right insula		13	42	8	1	3.52
Left middle frontal gyrus	260	10	-34	36	24	4.03
Left middle frontal gyrus		9	-34	33	34	3.86
Right cerebellum	139	-	26	-59	-19	4.02
Right cerebellum		-	36	-57	-17	3.77
Right posterior parahippocampal gyrus		30	26	-52	4	3.33
Right insula	164	13	36	-46	17	3.93
Right parietal lobe		13	32	-45	26	3.48
Left insula	57	13	-28	18	5	3.81
Right inferior parietal lobe	400	40	50	-37	44	3.81
Right inferior parietal lobe		40	36	-33	40	3.71
Left ventrolateral prefrontal cortex	23	10	-40	43	0	3.63
Right cerebellum	15	-	4	-64	-5	3.57
Right superior temporal gyrus	21	22	55	-46	12	3.52
Left putamen	14	-	-24	13	-4	3.52
Right middle frontal gyrus	9	9	48	15	34	3.51
Right ventricle gyrus	16	31	28	-54	6	3.51
Cingulate gyrus	13	31	6	-43	39	3.50
Left brainstem	24	-	-2	-31	0	3.49
Right middle frontal gyrus	19	10	38	38	24	3.48
Right dorsolateral frontal cortex		9	34	37	31	3.25
Left inferior frontal gyrus	19	9	-40	5	29	3.45
Right thalamus	21	-	2	-2	2	3.41
Right superior temporal gyrus	17	41	42	-38	7	3.38
Right fusiform gyrus	23	19	22	-71	-17	3.38
Left frontal lobe	13	-	-26	41	7	3.29

Note. BA = brodmann's area. All activations significant at $p<.001$. Indented rows indicate voxels in the same cluster as the non-indented row above them.

Table 5.

Regions Showing Significant Activation for Know Compared to New Responses.

			Talairach Coordinates			
Region	*Cluster size*	*BA*	x	y	z	*z-score*
Left putamen	621	-	-16	-2	-2	4.71
Left thalamus		-	-4	-17	8	4.28
Right posterior parahippocampal gyrus		-	20	-37	6	3.31
Right middle frontal gyrus	4855	6	28	0	46	4.54
Left medial frontal gyrus		6	-14	8	49	4.49
Right thalamus	102	-	10	-5	9	4.36
Right thalamus		-	16	-11	10	3.88
Posterior cingulate	415	23	2	-32	22	4.17
Cingulate gyrus		23	2	-28	29	4.16
Right inferior parietal lobe	539	40	42	-48	45	4.02
Right inferior parietal lobe		40	42	-40	48	4.01
Superior temporal gyrus	48	22	50	10	-2	3.98
Posterior cingulate	41	30	-6	-54	5	3.92
Right dorsolateral frontal cortex	195	9	37	36	26	3.90
Right dorsolateral frontal cortex		9	30	36	26	3.66
Right precuneus	12	7	18	-46	52	3.79
Right fusiform gyrus	36	19	40	-61	-17	3.71
Left cerebellum	63	-	-8	-28	-10	3.65
Left brainstem		-	2	-35	-7	3.37
Right brainstem	10	-	6	-22	-4	3.39

Note. BA = brodmann's area. All activations significant at $p<.001$. Indented rows indicate voxels in the same cluster as the non-indented row above them.

Figure Captions

Figure 1: a) a picture of SenseCam; b) the trial-by-trial procedure. Note, the final screen that participants view is dependent on whether participants respond "remember", "know" or "new" for the initial judgment.

Figure 2: Regions in MTL ROI where activation was greater for a) Remember than New responses; b) Remember than Know responses; c) Strong Remember than Weak Remember responses.

Figure 3: Regions in MTL ROI where activation was greater for: a) Know compared with New responses; b) New compared with Know responses. Percent signal change in right aPHG. Note. R = Remember; K = Know.

Figure 4: a) Regions in MTL parametrically modulated by weak know through to strong remember responses. The location of the hippocampus is outlined in black. b) Percent signal change in peak right hippocampus region; c) Percent signal change in right posterior parahippocampal gyrus; d) Percent signal change in right amygdala. Note. R = Remember; K = Know.

Figure 5: Whole brain analyses where activation was greater for: a) Remember than New responses; b) Know than New responses. The regions highlighted are all typically activated in recognition and autobiographical memory studies.

Figure 6: Common activation across the Remember compared to New and Know compared to New contrasts.

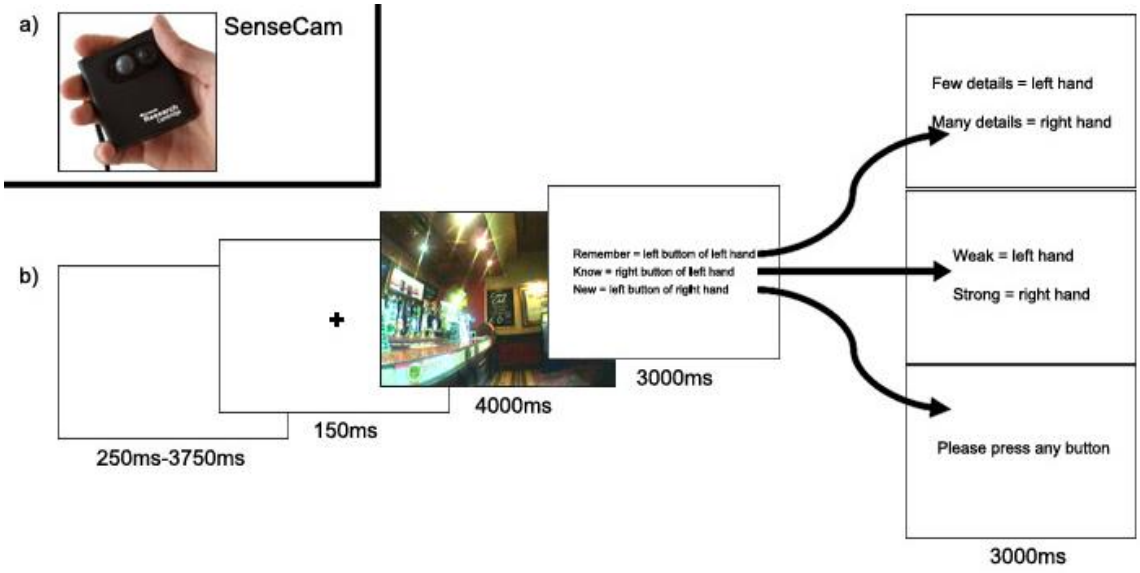
a)
SenseCam
b)
+
250ms-3750ms
150ms
4000ms
3000ms
Remember = left button of left hand
Know = right button of left hand
New = left button of right hand
Few details = left hand
Many details = right hand
Weak = left hand
Strong = right hand
Please press any button
3000ms

Figure 1.

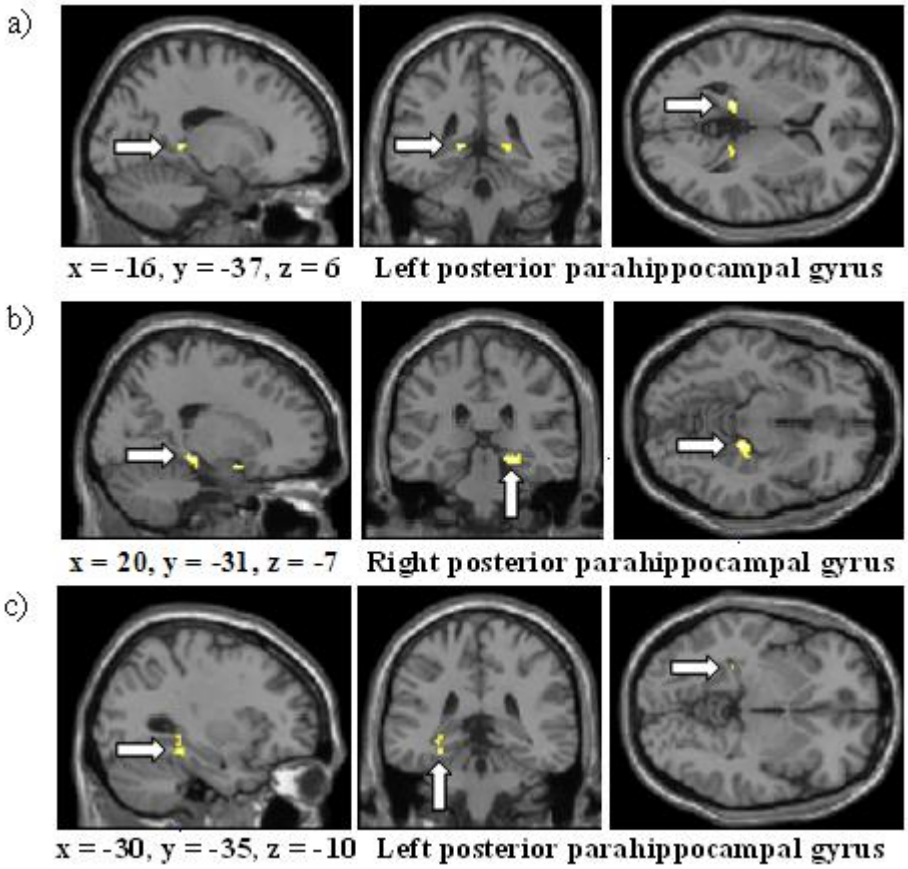
a)
x = -16, y = -37, z = 6
Left posterior parahippocampal gyrus
b)
x = 20, y = -31, z = -7
Right posterior parahippocampal gyrus
c)
x = -30, y = -35, z = -10
Left posterior parahippocampal gyrus

Figure 2.

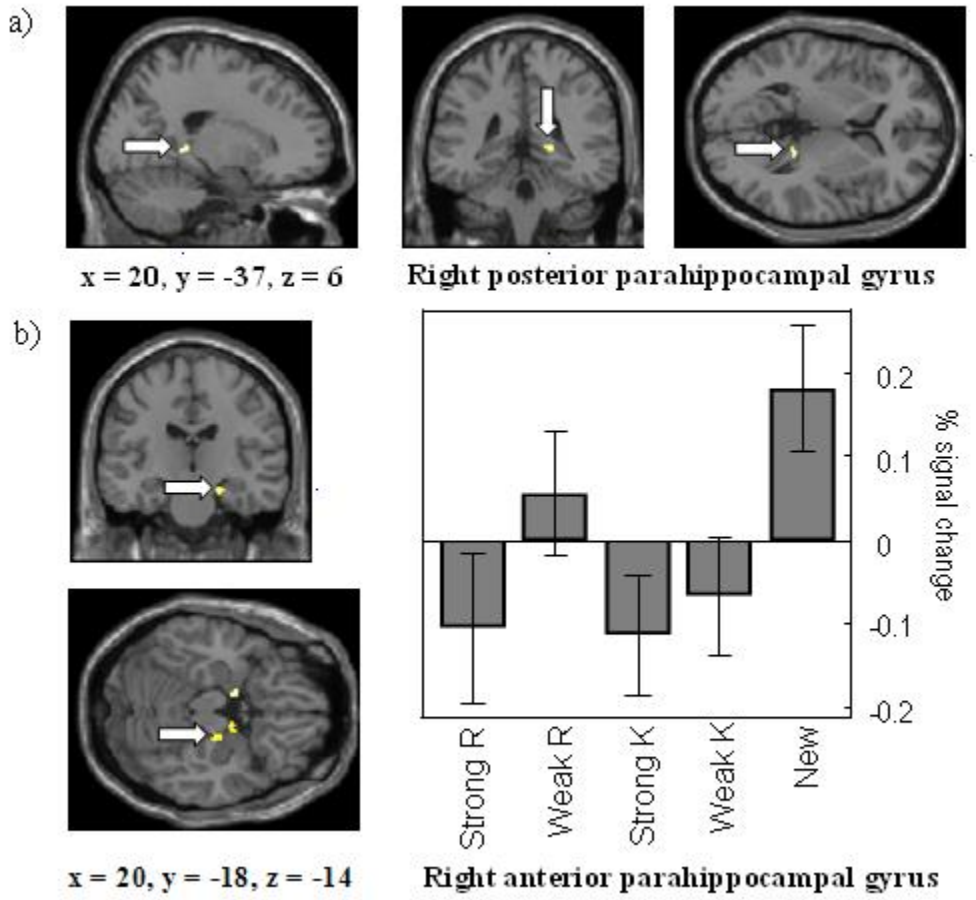
a)
x = 20, y = -37, z = 6
Right posterior parahippocampal gyrus
b)
x = 20, y = -18, z = -14
Right anterior parahippocampal gyrus
0.2
0.1
0
-0.1
-0.2
% signal change
Strong R
Weak R
Strong K
Weak K
New

Figure 3.

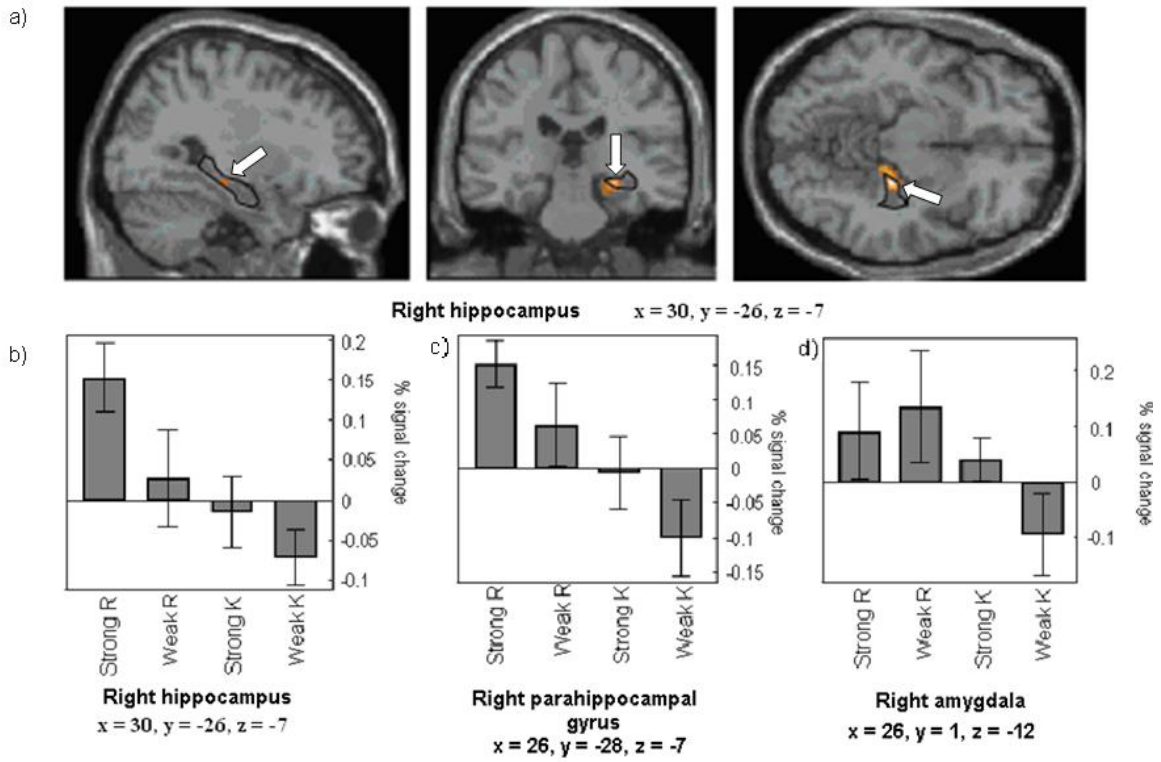
a)
Right hippocampus x = 30, y = -26, z = -7
b)
c)
d)
% signal change
Strong R
Weak R
Strong K
Weak K
Right hippocampus
x = 30, y = -26, z = -7
Right parahippocampal gyrus
x = 26, y = -28, z = -7
Right amygdala
x = 26, y = 1, z = -12

Figure 4.

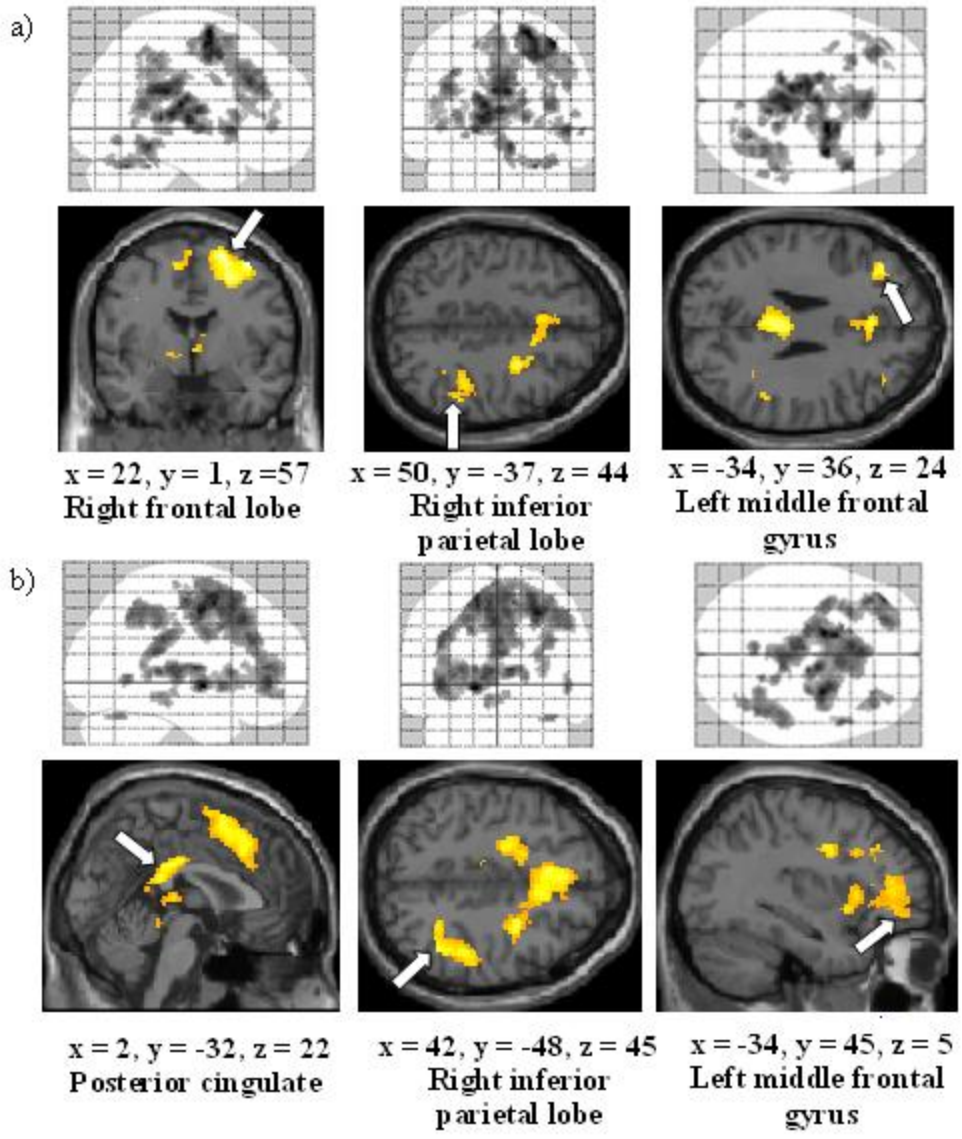
a)
x = 22, y = 1, z =57
Right frontal lobe
x = 50, y = -37, z = 44
Right inferior parietal lobe
x = -34, y = 36, z = 24
Left middle frontal gyrus
b)
x = 2, y = -32, z = 22
Posterior cingulate
x = 42, y = -48, z = 45
Right inferior parietal lobe
x = -34, y = 45, z = 5
Left middle frontal gyrus

Figure 5.

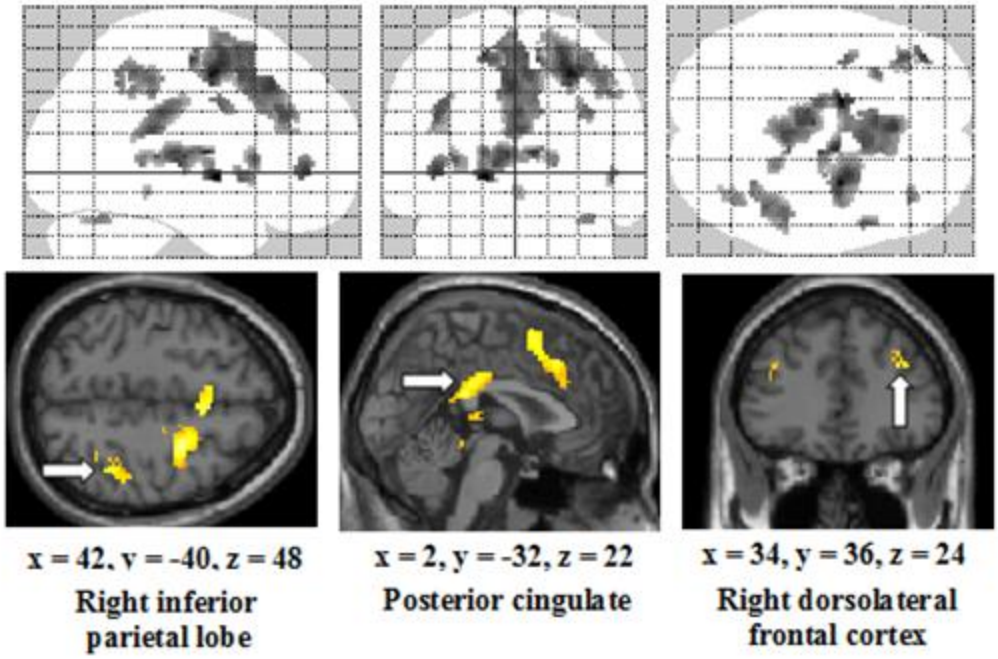
x = 42, y = -40, z = 48
Right inferior parietal lobe
x = 2, y = -32, z = 22
Posterior cingulate
x = 34, y = 36, z = 24
Right dorsolateral frontal cortex

Figure 6.

Appendix

Example responses from the post-scan interview for the four memory types.

	Participant Response
Strong Remember	"I was in church watching some people get baptised. They were wearing shorts and I remember thinking that was very strange."
	"I was looking for something for lunch on the way home. I remember looking at spaghetti carbonara but I thought it wasn't a good choice for lunch."
Weak Remember	"I was in a vintage clothing store in town, looking at some of the less stylish dresses."
	"I was in the bank, about to get some money out. I had to find my purse."
Strong Know	"I was in one of the corridors in the Medical School. I can't remember when it was taken. I might have been leaving the session, or getting a coffee, or something."
	"I had bumped into a friend so we went for a coffee. I recognise the event but not that moment."
Weak Know	"I was sitting on the kitchen table talking to my flatmate. I can't remember when it happened or what we were talking about."
	"I recognise that road. I must have been on my way to my study group."