Faces are special but not too special: Spared face recognition in amnesia is based on familiarity

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ABSTRACT

Most current theories of human memory are material-general in the sense that they assume that the medial temporal lobe (MTL) is important for retrieving the details of prior events, regardless of the specific type of materials. Recent studies of amnesia have challenged the material-general assumption by suggesting that the MTL may be necessary for remembering words, but is not involved in remembering faces. We examined recognition memory for faces and words in a group of amnesic patients, which included hypoxic patients and patients with extensive left or right MTL lesions. Recognition confidence judgments were used to plot receiver operating characteristics (ROCs) in order to more fully quantify recognition performance and to estimate the contributions of recollection and familiarity. Consistent with the extant literature, an analysis of overall recognition accuracy showed that the patients were impaired at word memory but had spared face memory. However, the ROC analysis indicated that the patients were generally impaired at high confidence recognition responses for faces and words, and they exhibited significant recollection impairments for both types of materials. Familiarity for faces was preserved in all patients, but extensive left MTL damage impaired familiarity for words. These results show that face recognition may appear to be spared because performance tends to rely heavily on familiarity, a process that is relatively well preserved in amnesia. In addition, the findings challenge material-general theories of memory, and suggest that both material and process are important determinants of memory performance in amnesia.

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What types of processes allow us to recognize events that we have experienced in the past, and how are they instantiated in the brain? Since the time of Aristotle, philosophers and scientists have distinguished between two forms of recognition memory: recollection and familiarity. The former reflects retrieval of qualitative information about a study event upon encountering a previously experienced stimulus, while the latter is a judgment of quantitative strength or fluent processing of an item, without any episodic details coming to mind (see Yonelinas, 2002 for review). In recent years, the field of cognitive neuroscience has made considerable progress in mapping the neural substrates of these two forms of recognition memory. An extensive body of research has indicated that the hippocampus is critical for recollection rather than familiarity, and that regions such as the perirhinal cortex are critical for familiarity (Aggleton & Brown, 1999; Brown & Aggleton, 2001; Bowles et al., 2007; Norman & O'Reilly, 2003; Quamme, Yonelinas, Widaman, Kroll, & Sauve, 2004; Yonelinas

et al., 2002; see Eichenbaum, Yonelinas, & Ranganath, 2007 for review).

While distinguishing between recollection and familiarity, dual process theories of recognition memory are material-general, in the sense that they are expected to characterize the processes that support recognition memory for a wide variety of different materials (Aggleton & Brown, 1999; Atkinson & Juola, 1974; Brown & Aggleton, 2001; Eichenbaum et al., 2007; Jacoby & Dallas, 1981; Mandler, 1980; Norman & O'Reilly, 2003; Yonelinas, 1994; see Yonelinas, 2002 for review). This material-general assumption leads to the prediction that memory is supported by the medial temporal lobes in similar ways for words, faces, scenes, or any other stimulus class. Thus, hippocampal damage should lead to impaired recollection, but spared familiarity, for all classes of items. Conversely, perirhinal cortex damage should impair familiarity but spare recollection, regardless of stimulus class. Finally, extensive medial temporal lobe damage should produce material-general deficits in both recollection and familiarity.

The material-general assumption is not isolated to dual process theories, but is also widely adopted in a host of other memory theories (e.g. Damasio, 1989; Davachi & Wagner, 2002; Eichenbaum,

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Otto, & Cohen, 1994; Giovanello, Schnyer, & Verfaellie, 2004; Squire, Cohen, & Nadel, 1984; Squire, Wixted, & Clark, 2007; Teyler & DiScenna, 1986; Tulving, 1983; Tulving & Markowitsch, 1998; Wickelgren, 1979). For example, the proposal that the medial temporal lobe memory system supports declarative memory in general, with the hippocampus and surrounding parahippocampal gyrus both supporting recollection and familiarity (Squire et al., 2007), generally assumes that memory is supported in an invariant way for different types of materials. Thus, larger MTL lesions should produce greater memory deficits in both recollection and familiarity, regardless of the type of material (Squire, Zola-Morgan, & Alvarez, 1994).

A number of findings from patients with damage to the medial temporal lobes appear to directly challenge this material-general assumption. For example, Carlesimo, Fadda, Turriziani, Tomaiuolo, and Caltagirone (2001) examined recognition performance in a global amnesic patient with a bilateral volume reduction in the hippocampus. Despite impaired item and associative memory for buildings and words, this patient showed sparing of both item and associative memory for faces. Similarly, Taylor, Henson, and Graham (2007) found that patients with selective hippocampal damage were impaired on recognition of scenes but had spared recognition for faces. When patients had damage that extended to medial temporal lobe structures beyond the hippocampus, however, both scene and face recognition memory were impaired. In addition, Bird and Burgess (2008) reviewed data from 10 amnesic patients for whom Recognition Memory Test (RMT) scores were available, and found that patients were significantly more impaired at word recognition than face recognition. In this case, however, face recognition appeared to be preserved in patients with selective hippocampal damage as well as patients with more extensive MTL damage.

The existing results suggest that the medial temporal lobe is critical for the recognition of materials like words and scenes, but that it is not necessary for the recognition of faces. Whether the pattern differs for patients with focal hippocampal or more extensive MTL lesions is not yet clear. In any case, the existing results directly challenge the prevalent material-general assumption.

How can these results be explained? Dual process models could account for these results if recognition memory for faces relies heavily on familiarity, whereas word recognition relies heavily on both recollection and familiarity. Because recollection is disproportionally disrupted in MTL amnesics (Yonelinas, Kroll, Dobbins, Lazzara, & Knight, 1998), they would be expected to have a greater impairment in word recognition than face recognition.

Unfortunately, the effects of medial temporal lobe damage on recollection and familiarity for faces and words has been examined in only three case studies, and the results are not entirely consistent. In each of these cases, recognition confidence judgments were used to plot receiver operating characteristics (ROCs), which were used to derive estimates of recollection and familiarity (Yonelinas, 1994). For example, patient VC, who suffered from bilateral hippocampal and left parahippocampal volume reductions related to migraine and seizures, was found to have deficits in both recollection and familiarity for words, but did not exhibit significant impairments on either recollection or familiarity for faces (Cipolotti et al., 2006). Patient RH, who suffered damage to the right hippocampus, was found to have preserved recollection and familiarity for both faces and words (Bird, Shallice, & Cipolotti, 2007). In addition, patient Jon, who suffered selective bilateral hippocampal damage in early infancy as a result of hypoxia, exhibited a deficit in recollection but not familiarity for words, but showed normal recollection and familiarity for faces (Bird, Vargha-Khadem, & Burgess, 2008; Brandt, Gardiner, Vargha-Khadem, Baddeley, & Mishkin, 2009). Although these case studies are not definitive, they do appear to challenge

the dual process account that face memory is preserved in amnesia because face recognition relies heavily on familiarity.

In the current study, we aimed to determine whether the material-specific deficits seen in amnesia are related to the differential contribution of recollection and familiarity to memory for faces versus words. Specifically, we examined recognition for faces and words in a group of amnesic patients, using the ROC method to estimate the contributions of recollection and familiarity. We included stroke patients who had damage to the hippocampus and surrounding cortex, but restricted to either the left or the right hemisphere, as well as patients who had suffered a hypoxic episode and were expected to have bilateral damage restricted to the hippocampus (see Gadian et al., 2000; Hopkins, Kesner, & Goldstein, 1995; Rempel-Clower, Zola, Squire, & Amaral, 1996). Since severe hypoxia increases the likelihood of damage outside the hippocampus (Kono, Kono, & Shida, 1983; Smith, Auer, & Siesjo, 1984), and leads to exceedingly profound memory impairments (e.g. Manns, Hopkins, Reed, Kitchener, & Squire, 2003), we only included patients who had suffered a mild hypoxic event as a result of cardiac arrest.

A previous study (Taylor et al., 2007) found that only hypoxic patients with selective hippocampal damage showed a greater word than face recognition deficit, while patients with extensive medial temporal lobe damage were impaired at recognition for both words and faces. However, there is also evidence that patients with damage that includes surrounding MTL can show spared face memory and impaired word memory (Bird & Burgess, 2008; Cipolotti et al., 2006). We therefore examined performance for the different patient groups separately, as well as the results for the overall patient group, in order to determine if the pattern of results differs as a result of different etiologies or lesion locations.

On the basis of previous studies, we expected to find that, in general, patients would be less impaired on face recognition than word recognition. The critical question was whether the material-specific dissociation could be attributed to a differential contribution of recollection and familiarity to face and word recognition. One possibility, consistent with dual-process theory, is that face recognition is relatively spared because it relies more heavily on familiarity, which is relatively preserved in amnesia (Yonelinas et al., 1998). Alternatively, both recollection and familiarity for faces may be unaffected by medial temporal lobe damage. Such a finding would directly challenge the material-general assumption commonly adopted by many current theories of MTL amnesia. Finally, it is possible that the dissociations between word and face recognition depend on the specific amnesic group (i.e. hypoxia versus broad MTL damage, or left versus right hemisphere lesions).

1. Method

1.1. Participants

Three patient groups took part in the experiments (see Table 1 for patient characteristics). The hippocampal (H) group consisted of four patients who had suffered a mild hypoxic episode as a result of cardiac arrest. Although we could not confirm that the damage in these patients was restricted to the hippocampus, mild hypoxia is less likely to affect extra-hippocampal structures than more severe hypoxic episodes (Gadian et al., 2000; Hopkins et al., 1995; Kono et al., 1983; Rempel-Clower et al., 1996; Smith et al., 1984).

The left hippocampal-plus (L H+) group included six patients with lesions to the left medial temporal lobe as a result of left posterior cerebral artery infarcts. An overlay of the lesion reconstructions for the left H+ patients is shown in Fig. 1a.[1] The right hippocampal-plus (R H+) group included four patients with lesions to the right medial temporal lobe as a result of right posterior cerebral artery infarcts. An overlay of the lesion reconstructions for the right H+ patients is shown in Fig. 1b. The damage in the infarct patients included the hippocampus, fornix, posterior portion

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[1] Scans were not available for one patient.

Table 1
Etiology, age, and neuropsychological test scores for the patients in the faces and words experiments.

Patient	Etiology	Age	Experiments	WMS-R Verb./Vis./Gen./Att./Del	WAIS-R IQ Verb./Perf./Full
H1	Hypoxic	61	Words	82/81/77/81/67	Not available
H2	Hypoxic	61	Faces	100/94/97/93/78	101 (full)
H3	Hypoxic	40	Both	62/130/79/97/83	96 (full)
H4	Hypoxic	42	Both	94/77/87/96/80	94 (full)
L1	L PCA	62	Both	73/81/81/85/69	96/88/92
L2	L PCA	54	Words	Not available	92/76/84
L3	L PCA	78	Both	82/92/81/93/69	113/109/112
L4	L PCA	85	Faces	Not available	Not available
L5	L PCA	71	Both	71/92/75/88/63	118/112/117
L6	L PCA	37	Faces	Not available	Not available
R1	R PCA	53	Both	98/126/106/98/113	96/115/104
R2	R PCA	33	Words	105/122/113/115/118	119/113/119
R3	R PCA	62	Both	125/115/126/137/125	126 (full)
R4	R PCA	62	Both	100/106/101/77/96	85 (full)

of the parahippocampal gyrus extending up to the posterior surface of the amygdala, and the surrounding fusiform and lingual gyri.

Data were collected on the face and word experiments at the same time, and patients were tested as they became available.

Nine age-matched control participants took part in the faces experiment. A separate group of eleven age-matched control participants took part in the words experiment.

1.2. Materials, design, and procedure

1.2.1. Memory for faces

Details of this task were described in a previous study examining face recognition in healthy participants (Yonelinas, Kroll, Dobbins, & Soltani, 1999). The participants first studied 120 colored drawings of faces of men, women, and children. To ensure that the faces were well encoded, each face was viewed twice—first, at a rate of one face every 4 s, and second, after being informed that they were now going to see the same faces for a second study trial, at a rate of 2 s per face. The faces were 4–6 in. wide and 5–7 in. high. The recognition test immediately followed the study phase. 60 studied faces were randomly mixed with 60 new faces, and participants rated their confidence that each face was new or old on a 1 (certain it is new) to 6 (certain it is old) scale.

1.2.2. Verbal memory

Details of this task were previously reported in Yonelinas et al. (2002). Results from the hypoxic and left hemisphere stroke patients were previously reported (Yonelinas et al., 2002). We report the data here for comparison to face memory, and include additional data from right hemisphere stroke patients. Participants took part in two sessions. In each session, 80 words were studied under pleasantness

encoding instructions and 80 under syllable counting instructions. The recognition test consisted of all studied words randomly mixed with 80 new words. Participants rated the confidence of their recognition response using a 1 (certain it is new) to 6 (certain it is old) scale. Performance was collapsed across the two sessions and encoding instructions because these factors did not change the pattern of results.

2. Results

2.1. Memory for faces

In order to assess recognition performance and estimate the contribution of recollection and familiarity, receiver operating characteristics (ROCs) were examined for each patient and control. The proportion of correct recognitions (hits) was plotted against the proportion of incorrect recognitions (false alarms) as a function of confidence, with the left-most point indicating the most confidently recognized items. The dual-process signal detection (DPSD) model was then fit to the ROCs to derive estimates of recollection and familiarity (Yonelinas, 1994, 2001). Recollection is measured as the y-intercept of the ROC, and familiarity as the degree of curvilinearity of the ROC.

Fig. 2a shows the aggregate face ROCs for the controls and each of the patient groups. An examination of that figure shows that the
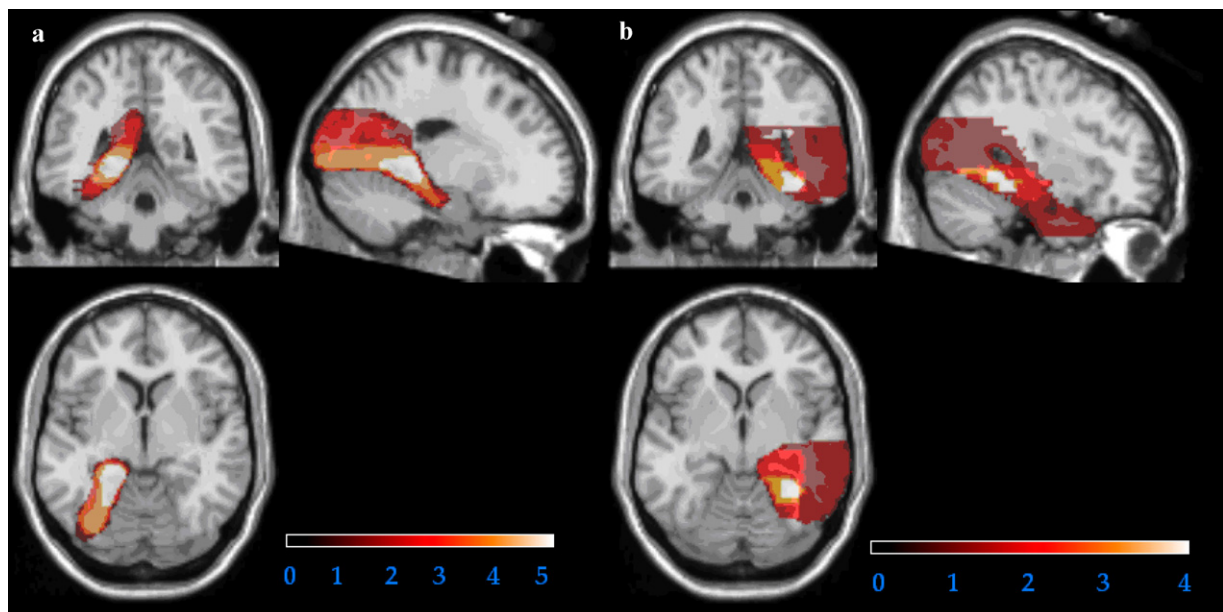
Fig. 1. Overlay of lesion reconstructions for the patients with left (a) and right (b) medial temporal lobe damage. Lighter shading indicates greater overlap across patients.
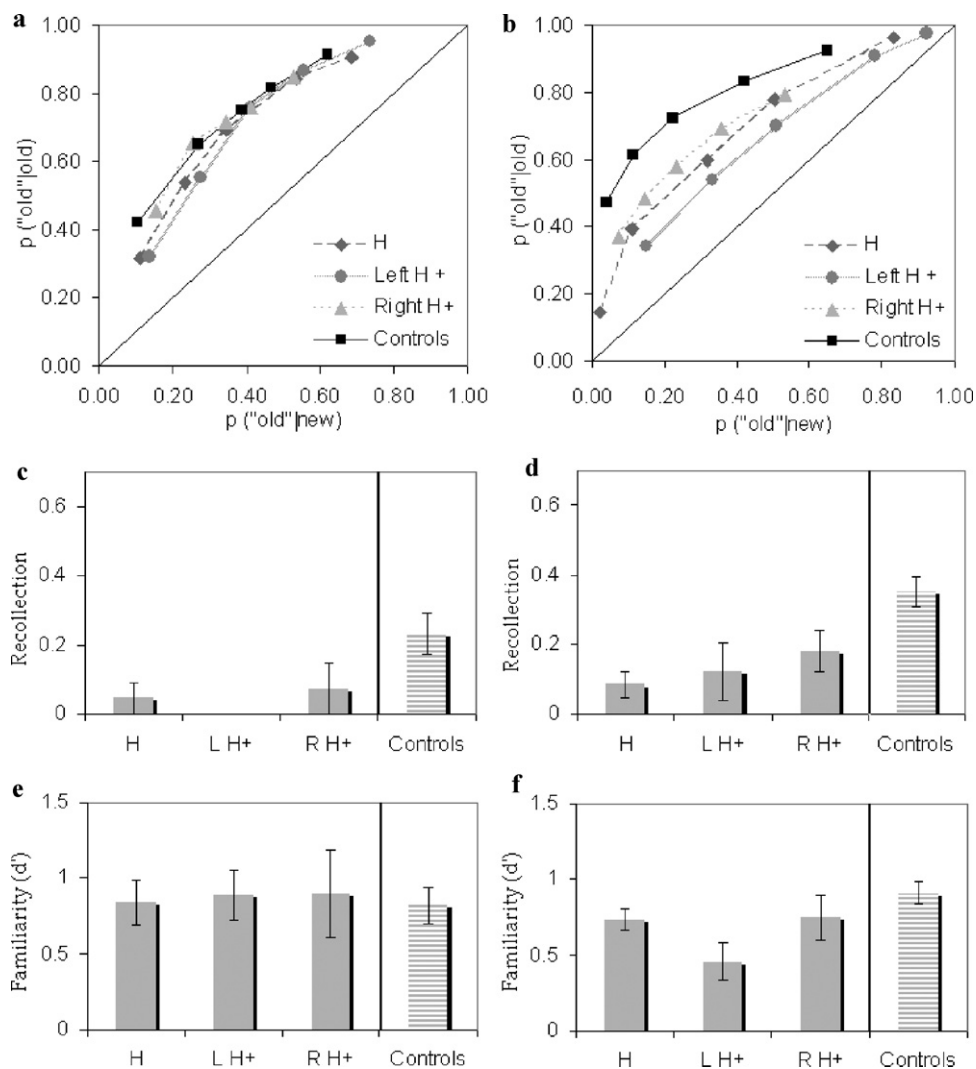
Fig. 2. Performance on the face (left column) and word (right column) tests for each patient group and the control group. (a and b) Receiver operating characteristics. (c and d) Recollection. (e and f) Familiarity.

patients and controls did not differ from one another in the middle of the ROCs, indicating that the patients did not show an overall impairment in recognition memory for faces. This was confirmed by an analysis of d' at the midpoint of the ROC, which showed that the patients did not differ significantly from controls, $t < 1$. This was consistent for all three patient groups (i.e. H, left H+, and right H+), all $t < 1$. However, the patients' ROCs did fall below that of the controls for the high confidence responses (i.e. the left most points). A d' analysis on the '6' confidence responses showed that the patients were significantly less accurate in these high-confidence responses than controls, $t(18) = 2.80$, $p = .006$. Inasmuch as recollection leads to high-confidence responses, this observation suggests that patients were impaired on recollection relative to controls.

This was confirmed by an examination of the recollection estimates (see Fig. 2c). Recollection estimates were significantly reduced in amnesics compared to the controls, $t(18) = 3.69$, $p < .001$. In addition, looking at the patient groups separately, each patient group was significantly impaired relative to the controls ($ps < .05$). Note that several patients had negative recollection estimates, so the analysis was repeated with the constraint than the recollection parameter remained greater than zero. Although constraining the estimates in this way underestimates the observed impairments,

the patients' recollection estimates were still significantly reduced compared to controls, $t(18) = 3.47$, $p = .001$.

Thus, the three methods of examining recollection converged in showing that the amnesic patients were impaired at recollection. Analyses of (1) d' at the high-confidence '6' responses, (2) recollection probability estimates that were constrained to be greater than or equal to zero, and (3) recollection probability estimates that were allowed to become less than zero all suggested that patients were impaired at recollection. Moreover, recollection deficits were seen in each of the patient subgroups, although the impairments were not always statistically significant because of the small sample sizes in the individual patient groups.

In contrast to recollection, the patients showed no evidence of an impairment in familiarity, $t < 1$. In addition, none of the patient groups showed any evidence of impaired familiarity, all $t < 1$, ns (see Fig. 2e).

2.2. Verbal memory

As with faces, we plotted ROCs for each patient and control and assessed the contribution of recollection and familiarity to word recognition (see Fig. 2b). As can be seen in the figure, the patients' performance fell below that of the controls across the entire range

of confidence responses, indicating that the patients were severely impaired at word recognition. d' analysis on the ROC midpoints and the high confidence points verified that the amnesics were impaired at both overall recognition, $t(20) = 5.55$, $p < .001$, and high confidence recognition, $t(20) = 4.47$, $p < .001$. The d' impairment at the ROC midpoints and high confidence points was seen for all patient groups, all $ps < .01$.

The impairment at high-confidence recognition was consistent with the analysis of recollection estimates, which revealed that amnesics were significantly impaired relative to the controls, $t(20) = 3.78$, $p < .001$. In addition, all three patient groups had significant recollection impairments relative to controls, $ps < .05$ (see Fig. 2d). As a group, the amnesics' familiarity estimates were reduced compared to controls, $t(20) = 2.45$, $p = .01$ (see Fig. 2f). However, only the left H+ group had a significant familiarity deficit, $t(13) = 3.066$, $p = .005$, whereas the H and right H+ groups were not significantly different from controls, $t(12) = 1.14$ and $t(13) = 1.05$, respectively, ns.

3. Discussion

Most dominant theories of recognition memory assume that the function of medial temporal lobe structures is invariant across different types of materials, such that their role does not depend on whether the to-be-remembered items are faces, words, or any other stimulus category. This has been true of the current dual process models as well as other models of MTL function, such as single process models (Aggleton & Brown, 1999; Atkinson & Juola, 1974; Brown & Aggleton, 2001; Damasio, 1989; Eichenbaum et al., 1994, 2007; Jacoby & Dallas, 1981; Mandler, 1980; Norman & O'Reilly, 2003; Squire et al., 1984, 2007; Teyler & DiScenna, 1986; Tulving, 1983; Tulving & Markowitsch, 1998; Wickelgren, 1979; Yonelinas, 1994).

Contrary to the material-general assumption inherent in these theories, several patient studies have found differential sparing and impairment of memory for different types of materials (Bird et al., 2007, 2008; Carlesimo et al., 2001; Cipolotti et al., 2006; Taylor et al., 2007) suggesting that memory for different materials has different neuroanatomical substrates. A particularly compelling finding has been that medial temporal lobe damage can lead to impaired recognition memory for words, while recognition of faces is spared (e.g. Bird & Burgess, 2008). In line with that research, we found that MTL amnesia is associated with a severe recognition impairment for words, whereas recognition for faces can appear well preserved.

The current results, however, indicated that the apparent sparing of face recognition in amnesia arose because performance relied heavily on familiarity. That is, when we examined overall recognition performance by collapsing across confidence, we found little evidence for a face recognition deficit. However, the ROC analysis revealed that recognition accuracy was impaired in the patients for the high confidence responses, and further indicated that the amnesics exhibited a deficit in recollection, but not familiarity-based recognition responses. Because recollection preferentially supports high confidence responses, the memory impairments for faces were largely masked when confidence was ignored.

In contrast to face recognition, the amnesics exhibited pronounced deficits in recognition for words, and these deficits were observed across the full range of the ROCs. Moreover, recollection was found to be significantly disrupted, whereas familiarity was less consistently impaired. That is, the hypoxics and right hemisphere lesion patients showed little evidence of a familiarity impairment, whereas the patients with left hemisphere MTL damage did exhibit a familiarity deficit. Thus, the word recognition deficit was further exaggerated for the left hemisphere

MTL patients because of their deficit in word familiarity. The greater deficit in word recognition compared to face recognition appears to be related to the finding that recollection played a greater role in word recognition. That is, because recollection was less likely to occur for faces than for words in the control participants, the recollection impairments in the patients were largely inconsequential in terms of overall accuracy in face recognition.

Three case studies have reported spared recollection and familiarity for faces in amnesia (Bird et al., 2007, 2008; Cipolotti et al., 2006). Why recollection for faces was not significantly impaired in those patients is unclear, but one possibility that cannot be ruled out is that it was related to low statistical power. For example, although patient VC (Cipolotti et al., 2006) did not exhibit a significant impairment in recollection compared to controls, recollection was numerically reduced in the patient (.21 compared to .36), and this reduction may have been significant with a larger sample size. Differences in lesion location may also be important. For example, patient RH (Bird et al., 2007) sustained a unilateral hippocampal lesion, which may not be sufficient to disrupt recollection for faces.

3.1. Neural substrates of recollection and familiarity

The current results are largely consistent with models that assume that the hippocampus is critical for recollection, whereas surrounding MTL regions, such as the perirhinal cortex, are important for familiarity (e.g. Aggleton & Brown, 1999; Eichenbaum et al., 2007; Norman & O'Reilly, 2003; Yonelinas et al., 2002). For example, the hypoxic patients were found to exhibit deficits in recollection but not familiarity. This is consistent with previous studies showing this pattern of deficits in word recognition (e.g. Quamme et al., 2004; Yonelinas et al., 2002), and it extends those results by showing that the same holds for faces. In addition, the finding that the left H+ group exhibited deficits in both recollection and familiarity for words is consistent with patient and neuroimaging studies implicating the left perirhinal cortex in familiarity for words (Bowles et al., 2007; Davachi, Mitchell, & Wagner, 2003; Ranganath et al., 2003; Uncapher, Otten, & Rugg, 2006; see Eichenbaum et al., 2007 for review). Finally, the deficits in the right H+ group replicate the finding that right MTL damage leads to deficits in recollection but not familiarity for verbal materials (Peters, Thoma, Koch, Schwarz, & Daum, 2009; see also Dobbins, Kroll, Tulving, Knight, & Gazzaniga, 1998).

In contrast to words, face familiarity was not disrupted in either the left or right hemisphere H+ groups. The current results suggest that face familiarity is either represented redundantly in the medial temporal lobe in both hemispheres (such that damage to the MTL in one hemisphere is not sufficient to disrupt it), or it is supported by regions outside the medial temporal lobe that were preserved in the patients (e.g. anterior temporal lobe or fusiform gyrus in one or both hemispheres). Evidence that face recognition may be bilaterally represented comes from imaging studies showing bilateral perirhinal cortex deactivations at retrieval related to familiarity-based memory for faces (Gonsalves, Kahn, Curran, Norman, & Wagner, 2005). Furthermore, Taylor et al. (2007) found that patients with extensive bilateral medial temporal lobe damage were impaired on face recognition. Evidence for a potential role of the fusiform gyrus in face familiarity comes from neuroimaging and patient research that implicates this region in both hemispheres in face processing (Barton, 2008; Goldsmith & Liu, 2001; Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Asgari, Gore, & McCarthy, 1996). Finally, the anterior temporal lobe has been implicated in the identification and imagery of faces (Barton, 2008; Kriegeskorte, Formisano, Sorger, & Goebel, 2007), and thus may also play a role in familiarity-based face memory. Whether these

regions are necessary for familiarity-based face memory remains to be determined.

3.2. Theoretical Implications

The current results have important implications for current memory theories of the MTL. First, the results indicate that the proposal that the MTL is not necessary for supporting episodic recognition memory for faces appears to be premature. MTL damage does lead to recollection impairments for both faces and words. Face recognition appears to be spared because it tends to rely more heavily on familiarity, which is relatively preserved in amnesia (Yonelinas et al., 1998). These findings are therefore consistent with dual-process models of recognition (Aggleton & Brown, 1999; Eichenbaum et al., 2007; Norman & O'Reilly, 2003; Yonelinas et al., 2002).

The current results do not fit easily into earlier single process models of the MTL (e.g. Squire et al., 1994). One potential account for the relative sparing of face recognition compared to word recognition is that face recognition is simply easier than word recognition, and it is only the more difficult tasks that rely on the MTL. However, in the current study, control participants performed slightly better in the word memory test than in the face memory test. Thus, it was not the case that the amnesics were simply less impaired on an easier recognition task.

An alternative to the dual-process interpretation of these results is the unequal-variance signal detection model, another two-component model that has sometimes been applied to recognition memory (Wixted, 2007). Although behavioral studies have largely ruled against this model (for review see Yonelinas & Parks, 2007; but also see Bird et al., 2007), it leads to the same general conclusions in the current study as the dual process view. That is, the current results could be described as reflecting the fact that amnesia is associated with a relatively selective reduction in the 'variance' component/process in recognition that leaves the 'strength' component less affected. If MTL damage reduces the variance component without greatly influencing the strength component of recognition, this could account for the lowering of high confidence hits in the amnesics. In addition, if the variance component was lower for faces than for words, then face recognition should be less impaired than word recognition. Consistent with this interpretation, the variance component was lower for faces than for words (controls' zROC slope was significantly higher for faces, $t(18) = 3.17$, $p = .003$). Moreover, the amnesics were impaired at overall discriminability for words (lower zROC intercept, $t(20) = 4.20$, $p < .001$), but not for faces, $t < 1$. Finally, amnesics had significantly higher zROC slopes compared to controls for both words, $t(20) = 3.77$, $p < .001$, and faces, $t(18) = 1.73$, $p = .01$, indicating that the old item variance was lower for amnesics than controls. Thus, both the dual-process and signal-detection approaches propose that amnesics are more reliant on a particular process (familiarity or strength), and are less impaired on face recognition because it relies heavily on this component.

3.3. Why do faces rely more on familiarity than words?

One possibility is that since the particular faces studied are not pre-experimentally familiar, each face receives a large boost in familiarity from being studied, and this allows familiarity judgments to be useful in discriminating between studied and unstudied faces at test. In contrast, words are pre-experimentally familiar, so any additional increment to familiarity as a result of study might be too small in some cases to discriminate between targets and lures at test. This becomes particularly apparent when one considers the number of words an individual has been exposed to in just the few minutes before the experiment (i.e. in conversa-

tion, reading, etc.). The words test, then, becomes akin to a source memory test in which the individual has to decide if the word is familiar because it has just been studied, or because it has been recently encountered but not in the study phase. On the other hand, the concepts associated with the studied words may bring to mind a number of pre-experimental associations, or trigger thoughts, emotions, or mental images related to those concepts, which can be used to support memory based on recollection. Such associations may be less likely to come to mind for unfamiliar faces, leading to a reduced role for recollection (see Bird & Burgess, 2008).

Another reason why face memory may depend largely on familiarity is the high feature overlap among faces, which may make the recollection of an individual feature undiagnostic of previous occurrence. Instead, the conjunction of features, or their configuration, is more diagnostic than individual features themselves. The perirhinal cortex may be involved in representing complex feature conjunctions, and has been implicated in face perception (Bussey, Saksida, & Murray, 2002; Bussey, Saksida, & Murray, 2005; Bussey & Saksida, 2005, 2007; Lee, Bussey, et al., 2005; Lee, Levi, Davies, Hodges, & Graham, 2007; Litman, Awipi, & Davachi, 2009), which might contribute to a familiarity-driven memory for faces.

3.4. Material or process?

The current results suggest that amnesia cannot be fully characterized on the basis of selectively affecting memory for particular materials (e.g. words, scenes, or faces) or for particular memory processes (recollection or familiarity). Rather, it is necessary to take into account material, process, and lesion location in order to understand the recognition deficits in amnesia. An important determinant of performance is whether the patient exhibits deficits in recollection and/or familiarity, and how heavily a given recognition task relies on recollection and familiarity. However, it is not the case that recollection and familiarity are entirely material-general, so it is important to consider how different lesion locations lead to dissociations across materials. For example, the left medial temporal lobe seems to be critical for familiarity for words, as seen from the current study as well as previous patient studies (e.g. Bowles et al., 2007) and neuroimaging studies (Davachi et al., 2003; Ranganath et al., 2003; Uncapher et al., 2006; see Eichenbaum et al., 2007 for review). Presumably this is because the left parahippocampal gyrus includes regions that are specialized for processing verbal materials. Left MTL damage, however, does not seem sufficient to disrupt familiarity for faces.

In addition, there is some evidence that the hippocampus may be particularly critical for processing complex scene information (e.g. Lee, Bussey, et al., 2005; Lee et al., 2007; Lee, Buckley, et al., 2005), and as such, damage to the hippocampus may lead to deficits in the initial encoding or identification of scenes, resulting in both recollection and familiarity-based memory deficits for these materials (for cases studies, see Bird et al., 2007, 2008). There are therefore clear limitations to material-general dual-process theories, and one needs to take into account the contributions of recollection and familiarity as well as the materials being tested and the site of the lesions in the patients in order to predict memory performance.

We propose that the hippocampus is critical for forming the novel associations that support subsequent recollection of both words and faces. Thus, selective hippocampal damage should disrupt recollection but not familiarity for faces and for words. It is possible that left versus right hippocampal damage can be more disruptive for word and face recollection, respectively, although we did not observe this in the current study. Furthermore, left parahippocampal gyrus damage should impair familiarity for words, but not for faces. Finally, bilateral medial temporal lobe damage may be necessary for face familiarity to be impaired.

4. Conclusions

The current results indicate that in order to determine whether amnesia will impact recognition memory, it is necessary to consider the materials that are being remembered as much as the retrieval process that is supporting that memory. An extensive body of research strongly supports the proposal that recollection and familiarity make distinct contributions to recognition. We propose that memory for different types of materials may depend more or less on recollection and familiarity, and these differences can be useful in explaining material-specific effects in amnesia. Nevertheless, differential contributions of recollection and familiarity are not the entire story, and it is necessary to also take into consideration the materials to be remembered as well as the lesions of the patients. It remains for future research to determine the boundaries of material generality and specificity.

Acknowledgments

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