Neural Bases of Autobiographical Support for Episodic Recollection of Faces

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ABSTRACT: Incidental retrieval of autobiographical knowledge can provide rich contextual support for episodic recollection of a recent event. We examined the neural bases of these two processes by performing fMRI scanning during a recognition memory test for faces that were unfamiliar, famous, or personally known. The presence of pre-experimental knowledge of a face was incidental to the task, but nonetheless resulted in improved performance. Two distinct networks of activation were associated with correct recollection of a face's prior presentation (recollection hits vs. correct rejections) on one hand, and with pre-experimental knowledge about it (famous or personally known vs. unfamiliar faces) on the other. The former included mid/posterior cingulate cortex, precuneus, and ventral striatum. The latter included bilateral hippocampus, retrosplenial, and ventromedial prefrontal cortices. Anterior and medial thalamic activations showed an interaction between both effects, driven by increased activation for recollection of unfamiliar faces. When recollecting the presentation of a famous or personally known face, hippocampal activation increased with participants' ratings of how well they felt they knew the person shown. Ventromedial prefrontal cortex showed significantly greater activation for personally known than famous faces. Our results indicate a dissociation between the involvement of retrosplenial vs. mid/posterior cingulate and precuneus in memory tasks. They also indicate that, during recognition memory experiments, the hippocampus supports incidental retrieval of pre-experimental knowledge about the stimuli presented. This type of knowledge likely underlies the additional recollection found for prior presentation of well known stimuli compared with novel ones and may link hippocampal activation at encoding to subsequent memory performance more generally. © 2009 Wiley-Liss, Inc.

KEY WORDS: hippocampus; retrosplenial cortex; medial prefrontal cortex; memory; fMRI

INTRODUCTION

A crucial aspect of the recollection of episodic memories is the concurrent retrieval of incidental "contextual" information that is not task-relevant. For instance, the "remember/know" procedure (Mandler, 1980; Tulving, 1985; Jacoby, 1991; see Yonelinas et al., 2001 for a review) operationalizes episodic recollection ("remembering") in terms of the ability to retrieve incidental information concerning the external (time, place, etc.) or internal (current thoughts, feelings, etc.) context of the event in question. More generally, events are often embedded within a rich context of incidental associations to other autobiographical and semantic knowledge (e.g., Burgess and Shallice, 1996; Tulving and Markowitsch, 1998; Conway and Pleydell-Pearce, 2000; Conway, 2001; Levine et al., 2004). These associations provide critical support for the process of retrieval. Nonetheless, the neural systems supporting the contribution of these incidental associations to episodic recollection have received relatively little direct study.

One way to manipulate the extent of incidental associative support for recollection comes from the choice of memoranda used in a recognition memory test. Thus, autobiographical stimuli often have rich contextual support, whereas novel laboratory stimuli presented within the experiment are relatively denuded of contextual support beyond internal thoughts or associations to the surrounding stimuli. Recent functional neuroimaging experiments have implicated a common network of brain regions in episodic memory retrieval, including the medial temporal lobe (MTL) (specifically the hippocampus, entorhinal, perirhinal, and parahippocampal cortices), as well as thalamus, retrosplenial cortex, inferior lateral parietal cortex, cerebellum, and multiple regions of prefrontal cortex (Schacter and Wagner, 1999; Cabeza and Nyberg, 2000; Fletcher and Henson, 2001; Moscovitch et al., 2005; Svoboda et al., 2006; Cabeza and St Jacques, 2007). However, consistent with the above discussion, the pattern of areas activated appears to be modulated by the nature of the material to be retrieved.

Memory for personally experienced real-world events (i.e., autobiographical stimuli) tends to produce strong activation of the MTL and medial frontal regions (Maguire and Mummery, 1999; Maguire et al., 2000; Ryan et al., 2001; Piefke et al., 2003; Addis et al., 2004; Cabeza et al., 2004; Gilboa et al., 2004; Greenberg et al., 2005; Viard et al., 2007). By contrast, episodic recollection of prior presentation of laboratory stimuli often shows a more prefrontal pat-

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tern of activation (e.g., Shallice et al., 1994; Tulving et al., 1994; Fletcher et al., 1998; Henson and Rugg, 2002; Gilboa, 2004), perhaps reflecting the increased interference resulting from the similarity of contextual cues across items (King et al., 2005). In addition, increased activation of amygdala, orbito-frontal cortex, and insula is seen for stimuli containing highly emotional content (Fink et al., 1996; Cahill and McGaugh, 1998; Hamann et al., 1999; LeDoux, 2000; Maratos et al., 2001; Piefke et al., 2003; Phelps, 2004; Strange and Dolan, 2004).

The importance of the hippocampal system and associated structures (including the anterior thalamic nuclei) for episodic recollection has long been clear from neuropsychological data (Scoville and Milner, 1957; O'Keefe and Nadel, 1978; Squire and Zola-Morgan, 1991; Cohen and Eichenbaum, 1993; Aggleton and Brown, 1999). Consequently, it has become important to characterize the factors contributing to activation of this system within neuroimaging experiments. Many authors have proposed that hippocampal activation reflects recollection of the prior occurrence of the memoranda (including, e.g., aspects of the context in which it occurred) rather than acontextual, familiarity-based recognition (e.g., Aggleton and Brown, 1999; Eldridge et al., 2000; Rugg and Yonelinas, 2003; Montaldi et al., 2006). Activation of the left hippocampus and medial prefrontal cortex has been specifically associated with personally relevant autobiographical events (Maguire and Mummery, 1999; Maguire et al., 2000).

Cabeza et al. (2004) measured brain activation using fMRI, as participants viewed photographs of familiar locations that had either been taken by the participant herself, or had been taken by a colleague and shown to the participant prior to the experiment, or were previously unseen. The participants classified the photos into own, other, or new. Stronger bilateral hippocampal and medial prefrontal activation was associated with the processing of their own photos vs. someone else's. The focus of Cabeza et al.'s experiment was on the different circumstances associated with the prior encoding of the picture (actually being there and taking the photo or simply having been shown it). Here, we have a slightly different aim as follows: to examine recollection of the recent prior presentation of stimuli in the standard laboratory paradigm and to look at how the participation of neural systems in this process is modulated as a function of the existence of prior autobiographical but non task-relevant associations to these stimuli.

The stimuli we chose are faces, which are well suited to this purpose for several reasons. The processing of faces does not necessarily involve the medial temporal lobe, whereas the hippocampus has been implicated in the processing of spatial scenes in perceptual tasks (Lee et al., 2005) and short term memory tasks (Hannula et al., 2006; Hartley et al., 2007). Thus, standard recognition memory tests using unfamiliar faces tend not to produce impairments in patients with focal hippocampal damage (Turriziani et al., 2004; Cipolotti et al., 2006; Bird et al., 2007; Taylor et al., 2007; Bird et al., 2008), whereas similar tests using unfamiliar scenes do produce

impairments (Cipolotti et al., 2006; Bird et al., 2007; Taylor et al., 2007; Bird et al., 2008). Recognition of words could be compared with recognition of nonwords but words come with pre-experimental associations that are less controllable and usually less personal. Thus recognition memory for words, unlike that for unfamiliar faces, is impaired by focal hippocampal damage (Bird and Burgess, 2008). Equally, the verbal descriptions of events most often used to test autobiographical memory are not well suited to a recognition memory paradigm. By contrast, presentation of familiar faces provides good experimental control compared with verbal descriptions and offers greater scope for being associated with personal information than most scenes. Thus, unknown faces provide a good baseline from which to look for additional effects of prior knowledge within the medial temporal lobe.

Klatzky and Forrest (1984) showed that recognition memory is better for famous faces than for unfamiliar faces. This performance advantage for famous faces reflected improved recognition of the previously presented faces rather than improved rejection of the foils or a difference in response bias. These data suggest that "the advantage of famous faces derives from the episode that is encoded when a face is viewed," explaining the absence of an advantage for the famous foil items. The advantage for famous faces did not simply reflect an increased ability to name the famous faces or an increased ability to recall the details of the face itself, suggesting that it "may reflect a nonverbal memory representation that is relatively abstract." There was also increased confidence in the correct responses for famous compared with unfamiliar faces. Overall, we suggest that the performance advantage for famous faces likely reflects a boost to episodic recollection provided by the richer context made available at encoding by the incidental pre-experimental associations of the familiar faces.

Previous neuroimaging studies of recognition memory for famous faces compared with unfamiliar faces have shown mixed results, some showing activation patterns similar to those for general episodic (Burgess et al., 2002) and autobiographical (event) memory (Maguire and Mummery, 1999; Maguire et al., 2000), including the medial temporal lobe (Leveroni et al., 2000; Haist et al., 2001; e.g., Bernard et al., 2004; Eger et al., 2005; Elfgren et al., 2006), and others not (Henson et al., 2003; Gobbini et al., 2004). One possibility is that famous faces vary in terms of their personal relevance, a participant can feel like they know some famous people almost as a friend, while only having a feeling of familiarity or factual knowledge about others (Westmacott and Moscovitch, 2003). In this study, we used pictures of faces of unfamiliar, famous, and personally known people and also asked participants how well they felt they knew each person. In this way, we could investigate the effect of a greater range of incidental personal knowledge (none for unfamiliar faces, a variable amount for famous faces, and plenty for personally known faces) on recognition memory.

During an encoding phase, we presented images of faces which were either (i) known personally; (ii) famous; or (iii) novel to the participant (novel and personally known face stim-
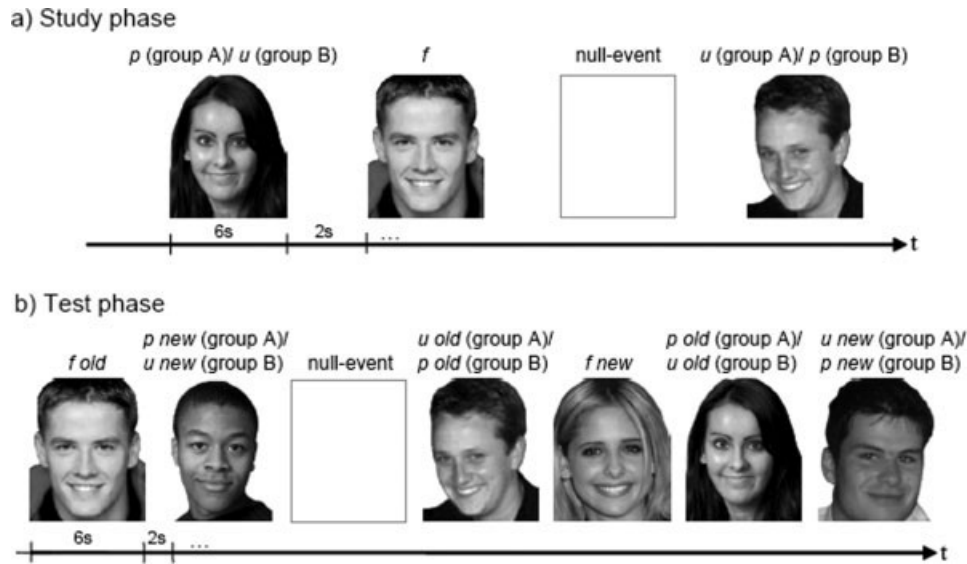
a) Study phase

b) Test phase

FIGURE 1.   **Experimental design. (a) Study phase (categorization task). Participants judge each face as famous (*f*), personally known (*p*), or unknown (*u*). (b) Test phase (recognition task). Faces from the study phase ("old"), and "new" faces were presented. Participants responded if they "clearly remembered" seeing the face during the study phase, including how they felt, or what came next (i.e., reflecting a process of "recollection"); "felt like they saw it in the first list, but without the above clarity and detail" (i.e., reflecting a feeling of "familiarity"); or if they knew that the face had "not" been presented previously.**

uli were drawn from the same set of faces, counterbalanced across participants). During a retrieval phase, we presented new faces and faces from the encoding phase from all three categories and asked participants to indicate which faces they could clearly recollect being presented in the presentation phase. Both phases occurred in an fMRI scanner. A postscan questionnaire asked participants to rate the attractiveness of the faces and, for personally known and famous faces, how well and for how long the person had been known, and how strong an emotional response was felt for each.

MATERIALS AND METHODS

Participants

Fourteen right-handed volunteers, aged between 20 and 23, were recruited. They were either "friends of A" (five female, two male) or "friends of B" (one female, six male). None had a history of neurological illness and all had either good eyesight or wore corrective contact lenses. Written consent was obtained in accord with the Institute of Neurology ethics committee.

Stimuli

One hundred forty-four face images were prepared, belonging to one of the three categories: famous faces, set A (friends of person A), and set B (friends of person B). Thus, on presentation of the whole range of stimuli, each group of participants viewed faces a third of which were famous (*f*), one third personally known (*p*), and one third unknown (*u*) to them. Half of each category's images were of females and half of males. Images of contemporary famous people's faces were obtained from the Internet. Care was taken to approximately match the famous faces to the other categories in depth and duration known as well as surface quality (similar expression, hairstyle, make up, etc.). Additionally, all faces were standardized into black and white pictures on a white background, see Figure 1.

Prescan Training

Immediately prior to scanning, participants undertook a shortened practice session of both tasks they would do in the scanner (the study phase and the test phase, see below), presented on a laptop computer. Participants responded by pressing three keys simulating the keypad used in the scanner. The 18 stimuli used for practice were extra faces that were not subsequently presented.

Scanning Experiment

Study phase: Categorization task "friend, famous, or unknown?"

Eighty-four faces were presented sequentially (28 famous, 28 personally known to group A, and 28 personally known to group B), plus 28 null events (presentation of a blank screen), using Cogent 2000 (http://www.vislab.ucl.ac.uk/Cogent/), implemented in MatLab 6.5 (The MathWorks Inc., Natick, MA). Participants indicated whether each stimulus face was famous, personally known, or unknown by pressing one of the three keys on a keypad.

In both the study phase and test phase (below), participants were instructed to respond as accurately and quickly as possible by pressing one of the three keys with their right hand. Response times were recorded. Stimuli were projected onto a screen, which the participants viewed by means of a mirror above their eyes in the scanner. Presentation of faces was pseudo-randomized in both parts of the experiment such that faces from the same category did not occur more than three times in a sequence. Each stimulus was presented for 6 s followed by a 2 s interval (a blank screen).

Test phase: Recognition task

The stimuli from the study phase were interleaved with 20 new faces from each category that participants had not seen before. As in the study phase, 28 null events were also interleaved. Participants were asked to press the left key if they "clearly remembered" seeing the face during the study phase, e.g., remembering how they felt or what came next; the middle key if they "felt like they saw it in the first list but without the above clarity and detail"; and the right key if they knew that the face had "not" been presented previously. The middle option was included to filter out responses based on a "feeling of familiarity" or guessing from those based on episodic recollection.

Postscan Questionnaire

Following scanning, participants completed a questionnaire about all 144 faces seen in the experiment. They assigned each face a category (famous, personally known, or unknown) and rated it for attractiveness (on a scale from 1 to 6). For the personally known and famous faces, they additionally answered as follows:

How long they had known the person (duration known), in years.

How well they felt they knew the person (from 1 to 6).

How strong an emotional response they felt for the person (1 to 6, positive, negative, or other).

fMRI Scanning

Forty T2*-weighted axial echoplanar images (EPI) per volume ($3 \times 3 \times 3$ mm voxels; $T_E = 30$ ms) with blood oxygenation level dependent (BOLD) contrast were acquired using a 3 Tesla Siemens Allegra scanner (Siemens, Erlangen, Germany). EPIs consisted of 2-mm thick axial slices (spacing = 1 mm), acquired in descending order. A total of 570 volumes were collected continuously with a repetition time (TR) of 2.6 s, with the first five volumes being discarded to allow for T1 equilibration effects. T1-weighted structural images were additionally obtained after completion of the task ($1 \times 1 \times 1$ mm voxels, 3D MDEFT acquisition sequence).

Data Analysis

Data were analyzed using Statistical Parametric Mapping (SPM5, Wellcome Trust Centre for Neuroimaging, UCL, UK).

The structural images underwent segmentation (into gray mater, white matter, and cerebro-spinal fluid), bias correction, and spatial normalization ("unified segmentation," (Ashburner and Friston, 2005)).

Functional images were realigned, unwarped, slice-time corrected, and normalized based on the spatial normalization parameters derived from the "unified segmentation" applied to the structural images. Finally, the functional images were spatially smoothed with an 8-mm FWHM Gaussian kernel. For each subject, the fMRI time-series was high-pass filtered (minimum cut-off period 128 s) and modeled as the weighted sum of regressors. Separate regressors were calculated according to each subject's own categorization of the faces during the study phase, i.e., "personally known" (p), "famous" (f), and "unknown" (u). Each regressor was defined as a series of delta functions timed 500 ms, after the appearance of the appropriate stimulus type, and convolved with SPM's standard hemodynamic response function.

For the test phase (i.e., the recognition test), the categorization of face type was based on subjects' responses during the study phase for "old" (i.e., previously presented) stimuli and according to their questionnaire responses for "new" (i.e., previously unseen) stimuli. The "old" stimuli were further subdivided into recollection-hits, guessed-hits, and misses, whereas "new" stimuli were subdivided into correct rejections and false alarms (including both "guessed" and "recollected" responses). In total, we generated 3 (face type) $\times$ 5 (recognition type) regressors and a separate regressor for the null-events.

The parameters for the best fitting model were estimated using SPM5. On the basis of these parameter estimates, the following second level analyses were performed: A 3×2 repeated measures ANOVA on data from the test phase over face type $\times$ recollection (recollection hits vs. correct rejections). Three conjunction models (Friston et al., 2005) were also calculated, bringing together pairwise comparisons of $p > u$, $p > f$, and $f > u$ from the study and the test phase.

Finally, three additional models for the study phase were generated, including parametric modulations of the above regressors. The first included the above regressors for p, f, and u faces, copies of them modulated by "attractiveness," the second the p and f regressors modulated by the parameter "duration known," and the third the p and f regressors modulated by the parameter "how well known", according to the postscanning questionnaire. For these models, single t-tests were run on the parameter estimates for each parametrically modulated regressor, revealing areas with an increase or decrease in activation according to (a) how attractive each face was rated ("attractiveness"), (b) the length of time each type of face had been known ("duration known"), and (c) "how well known" a face was rated. For these three analyses, we report activations in gray matter regions that fall within areas activated in the main effect of face type (see above). More generally, activations significant at $P < 0.001$, uncorrected, with a minimum cluster size of 20 voxels are reported. In addition, we tentatively report subthreshold activation in the medial temporal lobe, where it directly relates to a specific hypothesis under discussion.
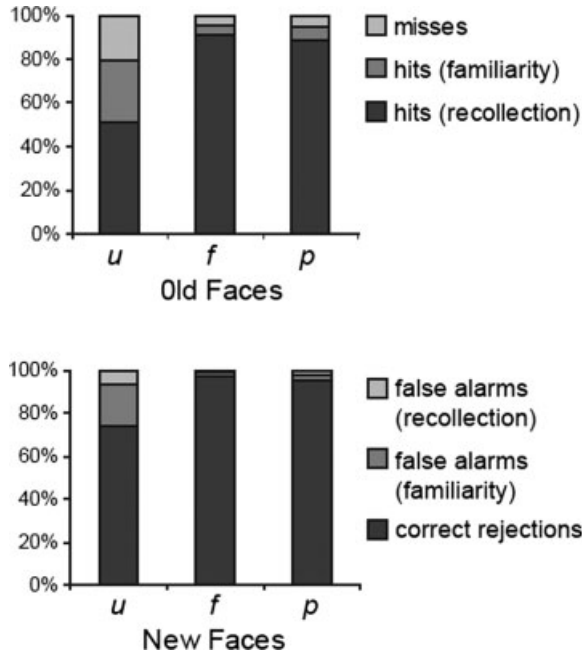
FIGURE 2. Behavioral data, showing average performance during the test phase recognition task, per face type: famous (*f*), personally known (*p*), unknown (*u*).

RESULTS

Behavioral Results

For the recognition task, analysis of variance (ANOVA) with factors face type (three levels) and recollection (two levels: hits vs. correct rejections) over the number of correct responses of each type revealed a significant effect of face type ($F_{2,26} = 16.4$ $P < 0.001$), a significant effect of recollection ($F_{1,13} = 15.0$, $P < 0.01$) and also a significant interaction ($F_{2,26} = 10.5$, $P < 0.001$), see Figure 2. Subsequent pairwise comparisons (Bonferroni corrected) showed that previous presentations of unknown faces were remembered less well than personally known ($P < 0.001$) and famous faces ($P = 0.027$), but there was no difference between personally known and famous faces ($P = 0.268$).

There is thus a behavioral effect of stimulus familiarity on old/new-recognition, which does not differentiate between famous and personally known faces.

Results From the Postscan Questionnaire

The results of the postscan questionnaire are summarized in Table 1. There was a significant difference between personally known and famous faces of "how well known" ($t_{13} = 3.47$, $P = 0.004$) and "duration known" ($t_{13} = 2.63$, $P = 0.02$). There was also a significant difference between personally known and famous faces for "emotionality" ratings ("How emotional do you feel about this person?" rescaled to -6 to -1 for negative emotions and $+1$ to $+6$ for positive emotions; $t_{13} = 2.35$, $P = 0.035$). The ratings of attractiveness varied significantly across all three face types (repeated measures one-way ANOVA $F_{2,26} = 40.15$, $P < 0.001$), with pairwise comparisons revealing that famous faces were more attractive than personally known and unknown faces (both $P < 0.001$). Personally known faces were rated more attractive than unknown faces ($P = 0.001$), even though personally known and unknown faces were counterbalanced across participants.

Notwithstanding the above differences, there was significant overlap in the ratings of how well participants felt they knew famous and personally known faces, with some famous faces achieving higher scores than some personally known ones, see Figure 3. Near ceiling performance for *f* and *p* faces (Fig. 2), as consistent with maximizing the fMRI signal for correct recollection of these faces, precludes a satisfactory item-by-item analysis of the effect of prior knowledge on performance. Nonetheless, consistent with Klatzky and Forrest (1984), the proportion of hits minus the proportion of false alarms is higher for the more-well-known (i.e., those above the subject's mean well-known rating) than less well known faces, but this difference does not reach significance (92.2% vs. 90.9%; $P = 0.3$). However, consistent with the overall difference in performance for *f* and *p* faces vs. *u* faces (Fig. 2), the more faces each subject rated as known during presentation (whether famous or personally known), the better their overall performance (correlation between number of correct responses and

TABLE 1.

Subjects' Ratings of the Faces From Postexperimental Questionnaire (Standard Deviation in Brackets)

|	Face category		
	Famous	Personally known	Unknown
Mean attractiveness ratings, scale = 1 to 6	3.73 (1.01)	3.06 (0.79)	2.24 (0.76)
Mean ratings of "duration known" ("How long do you know this person?"), in years	6.96 (1.78)	4.80 (2.47)	N/A
Mean ratings of "how well known" ("How well do you know this person?", scale = 1 to 6	1,90 (0,95)	2,83 (0,92)	N/A
Mean ratings of "emotionality" ("How emotional do you feel about this person?", scale = -6 to $+6$	1.69 (1.03)	2.35 (0.98)	N/A

Hippocampus
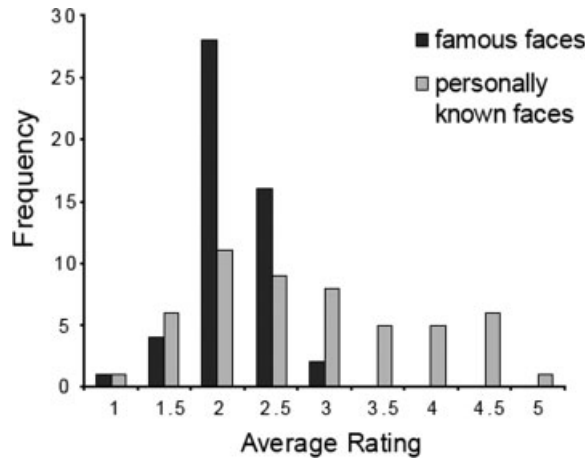
FIGURE 3. Frequency distribution of "How well known" ratings for famous and personally known faces, averaged across participants. Notice that some famous face stimuli received higher ratings than some personally known faces.

number of known faces over the 14 subjects: $r = 0.58$, $P = 0.03$).

fMRI Results: Recognition Test

A 3×2 ANOVA of face type $\times$ recollection of prior occurrence revealed two largely separate networks corresponding to the two main effects recollection of prior presentation on the one hand and pre-experimental knowledge (effect of face type) on the other hand. The main effect of recollection of prior occurrence was associated with bilateral activation in posterior cingulate, parieto-occipital sulcus, ventral striatum and precuneus (see Fig. 4a), and in precentral and middle frontal gyrus.

The main effect of face type was associated with extensive bilateral activation of the hippocampus, extending to amygdala, and ventromedial prefrontal cortex, extending dorsally (BA 9/10/11), retrosplenial cortex, parieto-occipital sulcus, and precuneus (BA 30/31/23), as well as angular gyrus (BA 39), anterior middle temporal cortex (BA 21), bilateral anterior insula (BA 13), and superior frontal gyrus (BA 8). See Figures 4a,b. An interaction between face type and recollection was seen in activation of the anterior and medial thalamus bilaterally. See Figure 4c.

To further examine these results, we plotted the percent signal change across conditions in several of our areas of interest. Activation in the posterior cingulate and parieto-occipital sulcus/precuneus was greater for hits than for correct rejections, showing an effect of prior presentation independent of face type (Fig. 5a), consistent with the significant effect of recollection in this area (see Table 2). By contrast, an adjacent activation in the retrosplenial cortex (see Fig. 4a for juxtaposition of the posterior activations) varied significantly with face type (Fig. 5bi), consistent with the significant effect of face type in this area (see Table 2), showing most activation for personally known faces, and more for famous faces than new faces, without significant modulation by prior presentation. A similar dependence on face type was seen in the ventro medial prefrontal cortex and hippocampus (Fig. 5bii,biii, and see Fig. 4). Finally, activation in the medial thalamus showed the strongest signal for correctly remembered unfamiliar faces compared with all
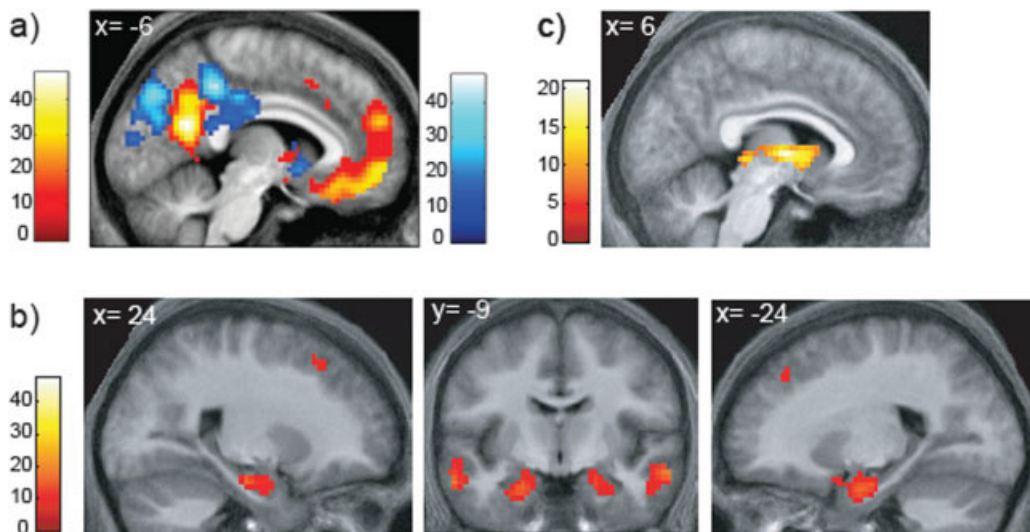

FIGURE 4. Activation corresponding to the main effects of recollection of prior presentation and of the presence of pre-experimental knowledge and to their interaction. (a) Activation for the main effects of recollection of prior presentation (blue) and of incidental pre-experimental knowledge (i.e., face type; red/yellow), showing activation of the precuneus and posterior cingulate (blue) and retrosplenial and medial prefrontal cortices (red/yellow). Activation is shown on the averaged normalized structural image across participants, both here and in the following figures. (b) Bilateral hippocampal activation corresponded to the main effect of prior knowledge (i.e., face type). (c) Dorsal thalamic activation showed an interaction between recollection and face type (greater activation for the recollection of prior presentation of unknown faces). Significance threshold: $P < 0.001$ uncorrected, extent threshold: 20 voxels. Colorbars show F-values. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]
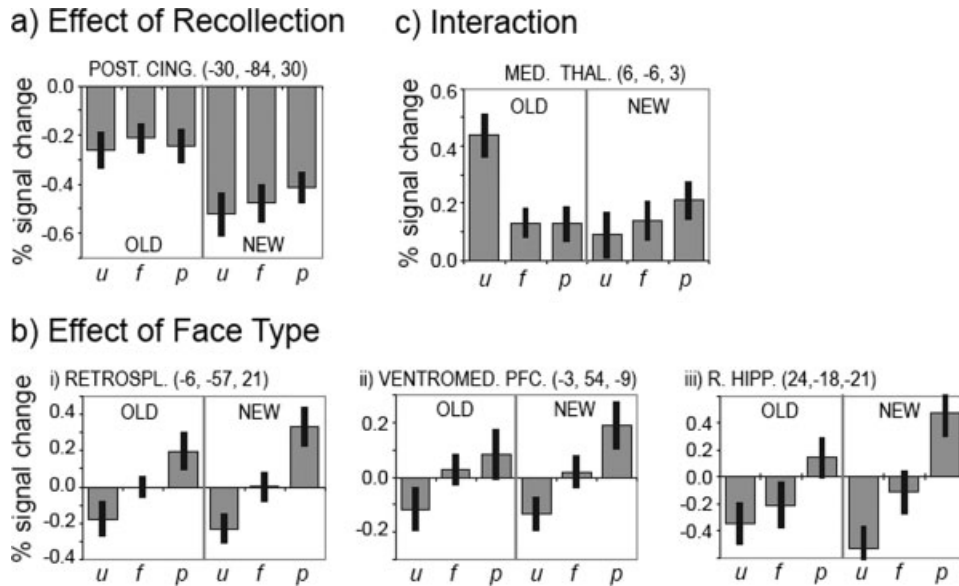
FIGURE 5. Percent signal change across conditions in various brain regions. (a) The posterior cingulate (at the location of the activation peak for the factor *recollection*) during the test phase recognition task. "old" = correctly remembered old faces; "new" = correctly rejected new faces; u = unknown; f = famous; p = personally known faces. (b) The activation peaks for the factor *face type* during the test phase recognition task. (i) retrosplenial cortex; (ii) ventromedial prefrontal cortex; (iii) right hippocampus. (c) Activation in anterior/medial thalamus shows a significant *interaction* effect, driven by activation for correct recollection of prior presentation of unknown faces.

other conditions, reflected in a significant face type × recollection interaction (see Table 2), see Figure 5c.

fMRI Results: Conjunctions Over Study and Test Phases

The comparison of $p > u$ yielded significant activations in the bilateral hippocampus, bilateral anterior middle temporal gyrus (BA 21), retrosplenial cortex (BA 30), and medial prefrontal/ orbitofrontal cortex (BA 9/10/11) common to both study and test phase. See Figure 6. The comparison of $f > u$ showed a similar but weaker pattern, with only the right anterior middle temporal gyrus (BA 21) and left orbitofrontal cortex (BA 11) surviving $P < 0.001$. Finally, the comparison of $p > f$ showed activations in ventromedial (BA 10/11) and dorsomedial (BA 9/10) prefrontal cortex that were common to both study and test phases, but no significant hippocampal activation. See Table 3. Thus actual personal knowledge for the person shown (compared with famous faces) was manifest in significant differences in ventromedial prefrontal activation, but not in medial temporal lobe activation.

Parametric Modulation of Activity by Subjective Ratings

Of the three parametric modulation models, only the model including the "how well known" parameter yielded significant results: activations in medial frontal cortex (BA9) and bilateral hippocampus were found to covary with "how well known" a personally known face was rated in the postscan questionnaire.

At a lowered threshold, of $P = 0.05$, activation in the hippocampus was found which covaried with "how well known" a famous face was rated. See Table 4.

DISCUSSION

We set out to explore the role of different degrees of incidental pre-experimental knowledge on the recollection of a recent previous presentation of a stimulus, using personally known and famous faces to embody prior knowledge in comparison to unknown faces. In terms of behavior we replicated a well documented advantage for familiar stimuli (Rogers et al., 1977; Klatzky and Forrest, 1984; e.g., Craik et al., 1999; Westmacott and Moscovitch, 2003), showing significantly better retrieval performance for personally known and famous faces compared with unknown faces. In terms of brain activation, our two-way ANOVA of face-type vs. recollection-of-prior-presentation revealed two distinct networks. The network reflecting the main effect of recollection-of-prior-presentation included the superior parietal gyrus, posterior parieto-occipital sulcus, and posterior cingulate (BA39/31/7/19), as well as the ventral striatum. These activations did not vary with the level of participants' pre-experimental knowledge of the stimuli. The complementary network, reflecting pre-experimental knowledge (the main effect of face type) included retrosplenial cortex/ anterior parieto-occipital sulcus, angular gyrus, together with the hippocampus, amygdala and lateral temporal cortices (BA 21). This latter network was found to be activated at both study

TABLE 2.

Significant Activations During the Test Phase Recognition Task for Different Factors (3 × 2 ANOVA; Face-Type × Recollection of Prior Presentation)

	Region		Hemisphere	Location	Z score	Extent
Effect of Face type	Inferior occipital gyrus	BA 19	L	−27 −78 −12	3.95	33
	Retrosplenial cortex, anterior precuneus	BA 30/31/23	L&R	−6 −57 21	7.50	543
	Angular gyrus	BA 39	L&R	−42 −63 24	4.88	197
				54 −48 15	3.92	103
	Hippocampus, extending to amygdala		L&R	−24 −18 −21	4.70	115
				24 −18 −21	4.68	68
	Anterior middle temporal gyrus	BA 21	L&R	−60 −18 −21	5.63	139
				63 −9 −15	5.04	155
	Basal forebrain		L&R	0 3 −9	4.62	22
	Globus pallidus		L	−9 3 3	3.79	24
	Cingulate sulcus	BA 6	L&R	3 18 39	4.56	79
	Anterior insula	BA 13	L&R	39 15 −6	3.85	41
				−33 21 −6	4.02	58
	Lateral orbital gyrus	BA 11	L	−36 27 −21	4.65	31
	Superior frontal gyrus	BA 8	L&R	21 27 48	3.80	22
				−18 36 42	4.87	45
	Ventromedial, extending to dorsomedial, prefrontal cortex	BA 10/9	L&R	−3 54 −9	7.17	986
				−3 −42 42	5.98	1559
Effect of Recollection	Posterior cingulate, superior parietal gyrus, posterior precuneus	BA 39/31/7/19	L&R	−6 −87 12	3.80	53
				−30 −84 30	4.36	227
	Calcarine sulcus		R	24 −69 3	4.01	31
	Precentral gyrus	BA 4	L&R	−39 −27 57	4.97	110
	Middle frontal gyrus	BA 6	L	−39 6 39	4.67	36
	Ventral striatum		L&R	12 9 −9	5.10	65
				−9 9 −6	4.36	47
Interaction Face type × Recollection	Anterior and medial thalamus		L&R	6 −6 3	5.29	186

The region (including Brodmann Area; BA, and laterality) is shown with the location of the peak activation in MNI coordinates (x, y, z), along with the Z-score equivalent to its reliability across subjects and the extent of the cluster in voxels. A significance threshold of $P < 0.001$ uncorrected and an extent threshold of 20 voxels were used.

and test, and, importantly, was not modulated by whether or not the face had been recently presented (hits vs. correct rejections).

Activation of the hippocampus, retrosplenial and medial prefrontal cortices during recollection of recent prior presentation is thus driven by retrieval of incidental pre-experimental knowledge, rather than by the act of recalling its recent presentation. Note that correctly recalling unknown faces did not yield MTL activation at all. By contrast, the main effect of recollection in the mid/posterior cingulate and precuneus shows equal signal change for correctly remembered unknown faces as well as famous and personally known faces. The interaction of the two main effects yielded greater activation for recognition of unfamiliar faces in the anterior and medial thalamus, suggesting modulation of retrieval-related activation by task difficulty since unknown faces were remembered significantly less well over all.

The network associated with pre-experimental knowledge, including the medial temporal lobe, yielded preferential activation for both famous and personally known faces compared with unknown faces, with several regions also showing a trend toward greater activation for personally known than famous faces. Thus personally known vs. famous faces were found to differ quantitatively rather than categorically in terms of retrieval of incidental pre-experimental knowledge. This interpretation is corroborated by the finding that medial temporal activation increased with how well known personally known faces were rated, with a similar but weaker (subthreshold) finding for famous faces. The increased activation of this network of areas with participant's increasing knowledge of the faces is also supported by a recent study using pictures of the faces of close relatives (Taylor et al., 2009). There was also a significantly higher proportion of recollection hits in the recognition of prior presentation of known faces (whether famous or personally known) than in the recognition of prior presentation of unknown faces (Fig. 2). Thus, hippocampal activation appears to correspond to the retrieval of incidental autobiographical information which in turn boosts recollection for familiar relative to unfamiliar items, rather than necessarily supporting recollection of the recent presentation of unfamiliar items themselves.
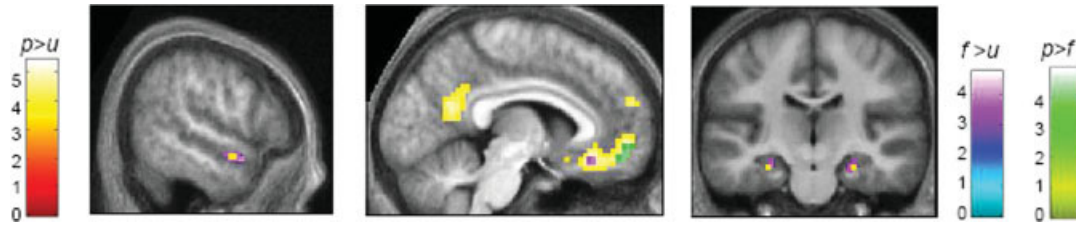
FIGURE 6. Superposition of the three conjunction contrasts over study and test phases, personally known vs. unknown (*p* > *u*; red/yellow), famous vs. unknown (*f* > *u*; blue/purple) and personally known vs. famous (*p* > *f*; green). Showing lateral temporal (left panel), retrosplenial and medial prefrontal (middle panel) and hippocampal (right panel) activation. Note how areas activated for *f* > *u* overlap the activations for *p* > *u*, with the *p* > *u* activated being much more prominent in retrosplenial and medial prefrontal areas. The medial prefrontal area includes a smaller activation for *p* > *f*. Significance threshold *P* = 0.001 uncorrected for *p* > *f* and *p* > *u*; *P* = 0.005 uncorrected for *f* > *u*. Color bars show equivalent Z scores. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

This interpretation is also consistent with the more general finding that items encoded with more contextual associations produce greater activation of the same network of areas, including the hippocampus, retrosplenial and ventromedial prefrontal areas (Peters et al., 2009). In addition, the retrieval of incidental contextual information at encoding may contribute to the link between hippocampal activation at encoding and subsequent memory performance (Wagner et al., 1998).

The idea that episodic retrieval is enhanced by autobiographical knowledge, when present, but can also function without it, is broadly consistent with Conway's idea that episodic memories can be embedded within autobiographical memory (Conway and Pleydell-Pearce, 2000; Conway, 2001) and with Tulving's proposal of parallel retrieval from semantic and episodic memory systems (Tulving and Markowitsch, 1998), see also (Burgess and Shallice, 1996; Levine et al., 2004). Our findings corroborate Klatzky and Forrest's (1984) suggestion that improved recognition of famous faces reflects enhanced encoding of the initial presentation supported by relatively abstract pre-experimental information. The network activated by pre-experimental knowledge, including the hippocampus, likely supports the incidental retrieval of this pre-experimental information, which in turn enhances episodic recollection.

Our results are consistent with the idea that public or semantic knowledge, such as that concerning famous people, often co-occurs with autobiographical information, such as

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TABLE 3.

Significant Activation Peaks for Conjunction Analyses of Activation Common to the Study and Test Phases

	Region		Hemisphere	Location	Z score	Extent
p > *u*	Retrosplenial cortex	BA 30	L&R	−3 −60 15	4.12	124
	Hippocampus		L&R	27 −21 −18	3.17	1
				−21 −12 −24	3.36	11
	Anterior middle temporal gyrus	BA 21	L&R	−57 −18 −18	3.72	18
				−51 9 −27	3.21	6
				57 0 −15	3.44	8
				42 18 −30	3.19	1
	Orbitofrontal cortex	BA 11	L&R	−3 15 −15	3.21	3
	Medial prefrontal cortex	BA 10		−9 33 −15	4.39	232
		BA 9/10		9 51 21	4.41	69
f > *u*	Hippocampus[a]		L&R	−27 −24 −18	3.00	4
				24 −21 −21	2.80	5
	Anterior middle temporal gyrus	BA 21	R	57 −3 −12	4.01	12
	Orbitofrontal cortex	BA 11	L	−6 30 −21	3.67	5
p > *f*	Parieto-occipital sulcus	BA 17	L&R	3 −63 21	3.19	1
	Subcallosal gyrus	BA 25	L&R	0 3 −12	3.75	8
	Orbitofrontal cortex	BA 11	R	9 36 −18	3.17	1
	Ventromedial prefrontal cortex	BA 10/11	L&R	0 45 −18	3.27	3
				−6 51 −12	4.13	21
	Dorsomedial prefrontal cortex	BA 9/10	L&R	9 48 18	4.12	18

Details as Table 2 unless indicated otherwise. No extent threshold applied.
p, personally known; *f*, famous; *u*, unknown faces.
[a] *P* < 0.005 uncorrected.

Hippocampus

Activation Peaks that Fall Within the Areas Activated by the Main Effect of Face Type Which Covary With how the Participants Felt that They Knew Each Face

	Region	Hemi-sphere	Location	Z score	Extent
p how well	Medial frontal gyrus BA 9		0 45 18	4.11	23
	Hippocampus[a]	L&R	24 −06 −27	3.16	1
			21 −9 −18	3.18	1
			−21 −12 −18	3.21	1
f how well	Hippocampus[b]	L	−27 −21 −21	2.10	5

Details as Table 2 unless indicated otherwise.
[a]no extent threshold.
[b]no extent threshold, $P < 0.05$ uncorrected.

remembering one's own actions and thoughts when acquiring that knowledge (see also Westmacott and Moscovitch 2003). The variability in how well participants feel they know different famous people may explain the variability of the activation of the classic autobiographical retrieval network, including the hippocampus, in previous studies using famous faces, compare, e.g., (Leveroni et al., 2000; Haist et al., 2001; Bernard et al., 2004; Eger et al., 2005; Elfgren et al., 2006) with, e.g., (Henson et al., 2003; Gobbini et al., 2004).

Our results are also consistent with the findings of recognition memory experiments using words and nonwords. Words provoke more recollective responses (compared with familiarity responses) during a recognition memory test than do nonwords (Gardiner and Java, 1990). Consistent with our interpretation of the classic episodic memory system as supporting the additional recollective performance found for stimuli with pre-experimental knowledge, amnesic patients do not show the pattern of increased recollection for words relative to nonwords found in healthy controls (Rajaram et al., 2002). Recollection of words has been seen to correspond to hippocampal activation (Henson et al., 1999; Eldridge et al., 2000). We would predict an absence of hippocampal activation in similar studies using nonwords.

An interesting dissociation was seen between adjacent posterior midline effects. Activation of the mid/posterior cingulate and posterior precuneus reflected recollection of prior presentation (Fig. 4a, blue), whereas activation of the intervening retrosplenial cortex/anterior precuneus reflected pre-experimental knowledge (Fig. 4a, red). The precuneus and parietal occipital sulcus have long been associated with memory retrieval, imagery and "attention to internal representations" (Fletcher et al., 1995; Burgess et al., 2001b; Maguire, 2001; Wagner et al., 2005; Wallentin et al., 2006; Byrne et al., 2007; Hassabis et al., 2007). However, the present findings indicate a functional division within the posterior midline cortex. The retrosplenial activation corresponding to the extent of incidental pre-experimental knowledge may reflect the generation of detailed visual imagery from long term representations (Burgess et al., 2001a; Byrne et al., 2007). By contrast, the posterior precuneus and mid/posterior cingulate activations may reflect

the represention of information specific to the recent presentation itself.

We also found a significant effect of face type in the amygdala which is consistent with the attribution of greatest emotionality to personally known faces in the post scan questionnaire, given the association of the amygdala with emotional processing (Cahill et al., 1995; Fink et al., 1996; Cahill and McGaugh, 1998; Hamann et al., 1999; LeDoux, 2000; Markowitsch et al., 2000; Markowitsch et al., 2003; Strange and Dolan, 2004). The lateral temporal activations are consistent with the reports of Sugiura et al. (2006), who investigated neural activity in a name detection task involving the visual presentation of personally familiar, famous, and unfamiliar names. These authors also found bilateral anterolateral temporal activation for personally known or famous names vs. unfamiliar names. These activations may reflect the retrieval of semantic information regarding personally known and famous stimuli, consistent with neuropsychological impairments resulting from semantic dementia and lateral temporal pole damage (Snowden et al., 1994; e.g., Graham and Hodges, 1997; Graham et al., 2003).

Finally, the area showing greatest difference in activation between personally known and famous faces (conjunction over study phase and recognition test of $p > f$) was the medial prefrontal cortex, both ventrally and more dorsally. In terms of behavioral findings, there was no significant difference in retrieval performance between personally known and famous faces, but according to questionnaire responses personally known faces were better and longer known and rated more emotional, all attributes of vivid autobiographical memory. This fits well with the consistent identification of the medial prefrontal cortex in neuroimaging studies of autobiographical memory (Maguire and Mummery, 1999; Maguire et al., 2000; Ryan et al., 2001; e.g., Addis et al., 2004; Cabeza et al., 2004; Gilboa et al., 2004), especially when the memory had the connotation of personal involvement, see Maguire et al. (2001). The fact that the incidentally retrieved memories by the personally known faces might be most "dear to the self" further supports the idea that this area is related to the representation of the "self" (Hodges and Gurd, 1994; Levine et al., 1998; Craik et al., 1999;

Gusnard et al., 2001; Maguire et al., 2001; Kelley et al., 2002; Wicker et al., 2003; Cabeza et al., 2004; Mitchell et al., 2006).

CONCLUSIONS

Recollection of the prior presentation of a stimulus is aided by the presence of incidental contextual associations to the stimulus. By varying the availability of incidental associations to the face stimuli used, we found two largely distinct networks supporting the recollection of a prior presentation of known faces on the one hand and the successful recognition of novel faces on the other hand. The hippocampus, retrosplenial and medial prefrontal cortices responded to known faces (both famous and personally known) during encoding and retrieval phases, irrespective of whether or not the face had been recently presented. By contrast, activation of mid/posterior cingulate, posterior medial parietal areas and the ventral striatum corresponded to recollection of prior presentation (hits vs. correct rejections) irrespective of face type. Our results also reveal several more detailed findings. There is a dissociation between retrosplenial activation for pre-experimental knowledge, similarly to medial temporal and medial prefrontal activation, and adjacent activations in precuneus and mid/posterior cingulate for recollection of recent prior presentation. The medial prefrontal activation was significantly greater for personally known than famous faces, consistent with a role in processing related to the "self". The hippocampal activations reflected the extent to how well the participant felt they knew the person whose face was shown.

Perhaps most importantly, our results indicate that activation of the hippocampus during recollection of recent prior presentation of a stimulus can reflect retrieval of incidental pre-experimental knowledge about the stimulus, rather than necessarily supporting correct recollection of a recent presentation per se (Bird and Burgess, 2008). The availability of additional pre-experimental contextual information, allowing stimulus presentation to trigger richer and more elaborated thoughts, likely underlies the recollection advantage of well known compared with novel stimulus items.

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REFERENCES

Addis DR, Moscovitch M, Crawley AP, McAndrews MP. 2004. Recollective qualities modulate hippocampal activation during autobiographical memory retrieval. Hippocampus 14:752–762.

Aggleton JP, Brown MW. 1999. Episodic memory, amnesia, and the hippocampal-anterior thalamic axis. Behav Brain Sci 22:425–490.

Ashburner J, Friston KJ. 2005. Unified segmentation. Neuroimage 26:839–851.

Bernard FA, Bullmore ET, Graham KS, Thompson SA, Hodges JR, Fletcher PC. 2004. The hippocampal region is involved in successful recognition of both remote and recent famous faces. Neuroimage 22:1704–1714.

Bird CM, Burgess N. 2008. Contextual support for familiar items may explain the hippocampal-dependence of recognition memory for words but not faces. Curr Biol 18:1932–1936.

Bird CM, Shallice T, Cipolotti L. 2007. Fractionation of memory in medial temporal lobe amnesia. Neuropsychologia 45:1160–1171.

Bird CM, Vargha-Khadem F, Burgess N. 2008. Impaired memory for scenes but not faces in developmental hippocampal amnesia: A case study. Neuropsychologia 46:1050–1059.

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

Burgess N, Becker S, King JA, O'Keefe J. 2001a. Memory for events and their spatial context: Models and experiments. Philos Trans R Soc Lond B Biol Sci 356:1493–1503.

Burgess N, Maguire E, O'Keefe J. 2002. The human hippocampus and spatial and episodic memory. Neuron 35:625

Burgess N, Maguire EA, Spiers HJ, O'Keefe J. 2001b. A temporoparietal and prefrontal network for retrieving the spatial context of lifelike events. Neuroimage 14:439–453.

Byrne P, Becker S, Burgess N. 2007. Remembering the past and imagining the future: A neural model of spatial memory and imagery. Psychol Rev 114:340–375.

Cabeza R, Nyberg L. 2000. Imaging cognition. II. An empirical review of 275 PET and fMRI studies. J Cogn Neurosci 12:1–47.

Cabeza R, St Jacques P. 2007. Functional neuroimaging of autobiographical memory. Trends Cogn Sci 11:219–227.

Cabeza R, Prince SE, Daselaar SM, Greenberg DL, Budde M, Dolcos F, LaBar KS, Rubin DC. 2004. Brain activity during episodic retrieval of autobiographical and laboratory events: An fMRI study using a novel photo paradigm. J Cogn Neurosci 16:1583–1594.

Cahill L, McGaugh JL. 1998. Mechanisms of emotional arousal and lasting declarative memory. Trends Neurosci 21:294–299.

Cahill L, Babinsky R, Markowitsch HJ, McGaugh JL. 1995. The amygdala and emotional memory. Nature 377:295–296.

Cipolotti L, Bird C, Good T, Macmanus D, Rudge P, Shallice T. 2006. Recollection and familiarity in dense hippocampal amnesia: A case study. Neuropsychologia 44:489–506.

Cohen NJ, Eichenbaum H. 1993 Memory, Amnesia and the Hippocampal System. Cambridge, Massachusettes: MIT Press.

Conway MA. 2001. Sensory-perceptual episodic memory and its context: Autobiographical memory. Philos Trans R Soc Lond B Biol Sci 356:1375–1384.

Conway MA, Pleydell-Pearce CW. 2000. The construction of autobiographical memories in the self-memory system. Psychol Rev 107:261–288.

Craik FIM, Moroz TM, Moscovitch M, Stuss DT, Winocur G, Tulving E, Kapur S. 1999. In search of the self: A positron emission tomography study. Psychol Sci 10:26–34.

Eger E, Schweinberger SR, Dolan RJ, Henson RN. 2005. Familiarity enhances invariance of face representations in human ventral visual cortex: fMRI evidence. Neuroimage 26:1128–1139.

Eldridge LL, Knowlton BJ, Furmanski CS, Bookheimer SY, Engel SA. 2000. Remembering episodes: A selective role for the hippocampus during retrieval. Nat Neurosci 3:1149–1152.

Elfgren C, van Westen D, Passant U, Larsson EM, Mannfolk P, Fransson P. 2006. fMRI activity in the medial temporal lobe during famous face processing. Neuroimage 30:609–616.

Fink GR, Markowitsch HJ, Reinkemeier M, Bruckbauer T, Kessler J, Heiss WD. 1996. Cerebral representation of one's own past: Neural networks involved in autobiographical memory. J Neurosci 16:4275–4282.

Fletcher PC, Henson RN. 2001. Frontal lobes and human memory: Insights from functional neuroimaging. Brain 124:849–881.

Fletcher PC, Frith CD, Baker SC, Shallice T, Frackowiak RSJ, Dolan RJ. 1995. The mind's eye—Precuneus activation in memory-related imagery. Neuroimage 2:195–200.

Fletcher PC, Shallice T, Frith CD, Frackowiak RS, Dolan RJ. 1998. The functional roles of prefrontal cortex in episodic memory. II. Retrieval. Brain 121:1249–1256.

Friston KJ, Penny WD, Glaser DE. 2005. Conjunction revisited. Neuroimage 25:661–667.

Gardiner JM, Java RI. 1990. Recollective experience in word and non-word recognition. Mem Cognit 18:23–30.

Gilboa A. 2004. Autobiographical and episodic memory-one and the same? Evidence from prefrontal activation in neuroimaging studies. Neuropsychologia 42:1336–1349.

Gilboa A, Winocur G, Grady CL, Hevenor SJ, Moscovitch M. 2004. Remembering our past: Functional neuroanatomy of recollection of recent and very remote personal events. Cereb Cortex 14:1214–1225.

Gobbini MI, Leibenluft E, Santiago N, Haxby JV. 2004. Social and emotional attachment in the neural representation of faces. Neuroimage 22:1628–1635.

Graham KS, Hodges JR. 1997. Differentiating the roles of the hippocampal complex and the neocortex in long-term memory storage: Evidence from the study of semantic dementia and Alzheimer's disease. Neuropsychology 11:77–89.

Graham KS, Lee AC, Brett M, Patterson K. 2003. The neural basis of autobiographical and semantic memory: New evidence from three PET studies. Cogn Affect Behav Neurosci 3:234–254.

Greenberg DL, Rice HJ, Cooper JJ, Cabeza R, Rubin DC, Labar KS. 2005. Co-activation of the amygdala, hippocampus and inferior frontal gyrus during autobiographical memory retrieval. Neuropsychologia 43:659–674.

Gusnard DA, Akbudak E, Shulman GL, Raichle ME. 2001. Medial prefrontal cortex and self-referential mental activity: Relation to a default mode of brain function. Proc Natl Acad Sci USA 98:4259–4264.

Haist F, Bowden GJ, Mao H. 2001. Consolidation of human memory over decades revealed by functional magnetic resonance imaging. Nat Neurosci 4:1139–1145.

Hamann SB, Ely TD, Grafton ST, Kilts CD. 1999. Amygdala activity related to enhanced memory for pleasant and aversive stimuli. Nat Neurosci 2:289–293.

Hannula DE, Tranel D, Cohen NJ. 2006. The long and the short of it: Relational memory impairments in amnesia, even at short lags. J Neurosci 26:8352–8359.

Hartley T, Bird CM, Chan D, Cipolotti L, Husain M, Vargha-Khadem F, Burgess N. 2007. The hippocampus is required for short-term topographical memory in humans. Hippocampus 17:34–48.

Hassabis D, Kumaran D, Maguire EA. 2007. Using imagination to understand the neural basis of episodic memory. J Neurosci 27:14365–14374.

Henson RNA, Rugg MD. 2002. Neural response suppression, haemodynamic repetition effects, and behavioral priming. Neuropsychologia 41:263–270.

Henson RN, Goshen-Gottstein Y, Ganel T, Otten LJ, Quayle A, Rugg MD. 2003. Electrophysiological and haemodynamic correlates of face perception, recognition and priming. Cereb Cortex 13:793–805.

Henson RN, Rugg MD, Shallice T, Josephs O, Dolan RJ. 1999. Recollection and familiarity in recognition memory: An event-related functional magnetic resonance imaging study. J Neurosci 19:3962–3972.

Hodges JR, Gurd JM. 1994. Remote memory and lexical retrieval in a case of frontal Pick's disease. Arch Neurol 51:821–827.

Jacoby LL. 1991. A process dissociation framework: Separating automatic from intentional uses of memory. J Mem Lang 30:513–541.

Kelley WM, Macrae CN, Wyland CL, Caglar S, Inati S, Heatherton TF. 2002. Finding the self? An event-related fMRI study. J Cogn Neurosci 14:785–794.

King JA, Hartley T, Spiers HJ, Maguire EA, Burgess N. 2005. Anterior prefrontal involvement in episodic retrieval reflects contextual interference. Neuroimage 28:256–267.

Klatzky RL, Forrest FH. 1984. Recognizing familiar and unfamiliar faces. Mem Cognit 12:60–70.

LeDoux JE. 2000. Emotion circuits in the brain. Annu Rev Neurosci 23:155–184.

Lee AC, Buckley MJ, Pegman SJ, Spiers HJ, Scahill VR, Gaffan D, Bussey TJ, Davies RR, Kapur N, Hodges JR, Graham KS. 2005. Specialization in the medial temporal lobe for processing of objects and scenes. Hippocampus 15:782–797.

Leveroni CL, Seidenberg M, Mayer AR, Mead LA, Binder JR, Rao SM. 2000. Neural systems underlying the recognition of familiar and newly learned faces. J Neurosci 20:878–886.

Levine B, Black SE, Cabeza R, Sinden M, McIntosh AR, Toth JP, Tulving E, Stuss DT. 1998. Episodic memory and the self in a case of isolated retrograde amnesia. Brain 121:1951–1973.

Levine B, Turner GR, Tisserand D, Hevenor SJ, Graham SJ, McIntosh AR. 2004. The functional neuroanatomy of episodic and semantic autobiographical remembering: A prospective functional MRI study. J Cogn Neurosci 16:1633–1646.

Maguire EA. 2001. The retrosplenial contribution to human navigation: A review of lesion and neuroimaging findings. Scand J Psychol 42:225–238.

Maguire EA, Mummery CJ. 1999. Differential modulation of a common memory retrieval network revealed by positron emission tomography. Hippocampus 9:54–61.

Maguire EA, Mummery CJ, Büchel C. 2000. Patterns of hippocampal-cortical interaction dissociate temporal lobe memory subsystems. Hippocampus 10:475–482.

Maguire EA, Vargha-Khadem F, Mishkin M. 2001. The effects of bilateral hippocampal damage on fMRI regional activations and interactions during memory retrieval. Brain 124:1156–1170.

Mandler G. 1980. Recognizing: The judgment of previous occurence. Psychol Rev 87:252–271.

Maratos EJ, Dolan RJ, Morris JS, Henson RN, Rugg MD. 2001. Neural activity associated with episodic memory for emotional context. Neuropsychologia 39:910–920.

Markowitsch HJ, Thiel A, Reinkemeier M, Kessler J, Koyuncu A, Heiss WD. 2000. Right amygdalar and temporofrontal activation during autobiographic, but not during fictitious memory retrieval. Behav Neurol 12:181–190.

Markowitsch HJ, Vandekerckhove MM, Lanfermann H, Russ MO. 2003. Engagement of lateral and medial prefrontal areas in the ecphory of sad and happy autobiographical memories. Cortex 39:643–665.

Mitchell JP, Macrae CN, Banaji MR. 2006. Dissociable medial prefrontal contributions to judgments of similar and dissimilar others. Neuron 50:655–663.

Montaldi D, Spencer TJ, Roberts N, Mayes AR. 2006. The neural system that mediates familiarity memory. Hippocampus 16:504–520.

Moscovitch M, Rosenbaum RS, Gilboa A, Addis DR, Westmacott R, Grady C, McAndrews MP, Levine B, Black S, Winocur G, Nadel L. 2005. Functional neuroanatomy of remote episodic, semantic and spatial memory: A unified account based on multiple trace theory. J Anat 207:35–66.

O'Keefe J, Nadel L. 1978. The Hippocampus as a Cognitive Map. Oxford: Oxford University Press.

Peters J, Daum I, Gizewski E, Forsting M, Suchan B. 2009. Associations evoked during memory encoding recruit the context-network. Hippocampus 19:141–151.

Phelps EA. 2004. Human emotion and memory: Interactions of the amygdala and hippocampal complex. Curr Opin Neurobiol 14:198–202.

Piefke M, Weiss PH, Zilles K, Markowitsch HJ, Fink GR. 2003. Differential remoteness and emotional tone modulate the neural correlates of autobiographical memory. Brain 126:650–668.

Rajaram S, Hamilton M, Bolton A. 2002. Distinguishing states of awareness from confidence during retrieval: Evidence from amnesia. Cogn Affect Behav Neurosci 2:227–235.

Rogers TB, Kuiper NA, Kirker WS. 1977. Self-reference and the encoding of personal information. J Pers Soc Psychol 35:677–688.

Rugg MD, Yonelinas AP. 2003. Human recognition memory: A cognitive neuroscience perspective. Trends Cogn Sci 7:313–319.

Ryan L, Nadel L, Keil K, Putnam K, Schnyer D, Trouard T, Moscovitch M. 2001. Hippocampal complex and retrieval of recent and very remote autobiographical memories: Evidence from functional magnetic resonance imaging in neurologically intact people. Hippocampus 11:707–714.

Schacter DL, Wagner AD. 1999. Medial temporal lobe activations in fMRI and PET studies of episodic encoding and retrieval. Hippocampus 9:7–24.

Scoville WB, Milner B. 1957. Loss of recent memory after bilateral hippocampal lesions. J Neurol Neurosurg Psychiatry 20:11–21.

Shallice T, Fletcher P, Frith CD, Grasby P, Frackowiak RS, Dolan RJ. 1994. Brain regions associated with acquisition and retrieval of verbal episodic memory. Nature 368:633–635.

Snowden JS, Griffiths HL, Neary D. 1994. Semantic dementia: Autobiographical contribution to preservation of meaning. Cog Neuropsych 11:265–288.

Squire LR, Zola-Morgan S. 1991. The medial temporal lobe memory system. Science 253:1380–1386.

Strange BA, Dolan RJ. 2004. Beta-adrenergic modulation of emotional memory-evoked human amygdala and hippocampal responses. Proc Natl Acad Sci USA 101:11454–11458.

Sugiura M, Sassa Y, Watanabe J, Akitsuki Y, Maeda Y, Matsue Y, Fukuda H, Kawashima R. 2006. Cortical mechanisms of person representation: Recognition of famous and personally familiar names. Neuroimage 31:853–860.

Svoboda E, McKinnon MC, Levine B. 2006. The functional neuroanatomy of autobiographical memory: A meta-analysis. Neuropsychologia 44:2189–2208.

Taylor MJ, Arsalidou M, Bayless SJ, Morris D, Evans JW, Barbeau EJ. 2009. Neural correlates of personally familiar faces: Parents, partner and own faces. Hum Brain Mapp 30:2008–2020.

Taylor KJ, Henson RN, Graham KS. 2007. Recognition memory for faces and scenes in amnesia: Dissociable roles of medial temporal lobe structures. Neuropsychologia 45:2428–2438.

Tulving E. 1985. Memory and consciousness. Can Psychol 26:1–12.

Tulving E, Markowitsch HJ. 1998. Episodic and declarative memory: Role of the hippocampus. Hippocampus 8:198–204.

Tulving E, Kapur S, Markowitsch HJ, Craik FI, Habib R, Houle S. 1994. Neuroanatomical correlates of retrieval in episodic memory: Auditory sentence recognition. Proc Natl Acad Sci USA 91:2012–2015.

Turriziani P, Fadda L, Caltagirone C, Carlesimo GA. 2004. Recognition memory for single items and for associations in amnesic patients. Neuropsychologia 42:426–433.

Viard A, Piolino P, Desgranges B, Chetelat G, Lebreton K, Landeau B, Young A, De La Sayette V, Eustache F. 2007. Hippocampal activation for autobiographical memories over the entire lifetime in healthy aged subjects: An fMRI study. Cereb Cortex 17:2453–2467.

Wagner AD, Schacter DL, Rotte M, Koutstaal W, Maril A, Dale AM, Rosen BR, Buckner RL. 1998. Building memories: Remembering and forgetting of verbal experiences as predicted by brain activity. Science 281:1188–1191.

Wagner AD, Shannon BJ, Kahn I, Buckner RL. 2005. Parietal lobe contributions to episodic memory retrieval. Trends Cogn Sci 9:445–453.

Wallentin M, Roepstorff A, Glover R, Burgess N. 2006. Parallel memory systems for talking about location and age in precuneus, caudate and Broca's region. Neuroimage 32:1850–1864.

Westmacott R, Moscovitch M. 2003. The contribution of autobiographical significance to semantic memory. Mem Cognit 31:761–774.

Wicker B, Ruby P, Royet JP, Fonlupt P. 2003. A relation between rest and the self in the brain? Brain Res Brain Res Rev 43:224–230.

Yonelinas AP, Hopfinger JB, Buonocore MH, Kroll NE, Baynes K. 2001. Hippocampal, parahippocampal and occipital-temporal contributions to associative and item recognition memory: An fMRI study. Neuroreport 12:359–363.