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Neuropsychologia 45 (2007) 2428–2438

NEUROPSYCHOLOGIA

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# Recognition memory for faces and scenes in amnesia: Dissociable roles of medial temporal lobe structures

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Received 8 September 2006; received in revised form 2 April 2007; accepted 3 April 2007
Available online 13 April 2007

**Abstract**

The relative contributions of the hippocampus and the perirhinal cortex to recognition memory are currently the subject of intense debate. Whereas some authors propose that both structures play a similar role in recognition memory, others suggest that the hippocampus might mediate recollective and/or associative aspects of recognition memory, whereas the perirhinal cortex may mediate item memory. Here we investigate an alternative functional demarcation between these structures, following reports of stimulus-specific perceptual deficits in amnesics with medial temporal lobe (MTL) lesions. Using a novel recognition memory test for faces and scenes, participants with broad damage to MTL structures, which included the hippocampus and the perirhinal cortex, were impaired on both face and scene memory. By contrast, participants with damage limited to the hippocampus showed deficits only in memory for scenes. These findings imply that although both the hippocampus and surrounding cortex contribute to recognition memory, their respective roles can be distinguished according to the type of material to be remembered. This interaction between lesion site and stimulus category may explain some of the inconsistencies present in the literature.


*Keywords:* Recognition memory; Spatial memory; Amnesia; Hippocampus; Perirhinal cortex; Medial temporal lobe

Impairments in recognition memory are widely believed to be a key feature of medial temporal lobe (MTL) amnesia. Whether the hippocampus and perirhinal cortex make different contributions to this type of memory, however, remains controversial. One prominent theory proposes that both structures form part of a unitary declarative memory system supporting conscious recall of past experiences, and therefore, both are essential for intact recognition memory (Squire, Stark, & Clark, 2004; Squire & Zola-Morgan, 1991). An alternative view predicts that a network involving perirhinal cortex may be sufficient to support familiarity-based recognition memory for single items, in the absence of the hippocampus (Aggleton & Brown, 1999; Brown & Aggleton, 2001; Holdstock, 2005). According to this view, tasks requiring contextual information about the learning episode are hippocampally dependent and consequently hippocampal damage will impair performance on such tests.

In support of the latter theory, studies in hippocampal patients have reported intact recognition memory for single items coupled with impaired recall and/or impaired recognition memory for (cross-modal) associations (Aggleton et al., 2005; Baddeley, Vargha-Khadem, & Mishkin, 2001; Barbeau et al., 2005; Bastin et al., 2004; Holdstock, Mayes, Gong, Roberts, & Kapur, 2005; Mayes, Holdstock, Isaac, Hunkin, & Roberts, 2002; Mayes et al., 2004; Turriziani, Fadda, Caltagirone, & Carlesimo, 2004; Vargha-Khadem et al., 1997). Conversely, Squire and colleagues consistently find impaired recall and recognition memory for both single items and associations in their focal hippocampal patients (Manns, Hopkins, Reed, Kitchener, & Squire, 2003; Manns & Squire, 1999; Stark, Bayley, & Squire, 2002; Stark & Squire, 2003; Wais, Wixted, Hopkins, & Squire, 2006). For example, Gold et al. (2006) report deficits in item and source memory for words in patients with damage limited to the hippocampus. In addition, use of a similar task in functional magnetic resonance imaging (fMRI) revealed activation of the hippocampus and perirhinal cortex in healthy participants.

An alternative view that may partially explain this controversy is that different regions within the MTL may be involved in the processing of different stimulus categories, with the hippocampus and perirhinal cortex playing a critical role in spatial and object processing, even when there is minimal demand for

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doi:10.1016/j.neuropsychologia.2007.04.004

declarative memory. Much of the evidence in support of this view has come from investigations in rats and monkeys that have focused on object perception after perirhinal lesions (Buckley, Booth, Rolls, & Gaffan, 2001; Buckley & Gaffan, 2006; Bussey, Saksida, & Murray, 2002; Bussey, Saksida, & Murray, 2003; Eacott & Gaffan, 2005). For example, monkeys with perirhinal lesions were found to be impaired on concurrent object discriminations with a high, but not low, degree of 'feature ambiguity', a property of visual discrimination problems that emerges when discriminating between objects with a large number of features in common (Bussey et al., 2002). In contrast, monkeys with hippocampal lesions performed normally on such tasks (Saksida, Bussey, Buckmaster, & Murray, 2006), a pattern also true of human amnesics with selective hippocampal damage (Barense et al., 2005).

The findings from these experiments have been interpreted as support for a view of visual processing in which the perirhinal cortex functions as the apex of the ventral visual processing stream, with perirhinal cortex containing representations of complex conjunctions of stimulus features, whereas more caudal regions (e.g., V4, TEO) house the components from which these conjunctions are formed (Bussey & Saksida, 2005). Lee, Buckley et al., 2005, Lee, Levi, Davies, Hodges, & Graham (2007) have recently proposed a similar role for the hippocampus in the processing of complex spatial scenes or spatial configurations based on data using a four-choice odd-one-out paradigm adapted from animal studies (Buckley et al., 2001). Lee, Buckley et al. (2005) observed deficits in patients with focal hippocampal lesions in the perceptual discrimination of virtual reality scenes, but not faces. A second group of patients with broader MTL damage that included the hippocampus and perirhinal cortex were impaired on both face and scene conditions, confirming a role for human perirhinal cortex in the discrimination of faces (see Buckley, 2005, for a review of similar experiments in monkeys with perirhinal lesions). These deficits were limited to trials where stimuli were presented from different, but not same, viewpoints, suggesting that view-invariant but not view-specific representations were impaired in these patients. These studies, when considered alongside other investigations revealing double dissociations in the involvement of MTL structures in object and spatial processing (e.g., early gene imaging, Aggleton & Brown, 1999, 2005; lesion studies, Winters, Forwood, Cowell, Saksida, & Bussey, 2004, in rats), highlight a key difference between stimulus categories that may be particularly important for understanding human recognition memory.

Here we investigate whether the stimulus specific effects seen on perceptual tasks in amnesic patients extend into the memory domain, by testing patients with amnesia on a novel recognition memory test for faces and scenes (existing standardised tests do not allow direct comparison of performance on these two stimulus categories). We tested whether deficits in the memory domain are limited to tasks requiring view-invariant representations by incorporating same and different view conditions. We predicted that hippocampal patients would show normal recognition memory for faces, but not scenes, whereas individuals with broader MTL lesions involving perirhinal cortex would show poor recognition memory regardless of stimulus type.

## 1. Materials and methods

### 1.1. Participants

Six amnesic patients with focal brain lesions participated in this study. Structural magnetic resonance imaging (MRI) scans in five of the patients were evaluated (see Section 1.2), and on the basis of these evaluations, patients were categorised into the following two groups: (1) individuals with selective hippocampal damage (HC group, $n = 3$) and (2) participants with broader MTL damage, including perirhinal cortex, in addition to the hippocampus (MTL group, $n = 3$). Of the three patients included in the MTL group (age = 69.7 years; education = 10.3 years; one female, two males), two had been diagnosed with viral encephalitis and the third had experienced traumatic intracerebral bleeding. Of the three patients categorised in the hippocampal group (age = 48.7 years; education = 13 years; all female), one had a diagnosis of viral encephalitis, another had cerebral anoxia in the context of suspected encephalitis, and the third had carbon monoxide induced hypoxia. One patient from the HC group (referred to as HC5) did not wish to undergo further scanning. We were unable to retrieve her previous scan, but the radiological report indicated selective hippocampal damage and her performance on standard neuropsychological tests was indistinguishable from the other cases with selective hippocampal damage. Exclusion of this patient from the analyses did not significantly alter the experimental findings.

Since the two patient groups were not matched in terms of age ($p < 0.05$) or sex, for the experimental tests, two groups of 12 healthy controls were recruited to match the two patient groups in terms of age, education and sex: HC controls: age = 48.8 years; education = 14.7 years; all female; MTL controls: age = 69.0 years; education = 11.6 years; 4 females, 8 males (all $p > 0.19$).

All participants gave informed consent before undertaking the study. This investigation received ethical approval from the Cambridge and Southampton Health Authority Local Research Ethics Committees (UK).

### 1.2. Scan rating method

The MRI scans from the patients were assessed using (a) detailed rating of a number of temporal lobe brain regions, based on a rating scale that focused on MTL regions (Barense et al., 2005; Galton et al., 2001; Lee, Bussey et al., 2005) and (b) MRIcro (Rorden & Brett, 2000) to delineate which brain regions highlighted from the rating scale were damaged in the two groups. The results of these evaluations are shown in Table 1 and Fig. 1. One hippocampal patient was not included in either analysis for the reasons given above. A further patient, referred to as MTL2, was not included in the second analysis since an electronic version of his scan was not available. Exclusion of either, or both, of these patients did not significantly alter the experimental findings.

The visual rating method assesses a total of nine regions, including (1) *anterior hippocampus*, which was rated on the anterior-most pontine slice and based on the widths of the choroid fissure and temporal horn and the height of the hippocampal formation; (2) *anterior temporal lobe*, which was based on the cerebral spinal fluid space between the back of the orbit and temporal pole; (3) *amygdala*, which was rated on the scan-slice anterior to the tip of the temporal horn; (4) *lateral temporal lobe*, which was rated on the same slice as the anterior hippocampus and was based on the cortical thickness of the superior and middle temporal gyri; (5) *posterior hippocampus*, which was rated on the anterior-most slice through the cerebral aqueduct in parallel with the anterior measure and according to the width of the temporal horn and the height of the hippocampal formation; finally (6) *anterior parahippocampal gyrus*; (7) *medial bank of the collateral sulcus*; (8) *lateral bank of the collateral sulcus*; (9) *occipitotemporal suclus*, which were all rated on the slice showing the collateral sulcus at its longest. Other than the anterior hippocampus, which was rated on a five point scale (normal = 0, severe atrophy = 4) based on Scheltens et al. (1992), all regions were assessed using a four point scale (normal = 0, severe atrophy = 3), with ratings for each area averaged across both hemispheres.

Table 1 displays the ratings for each individual patient and the mean scores for each of the three subject groups (HC, MTL and control). A repeated measures ANOVA with a within-group factor of 'region' and a between-group factor of 'subject group' revealed a significant difference in scores across the nine brain areas rated (Greenhouse-Geisser corrected $F_{(3.6, 50.7)} = 4.78$, $p < 0.01$).

Table 1
Structural MRI scan ratings for various brain regions (ordered from anterior to posterior), averaged across both hemispheres, for each individual patient

| | AntTemp | Amyg | PHG | MBCS | LBCS | MBOS | Ant-HC | LatTemp | PostHC |
|---|---|---|---|---|---|---|---|---|---|
| HC2 | 0 | 0.5 | 0.25 | 0.5 | 0.25 | 0 | 2* | 0 | 0.25 |
| HC3 | 0 | 0 | 0.75* | 0.75 | 0.5 | 0.25 | 1.25* | 0.5 | 1 |
| MTL1 | 2* | 2.25* | 1.5* | 1* | 1.25* | 2* | 1.75* | 1.75* | 1.75* |
| MTL2 | 2* | 3* | 2.5* | 2.75* | 2.5* | 2* | 3* | 1 | 2.75* |
| MTL3 | 1.75* | 2.75* | 2.75* | 2.75* | 2.5* | 2.5* | 2* | 0.5 | 2* |
| HC group | 0 (0) | 0.250 (0.354) | 0.500 (0.354) | 0.625 (0.177) | 0.375 (0.177) | 0.125 (0.177) | 1.625* (0.530) | 0.250 (0.354) | 0.625 (0.530) |
| MTL group | 1.917* (0.144) | 2.667* (0.382) | 2.250* (0.661) | 2.167* (1.01) | 2.083* (0.722) | 2.167* (0.289) | 2.25* (0.661) | 1.083 (0.629) | 2.167* (0.520) |
| Control group | 0.313 (0.284) | 0.375 (0.483) | 0.188 (0.188) | 0.521 (0.291) | 0.271 (0.310) | 0.333 (0.289) | 0.458 (0.382) | 0.458 (0.411) | 0.271 (0.361) |

As a comparison, the mean ratings for the control group (with standard deviations) are also shown. *Signifies significant atrophy ($p < 0.05$). A range of 0–3 (0–4 for the anterior hippocampus) was used where 0: no visible damage and 3/4: complete absence of area. The mean ratings and standard deviations of both patient groups and the control group are also shown. HC5 does not appear since her scan was not available for rating. Patient labels refer to those used in Lee, Bussey et al. (2005) where applicable. HC: hippocampal; MTL: medial temporal lobe; AntTemp: anterior temporal cortex; Amyg: Amygdala; PHG: parahippocampal gyrus (corresponding to entorhinal cortex); MBCS: medial bank of collateral sulcus (corresponding to the transition between entorhinal and perirhinal cortex); LBCS: lateral bank of collateral sulcus (corresponding to perirhinal cortex); MBOS: medial bank of occipitotemporal sulcus (corresponding to the transition between perirhinal and isocortex); AntHC: anterior hippocampus; LatTemp: lateral temporal cortex (likely to correspond to TE); PostHC: posterior hippocampus.

One-way ANOVAs confirmed a significant group difference on all brain areas (all $F_{(2,14)} > 15.4$, $p < 0.001$) other than the lateral temporal lobe measure which was not significant ($p > 0.1$). Post hoc analyses comparing the HC group with their matched controls, on the regions in which there was a significant overall group difference, indicated significantly greater atrophy of the anterior hippocampus ($p < 0.01$) but no other significant differences. In contrast, the MTL group received significantly greater rating scores compared to the control group on all measures (all $p < 0.001$) for which the one-way ANOVAs revealed significant group differences.

In addition to this rating scale, regions of atrophy within the temporal lobe were delineated for the two patients from each group for whom appropriate scans were available using MRIcro (Rorden and Brett, 2000). The structural scans were first warped into Montreal Neurological Institute (MNI) space in SPM99 (Wellcome Department of Functional Neuroscience, London, UK) using a standard procedure for brain images with focal lesions (Brett, Leff, Rorden, & Ashburner, 2001). To do this, a mask was created in MRIcro for each of the subjects' lesions, by delineating regions of cerebral spinal fluid in the middle cranial fossae, including the inferior horn and choroidal fissure, up to a posterior limit of the end of the hippocampus. These masks were then used for cost function masked normalisation of each brain to a standard T1 MNI template. Following warping, the lesions of each patient were then redrawn, and finally overlaid onto an average brain T1 MNI template using MRIcro. Overlapping regions of damage within the temporal lobe are shown for each patient group in Fig. 1a and b. This process confirmed the results from the rating scale. The region of overlapping damage across the two patients classified in the hippocampal group was limited to the hippocampus bilaterally. By contrast, the MTL patients had broader MTL damage encompassing the hippocampus and perirhinal cortex. Fig. 1b shows an increased amount of cerebral spinal fluid in the region of the collateral sulcus and corresponding to the ventromedial aspect of the temporal pole, in line with recent descriptions of the perirhinal cortex (Davies, Graham, Xuereb, Williams, & Hodges, 2004; Insausti et al., 1998; Suzuki & Amaral, 1994).

### 1.3. Neuropsychological battery

The cognitive abilities of the patients were assessed using a series of standardised neuropsychological tests, the results of which can be found in Table 2. Performance was evaluated by comparison with standard published norms where available. Both patient groups performed poorly on tests of recall (Logical Memory Stories 1 and 2, immediate and delayed recall; Rey Complex Figure delayed recall, Ostterrieth, 1944). Similarly, recognition memory, as assessed by both the Logical Memory Test and the words subtest of the Warrington Recognition Memory Test (Warrington, 1984), was impaired in both groups, with the exception of the patient HC2 who performed between the 10th and 25th percentile on the RMT words subtest. Scores on the face subtest of Warrington's RMT however, were of particular interest: whereas the MTL group was impaired, the HC group performed in the normal range. Visuoperceptual processing was within the normal range in both groups across all tasks (Benton Face Test, Benton, Hamsher, Varney, & Spreen, 1983; Visual Object Space Perception battery, Warrington & James, 1991; Rey Complex Figure copy, Ostterrieth, 1944). It should be noted, however, that these tasks are not sufficiently taxing to reveal the perceptual deficits of the type previously observed in these patients (Lee, Buckley et al., 2005; Lee, Bussey et al., 2005). Tests of semantic memory revealed mild impairments in the MTL group but not the HC group as measured by Category Comprehension; the Pyramids and Palm Trees Test (Howard & Patterson, 1992) and Naming. Both groups performed in the normal range on executive tasks (Wisconsin card sorting, Nelson, 1976; forwards and backwards digit span; Tower of London Test, Shallice, 1982; Raven's Coloured Progressive Matrices, Raven, 1962), with the exception of MTL3 who showed an impairment in backwards digit span.

### 1.4. Materials

The stimuli consisted of 256 photographs of faces and 256 photographs of scenes. The pictures were grouped into 64 sets of four for each stimulus type. Each set contained two similar faces or scenes, each shown from two different views. In the case of the faces, pairs were selected from the Facial Recognition Technology (Feret) Database (Phillips, Moon, Rizvi, & Rauss, 2000; Phillips,

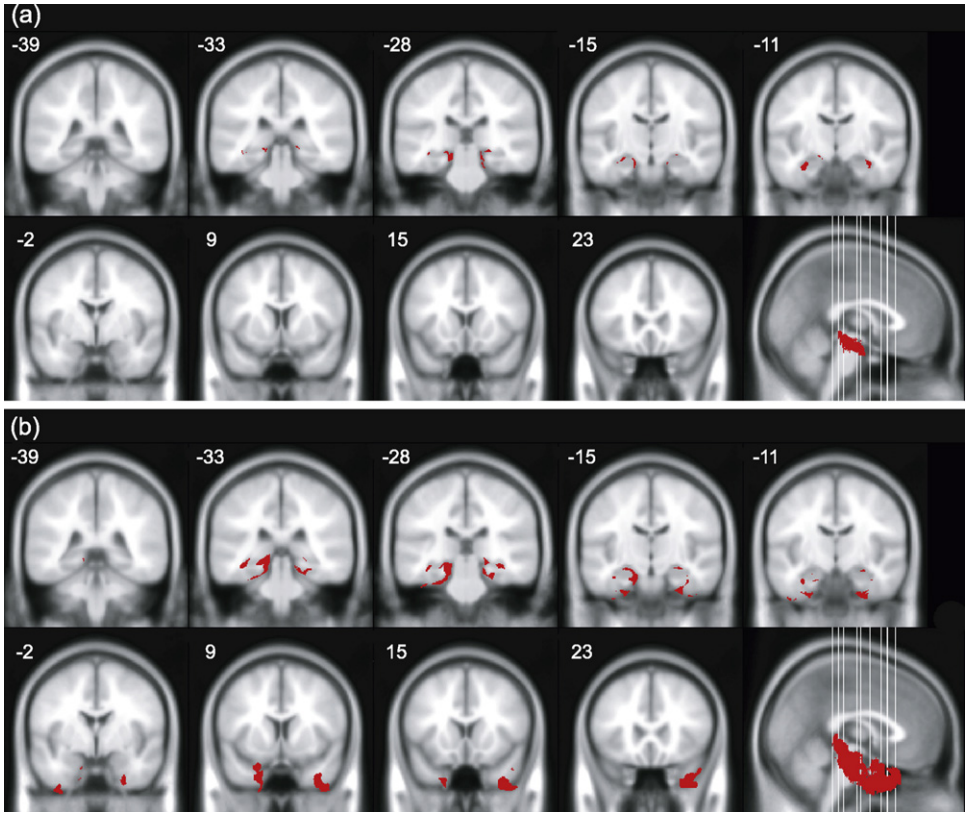


Fig. 1. Overlapping regions of atrophy within the temporal lobe are shown (in red) for (a) HC ($n = 2$) and (b) MTL ($n = 2$) patients with structural MRI scans, superimposed on a Montreal Neurological Institute average brain template.

Table 2
The six patients' individual and group performance on a brief neuropsychological battery

| | HC5 | HC2 | HC3 | HC mean | HC mean % score | MTL1 | MTL2 | MTL3 | MTL mean | MTL mean % mcore |
|---|---|---|---|---|---|---|---|---|---|---|
| Recall | | | | | | | | | | |
| LM immediate recall (75) | 6 | 31 | 22 | 19.7 | 26.2 | 12 | 29 | 13 | 18.0 | 24.0 |
| LM delayed recall (50) | 0 | 24 | 4 | 9.3 | 18.7 | 3 | 0 | 4 | 2.3 | 4.7 |
| Rey delayed recall (36) | 1 | 18 | 3 | 7.3 | 20.4 | 7 | 0 | 4.5 | 3.8 | 10.6 |
| Recognition | | | | | | | | | | |
| LM Recognition (30) | 16 | 24 | 19 | 19.7 | 65.6 | 19 | 19 | 23 | 20.3 | 67.8 |
| WRMT – Words (50) | 37 | 42 | 33 | 37.3 | 74.7 | 19 | 31 | 31 | 27.0 | 54.0 |
| WRMT – Faces (50) | 42 | 48 | 44 | 44.7 | 89.3 | 32 | 32 | 30 | 31.3 | 62.7 |
| Visuoperceptual | | | | | | | | | | |
| Rey copy (36) | 36 | 36 | 35 | 35.7 | 99.1 | 33 | 36 | 30.5 | 33.2 | 92.1 |
| VOSP (all sub-tests) | P | P | P | – | – | P | P | P | – | – |
| Benton face recognition (54) | 48 | 46 | 47 | 47.0 | 87.0 | 41 | 45 | 42 | 42.7 | 79.0 |
| Semantic | | | | | | | | | | |
| Picture naming (64) | 62 | 62 | 64 | 62.7 | 97.9 | 28 | 55 | 46 | 43.0 | 67.2 |
| Category comprehension (64) | 63 | 64 | 64 | 63.7 | 99.5 | 57 | 59 | 54 | 56.7 | 88.5 |
| Pyramid and palmtrees (52) | 52 | 51 | 52 | 51.7 | 99.4 | 45 | 49 | 46 | 46.7 | 89.7 |
| Executive | | | | | | | | | | |
| WCST (categories, 6) | 6 | 6 | 6 | 6.0 | 100.0 | n.t. | 6 | 6 | 6.0 | 100.0 |
| Digit span – forwards | 5 | 6 | 6 | 5.7 | – | 7 | 8 | 6 | 7.0 | – |
| Digit span – backwards | 4 | 4 | 6 | 4.7 | – | 4 | 7 | 2 | 4.3 | – |
| TOL (correct solutions, 16) | 16 | 16 | 16 | 16.0 | 100.0 | 11 | 13 | n.t. | 12.0 | 75.0 |
| RCP (36) | 34 | 34 | 34 | 34.0 | 94.4 | 19 | 33 | 22 | 24.7 | 68.5 |

Maximum scores are given in brackets where applicable. LM: Logical Memory; Rey: Rey Complex Figure; WRMT: Warrington Recognition Memory Test; WCST: Wisconsin Card Sorting Test; TOL: Tower of London; RCP: Raven's Coloured Matrices; n.t.: not tested.

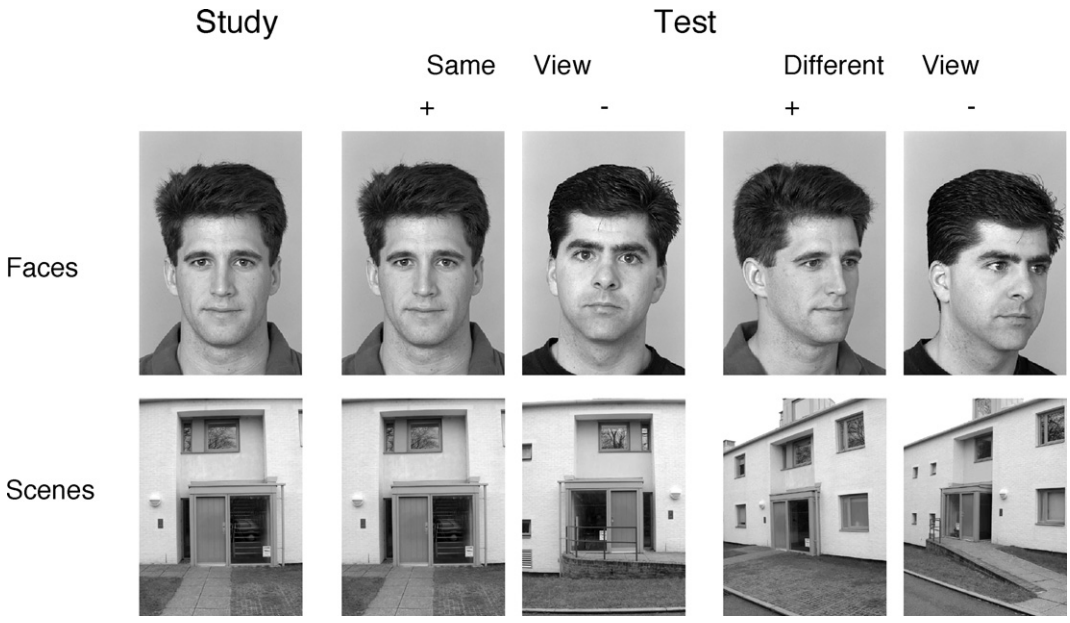


Fig. 2. Examples of one trial from each condition in the experiment. (+) Indicates correct stimulus; (−) indicates incorrect stimulus. NB. The same items appear in the same and different view conditions presented here for illustrative purposes only. All items in the experiment were trial unique and assigned to a single condition only.

Wechsler, Huang, & Rauss, 1998) that were judged to look as similar as possible. For each subject, a frontal view, and a second view with the subject facing to their left by approximately 40° were used. In the case of the scenes, pairs of locations were found around Cambridge and London that shared the same general form but that differed in the shape and/or configuration of some features. These included pictures of both the inside and outside of buildings, as well as gardens and fields, etc. Pictures from a range of angles were initially taken, and for each pair, two views were subsequently chosen. The difference in viewing angle between the two views ranged from approximately 30–90° across different sets, but was kept as similar as possible between pairs within each set.

### 1.5. Method

Testing was conducted using an LCD touchscreen. Before testing began, subjects were given the opportunity to make themselves comfortable and to familiarise themselves with the touchscreen. A short practice block was administered prior to each encoding block to ensure subjects understood the instructions and to give them experience of the same and different view manipulation.

There were two study blocks, one for each stimulus set. For each of these study blocks, subjects were required to view a series of 64 pictures on the touchscreen and indicate whether they found each picture pleasant or unpleasant by pressing the appropriate button on the screen. Each picture was presented for 5 s regardless of when the pleasant/unpleasant response was made. On trials where no response had been made within this time, subjects were shown a brief message asking them to try to respond more quickly on subsequent trials. Two test blocks, one same view, and one different view followed each study block, after a short delay (approximately 1 min).

There were four test conditions, assigned to separate blocks: *same view faces; different view faces; same view scenes* and *different view scenes*. For each of these blocks, subjects were presented with a series of 32 matched pairs of stimuli, one of which they had seen at study, and one of which was new, presented side by side. They were instructed to indicate which stimulus had been presented previously by touching that picture on the screen. The next pair was then presented. There was no time limit for making a response but subjects were encouraged not to spend too long and to "go with their gut feeling" if they were unsure. For the *same view* test blocks, the target stimulus was shown from the same view as it was presented at study. For the *different view* test blocks, the target stimulus was shown from a different view to that seen at study. In both cases, where applicable, the foil was presented from the same orientation as the target picture. Examples of a trial from each condition are shown in Fig. 2.

The assignment of stimuli to conditions and the presentation order of the two tasks (faces and scenes) were counterbalanced across subjects. Given that pilot studies showed that the different view conditions were more difficult than the same view conditions, subjects were tested on the different view block before the same view block in an attempt to better match performance.

### 1.6. Statistics

A repeated measures analysis of variance (ANOVA) was conducted on all the performance data.[1] Two within-subject factors each with two levels were included: "stimulus", with the levels face and scene, and "view" with the levels same and different. In addition, two between-subject factors each with two levels were included: "health", with the levels control and patient, and "lesion type" with the levels HC and MTL (used to classify both patients and their matched controls). As noted earlier, the two patient groups were not matched in terms of age or sex so direct comparisons of performance should not be made between the two groups of patients across the various tasks. The statistical design described enables us, however, to compare the two groups of patients with respect to their individual matched control groups, in other words, it enables us to contrast the relative levels of *impairment* between the two groups of patients. An interaction between "health" and "lesion" indicates that the level of *impairment* on a given condition or set of conditions differs between the two groups of patients. An interaction between "health", "lesion" and "stimulus" and/or "view" indicates that the magnitude and/or direction of the difference in impairment between the two patient groups differs across the various conditions in the experiment. A four-way interaction was, in fact, observed and investigated as follows. We were initially interested in whether the pattern of impairment differed across the various conditions within each patient group. The data from the two sets of patients and matched controls were therefore subjected to two separate two-way ANOVAs. Significant interactions between "health" and "stimulus" and/or "view" indicated that the level of impairment differed between conditions; such interactions were examined further using independent-sample *t*-tests. In order to directly compare the level of impairment between the two patient groups on each condition, a further four univariate ANOVAs were performed, each with the

[1] The use of parametric statistics was deemed appropriate since an analysis of the distribution of the residuals of the data revealed no outliers or departures from normality, and therefore the underlying assumptions of the general linear model were met.

Table 3
Mean % correct (with standard deviations) for each group on each of the four conditions (chance performance = 50%)

| | HC controls | HC patients | MTL controls | MTL patients |
|---|---|---|---|---|
| Same view faces | 92.7 (7.9) | 88.5 (6.5) | 89.8 (7.1) | 72.9* (1.8) |
| Different view faces | 83.6 (8.5) | 81.3 (0.0) | 78.6 (8.8) | 53.1* (20.5) |
| Same view scenes | 84.1 (11.9) | 61.5* (1.8) | 82.2 (7.5) | 52.1* (9.0) |
| Different view scenes | 75.5 (9.7) | 60.4* (4.8) | 68.0 (10.4) | 55.2* (4.8) |

*Significant impairment relative to the matched control group ($p < 0.05$). HC: hippocampal; MTL: medial temporal lobe.

same two between-subject factors "health" and "lesion". Since our predictions regarding the performance of the patients compared with their respective control groups were directional, all quoted $p$ values are one-tailed.

## 2. Results

The mean performance level of all control and patient groups can be found in Table 3. For illustration purposes, difference scores between each patient group and its corresponding control group can be found in Fig. 3(a). Statistical analyses revealed a significant "stimulus" × "view" × "health" × "lesion" interaction ($F_{(1,26)} = 4.12$; $p < 0.05$) indicating that the difference in performance between the two patient groups relative to their matched controls varied across the four conditions.

As described above, two separate three-way ANOVAs were then performed, one for each set of patients plus their matched controls. In the HC group analysis, there was a significant two-way interaction between "stimulus" and "health" ($F_{(1,13)} = 21.18$; $p < 0.001$). This interaction reflects poorer performance in the HC group in the scene compared with the face conditions. *T*-tests revealed that whereas the HC group performed in the normal range on both face conditions (both $p > 0.22$), they were significantly impaired on both scene conditions (same view: $t = 4.66$; $p < 0.001$; different view: $t = 3.05$; $p < 0.01$). In the MTL group analysis, there was a significant three-way interaction between "stimulus", "health" and "view" ($F_{(1,13)} = 11.53$; $p < 0.01$), which is likely to be the result of floor effects. More importantly, *t*-tests revealed that the MTL group was significantly impaired on all four conditions compared to their control group (all $t > 2.0$, $p < 0.05$).

Further analyses were then performed on each condition in turn in order to contrast the level of impairment between the two patient groups on each condition. The analyses of both the *same view* and *different view faces* conditions revealed a significant "health" × "lesion" interaction (same view: $F_{(1,26)} = 3.66$; $p < 0.05$; different view: $F_{(1,26)} = 6.23$; $p < 0.01$) indicating that the MTL group were significantly more impaired than the HC group on both face conditions. In the analyses of both scene conditions, no such interactions were observed (both $p > 0.15$), indicating that the level of impairment did not significantly differ between the two groups on either of the scene conditions.

Individual scores for each subject are provided for each condition in Fig. 3(b). Both groups are clearly impaired on the two scene conditions, as found in the analyses above, although floor effects limit the observable levels of impairment on the *different view scenes* condition. One could argue that a slight ceiling effect in controls is masking a significant impairment in the HC group on the *same view faces* condition. The same cannot be said of the *different view faces* condition, however, since no controls performed without error, and scores were well distributed. In the MTL group, one patient scored within the control range on the *different view faces* task, but in general, memory for faces and scenes in this group was impaired.

## 3. Discussion

Contrary to most theoretical accounts of recognition memory, amnesic individuals with either selective hippocampal damage or more extensive injury that included perirhinal cortex showed distinct patterns of performance on a novel recognition memory test that contrasted faces and spatial scenes. Patients with broad MTL lesions were impaired on recognition memory for faces and scenes regardless of view. By contrast, cases with bilateral hippocampal damage performed within the normal range on both same and different view faces, but had poor memory for same and different view scenes. These results challenge current conceptualisations of recognition memory by suggesting that although both the hippocampus and perirhinal cortex are critical to recognition memory, the role played by these two regions appears to be limited to particular stimulus categories.

Consistent with our findings, in a brief review of published cases, Aggleton and Shaw (1996) noted normal face recognition memory in some patients with focal hippocampal damage. A similar large scale study of recognition memory in patients with unilateral temporal lobe pathology revealed that damage in non-hippocampal MTL regions, but not the hippocampus, was a good predictor of impairment on the same test (Baxendale, 1997). In addition, three case studies have shown impaired recognition memory for topographical stimuli in the context of preserved recognition memory for unfamiliar faces following hippocampal damage (Bird, Shallice, & Cipolotti, 2007; Carlesimo, Fadda, Turriziani, Tomaiuolo, & Caltagirone, 2001; Cipolotti et al., 2006), although no direct statistical comparisons between performance on these two stimulus categories were provided. Our study, therefore, which is the first to directly contrast recognition memory for faces and scenes in the same experimental paradigm, extends these preliminary investigations and confirms that recognition memory is not a single process that can be easily mapped onto a single MTL structure.

A direct prediction from the view that the MTL functions as a single declarative memory system, is that all types of recognition memory should be deficient in amnesic individuals with MTL damage, regardless of their specific lesion site. Furthermore, a direct relationship should be evident between extent

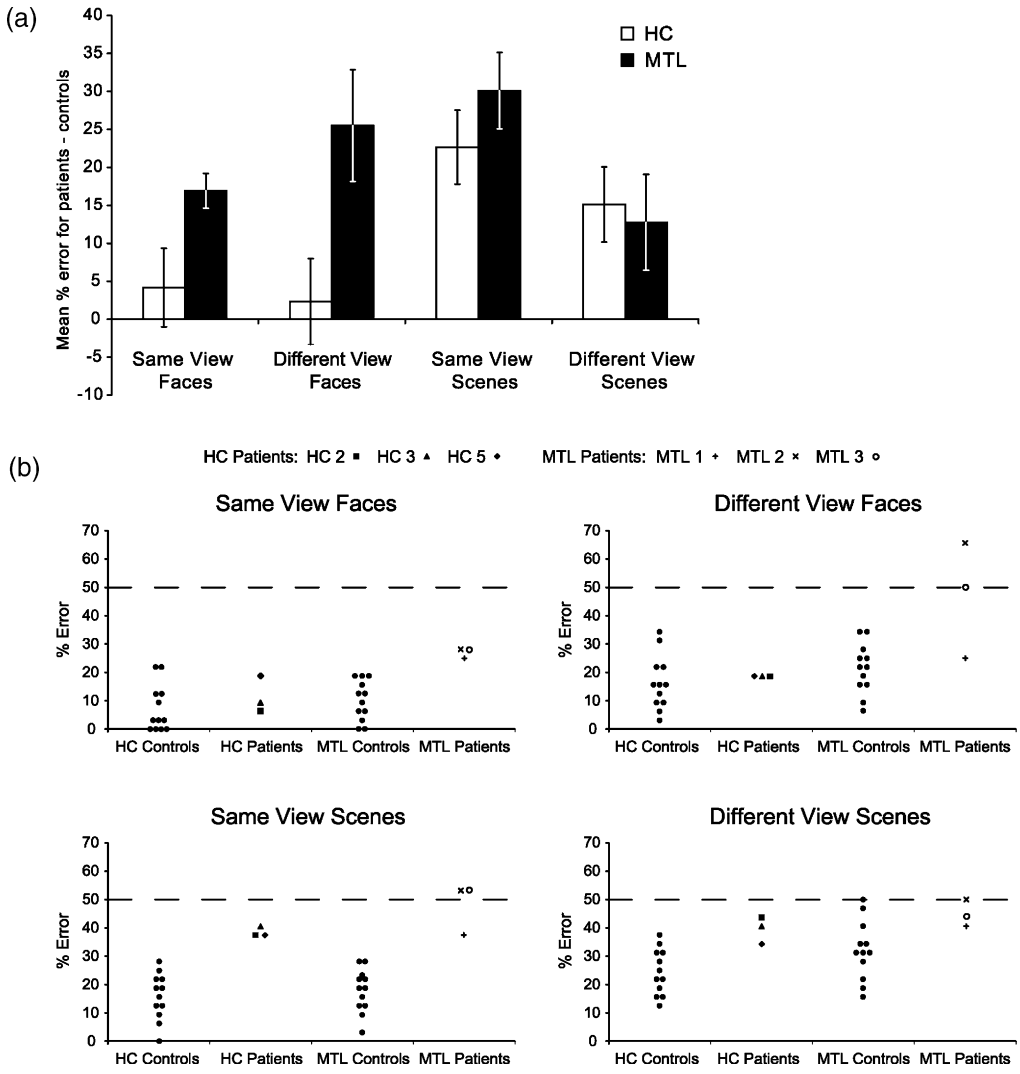


Fig. 3. Performance on the task illustrated as (a) mean % error (±S.E.) for each patient group minus its matched control group and (b) individual scores (errors) for each of the four conditions (chance performance = 50%).

of lesion and degree of deficit (Gold et al., 2006). Although the two patient groups examined here differed by the additional involvement of non-hippocampal MTL structures (in the MTL group), and it is this extra lesion that we are attributing to the poor face recognition memory, it is important to note that the size of the hippocampal lesion was also predictably bigger in the MTL participants. It is possible, therefore, that this difference in lesion size explains the patterns seen in the two patients groups, in particular the normal performance of the HC group on the face compared to scene tasks, which were not matched for overall difficulty. Such an explanation may also seem intuitively appealing given our expertise, as humans, at recognising faces, which may render this skill more robust in the context of memory impairment.

There are a number of reasons why we feel this explanation is unlikely to be underlying the effects observed. First, although the face conditions were easier than the scene conditions overall, a comparison of the *different view face* and *same view scene* conditions reveals that control performance was matched across these two conditions (see Table 3 and Fig. 3(b)). Despite this, the HC group was significantly impaired on the *same view scene* but not the *different view face* condition, a pattern inconsistent with an explanation based on differences in difficulty across conditions. Second, there is increasing converging evidence of dissociations in performance along similar lines to those reported here from both human and animal studies, including observations of the reverse dissociation, in other words, impaired memory for faces in the context of preserved memory for scenes. For example, good scene recognition memory in the context of poor face recognition memory (albeit on recognition memory tasks that were not as well-matched) has been documented in patients with semantic dementia (Cipolotti & Maguire, 2003; Maguire & Cipolotti, 1998). This finding is particularly interesting as it suggests that not all patients with memory problems show an advantage for faces over scenes. Further support comes from double dissociations that have been demonstrated in both the imaging and animal literature. In a recent functional neuroimaging study, Pihlajamaki et al. (2004)

found activation in perirhinal cortex when a novel object was presented (see also Lee, Bandelow, Schwarzbauer, Henson, & Graham, 2006), whereas the posterior hippocampus was activated in response to novel *rearrangements* of familiar objects. In addition, rat lesion and early gene imaging studies have also highlighted critical roles for perirhinal cortex and hippocampus in object and spatial memory, respectively, including documenting double dissociations in performance (Aggleton & Brown, 2005; Winters et al., 2004). There is increasing convergent evidence, therefore, that the MTL, across species, may be functionally specialised according to spatial and object processing.

The impairment seen in both patient groups on same view scenes seems, at first glance, inconsistent with some theoretical accounts of the hippocampus, such as the cognitive map theory (O'Keefe & Nadel, 1978), in which the hippocampus is involved in allocentric but not egocentric spatial processing. Using novel virtual reality environments, large deficits in recognition memory for shifted-view scenes has been documented in a patient with bilateral hippocampal damage (King, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2002). Strikingly, the patient's memory for same-view scenes was normal, except in conditions where participants were required to remember 10 or more items. The authors propose that greater list lengths may force an increasing reliance upon allocentric processing, and consequently hippocampal function. If true, individuals with hippocampal damage may perform more poorly on same view scene recognition memory when larger sets of stimuli are presented. The data reported here are consistent with this hypothesis: patients showed poor memory for same view scenes when asked to remember 64 consecutively presented images. Notably, however, the effects seen on recognition memory performance by increasing stimuli set size may not necessarily be due to increased allocentric processing. Such a manipulation is also likely to increase the need for discriminating between spatially ambiguous scenes, a process that may require increasing access to conjunctions of spatial features stored within the hippocampus (Buckley, Charles, Browning, & Gaffan, 2004; Lee, Buckley et al., 2006).

Similarly, our finding that different structures in the MTL may be differentially involved in accurate recognition memory for complex scenes and faces does not necessarily invalidate dual process theories of recognition memory, in which the hippocampus is thought to play a key role in recollective aspects of recognition, and perirhinal cortex in familiarity for previously studied items (irrespective of type, Aggleton & Brown, 1999; Brown & Aggleton, 2001). It seems plausible that successful recognition memory for these two types of stimuli may place differential demands upon recollection and familiarity. For example, the processing of faces holistically, as a "gestalt" (Schiltz & Rossion, 2006; Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987), may increase reliance upon a signal detection-like familiarity process in perirhinal cortex (Yonelinas, Kroll, Dobbins, & Soltani, 1999). Memory for complex scenes, on the other hand, may stress memory for associations between the various elements comprising the scene, which may not be adequately supported by familiarity and may therefore require hippocampally dependent recollection (Yonelinas, 1997, 2002). Notably, counter to this account, intact recollection of faces in two focal hippocampal cases, VC and RH, has recently been reported by Cipolotti and colleagues (Bird et al., 2007; Cipolotti et al., 2006) a pattern that implies that recollection, at least as measured by ROC analyses in these cases, can be supported by non-hippocampal structures.

Furthermore, although it is difficult to disentangle this type of 'process' account from a 'stimulus' account based on findings from our current study, it is not clear that re-framing our dissociation in terms of recollection and familiarity provides a sufficient explanation. Strictly speaking, recollection normally refers to associations between a stimulus and the episodic context in which it was studied and the question then remains as to why scenes engender stronger item-context associations than do faces. Moreover, the types of associative memory that have been shown to require recollection generally involve pairwise recombinations of studied items such that familiarity for the two elements of each test item, be it target or foil, should be equivalent (for example, Mayes, Montaldi, & Migo, 2007; Mayes et al., 2004; Yonelinas, 1997; Yonelinas et al., 1999). Since the scene stimuli used in the current experiment were not recombinations of studied elements, it is not immediately obvious why assessing the relative familiarity of target and foil items would not be sufficient to solve the task. The current findings could, however, be accommodated by related theories which propose a role for perirhinal cortex in memory for unitised and within-domain associations, and for the hippocampus in between-domain associations, in this case, items and their locations (Mayes et al., 2007; see also Cohen & Eichenbaum, 1993; Moses & Ryan, 2006). Further studies that take into account how measures of recollection and familiarity interact with successful recognition memory for different stimulus types should provide further data to help address this issue.

The profiles of performance seen in the recognition task across different view scene and face conditions have been shown to extend to tasks that do not contain an overt long-term memory demand. Lee, Buckley et al. (2005) found that the hippocampal group were unable to discriminate between different view virtual reality scenes, whereas the MTL group, with more extensive lesions that included perirhinal cortex, were additionally impaired on different view oddity judgement for faces. In contrast to the current study, deficits in same view conditions were not observed. This could either be due to the precise nature of the stimuli used in each study (for example Lee, Buckley at al. utilised virtual reality rather than real world scenes), or a reflection of the increased demands of mnemonic versus perceptual tasks. Even without this extra complication, it is not entirely clear how the deficits in recognition memory relate to the perceptual impairments seen in the patients. One plausible account is that the memory deficits are a consequence of poor perception (Gaffan, 2001). More specifically, that the hippocampus and perirhinal cortex store conjunctions of spatial and object information, respectively, and that incomplete representations, present after brain damage, inevitably result in deficient and erroneous memory. Another possibility is that functionally distinct neuronal populations may underlie mnemonic

and perceptual processing. For example, electrophysiological recordings from perirhinal cortex have revealed neurons that show decreased firing rates in response to previously seen objects, whereas other neurons show stimulus-specific effects in the absence of familiarity- or repetition-related response changes (Xiang & Brown, 1998).

The current findings provide evidence against the view that all structures within the MTL play an essential role in recognition memory (Manns et al., 2003). How do we explain, therefore, studies which document poor recognition memory in hippocampal patients (Gold et al., 2006; Manns et al., 2003; Manns & Squire, 1999; Stark et al., 2002; Stark & Squire, 2003; Wais et al., 2006)? It seems most likely that contradictory findings across published articles stem from differences in the stimuli and procedures used in these experiments. For example, recognition of verbal material may well be hippocampally dependent: not only do a number of studies report poor verbal recognition memory (Gold et al., 2006; Manns et al., 2003; Wais et al., 2006), but all the hippocampal patients reported here also present with deficient memory for words. Impairments have also been demonstrated using nonverbal material but these tests typically involve memory for scenes and associations (Manns & Squire, 1999; Stark & Squire, 2003), incorporate a yes/no test format (Stark et al., 2002) and/or long delays between study and test (Manns et al., 2003) making these results incomparable to those reported here. When immediate forced choice recognition memory for faces has been tested (Reed & Squire, 1997), it is notable that hippocampal patients were not significantly impaired.

In summary, we report the first systematic comparison of recognition memory for faces and spatial scenes following MTL lesions in humans. Whereas both hippocampal and non-hippocampal MTL lesions affect recognition memory, we have provided strong evidence to suggest that different MTL structures play unique roles in processing information about different stimulus categories (scenes and faces). These findings complement recent neuropsychological studies of visual discrimination in amnesia, and taken together, these investigations suggest a radical revision to models of MTL function, taking into account the role played by the hippocampus and perirhinal cortex in space and object processing.

## Acknowledgements

The authors are grateful to the patients and control volunteers for their participation in this study. This work was funded by the Medical Research Council. Portions of the research in this paper use the FERET database of facial images collected under the FERET program, sponsored by the DOD Counterdrug Technology Development Program Office.

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