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Report

The Hippocampus Supports Recognition Memory for Familiar Words but Not Unfamiliar Faces

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Summary

Bilateral damage to the human hippocampus profoundly impairs the ability to form long-term, consciously accessible memories, producing a classic amnesic syndrome. However, the effect of hippocampal damage on our ability to recognize items via a feeling of familiarity is hotly disputed. Dual-process theory predicts no effect [1–4], whereas declarative memory theory predicts impairment of all types of recognition memory [5]. Here, we demonstrate a striking material specificity in the effect of focal hippocampal damage: Recognition memory is impaired for words but intact for faces. The latter finding is incompatible with declarative memory theory, whereas the former constrains dual-process theory by revealing the limitations of postulated extrahippocampal familiarity-based processes. We suggest that the hippocampus boosts recognition of well-known stimuli (high-frequency words) by activating pre-experimental associations that enrich the context of their presentation. By contrast, recognition memory for some kinds of previously unfamiliar stimuli (unfamiliar faces) may be supported by extrahippocampal familiarity-based processes, at least over short intervals.

Results

We retrospectively analyzed data from all patients in the literature with selective damage to the hippocampal formation that had been assessed on the Recognition Memory Test (RMT) [6]. Details of these ten patients are given in Table 1 (see Experimental Procedures and Supplemental Data, available online, for more details). The patients were compared with a large sample of neurologically healthy adult "controls." The RMT is a clinical test of recognition memory with two subtests that employ an identical administration procedure but different memoranda (high-frequency words or unfamiliar faces). In each subtest, 50 stimuli are presented in a study phase, followed by presentation of 50 test stimuli. The test stimuli comprise two items: Each "target" from the study phase is paired with a new stimulus or "foil." Participants must indicate which of the two items on the test stimulus was in the presentation list. The two subtests of the RMT allowed us to investigate whether or not recognition-memory deficits are a pervasive feature of hippocampal amnesia or whether performance depends upon the nature of the memoranda.

Figure 1 shows the performance of patients and controls on the two subtests of the RMT. Overall, the patients' scores are below those of the controls. However, there is a significant subtest-by-group interaction; the controls performed better with words, whereas the patients performed better with faces. Direct comparison of the two groups' performances on each subtest reveals that the interaction results from a significant difference between patients and controls for words, but similar performance for faces.

Because two of the patients had evidence of additional damage to the parahippocampal gyrus (VC and PH; see Table 1), we performed the analysis again, excluding data from these patients. This did not alter the results; there was still a main effect of group ($F[1, 115] = 14.1$, $p = 0.0003$) and a significant subtest-by-group interaction ($F[1, 115] = 4.3$, $p = 0.040$). Again, the difference between the patients and controls was significant for the words subtest ($t[115] = 4.4$, $p < 0.0001$), but not for the faces subtest ($t[115] = 1.17$, $p = 0.242$).

Discussion

This is the largest group study of recognition memory in patients with isolated damage to the hippocampal formation. Single-word recognition was impaired in these patients. Interestingly, however, on the test that employed unfamiliar faces as memoranda but otherwise had an identical test procedure, performance of the patients was no different from that of the controls. This material-specific effect must be a consequence of differences in how the test items are processed. Here, we discuss possible explanations for these differences and relate them to current theories of hippocampal function.

Word recognition of the patients was significantly impaired compared to that of the controls. Indeed, the overall performance of the patients on the RMT was significantly below that of the controls. A number of previous group studies of hippocampal damage in humans have also found single-word recognition to be impaired [7–9] and recognition memory in general to be impaired when performances across different test materials were averaged together [10]. These findings are consistent with declarative memory theory, which proposes that recognition memory, like all forms of consciously accessible (declarative) knowledge, relies on the hippocampus for its acquisition [5]. In contrast, dual-process theory proposes that single items, such as words, are treated as "units" and can be recognized thorough a familiarity process that is independent of the hippocampus [1–4]. Therefore, on the face of it, impaired word recognition is at odds with dual-process theory.

However, a very different pattern of performance was observed on the face recognition-memory subtest; patients' scores were no different from the controls'. This is impressive when one considers that healthy adults generally obtain lower scores on the faces subtest than the words subtest (see [6] and Figure 1), ruling out a simple explanation of our results in terms of task difficulty. A number of studies have highlighted the fact that recognition memory for faces can be spared in hippocampal amnesia [11–15]. The finding is also consistent with a study of the effects of damage to the fornix (the major subcortical connection of the hippocampus) on memory: Reduced fornix

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Table 1. Participant Details

Patient	Citing Reference	Sex	Lesion Location	Age	IQ	RMT (Words)	RMT (Faces)
LM	[32, 43]	M	bilateral hpc lesions (CA1, CA2, and CA3) slightly greater on the left; some cell loss in entorhinal cortex	60	109	43	43
PH	[32, 44, 45]	M	bilateral hpc and parahpc volume reduction of 30%	74	120	33	41
LJ	[32, 44, 46]	F	bilateral hpc volume reduction of 46%	59	98	46	40
WH	[32, 43]	M	bilateral hpc lesions (CA1, CA2, and CA3 dentate gyrus) slightly greater on the left; some cell loss in entorhinal cortex (left > right)	71	113	28	39
GD	[43, 47]	M	bilateral hpc lesions (CA1)	46	92	43	35
VC	[13, 48]	M	bilateral hpc volume reduction of 46%; left parahpc volume reduction of 32%	72	125	36	39
BE	[49, 50]	M	bilateral hpc volume reduction of 38%; possibility of extrahippocampal damage detected by FDG PET scan (left > right)	46	128	39	42
YR	[51]	F	bilateral hpc volume reduction of 46%	58	102	45	48
PS	[52]	F	bilateral hpc volume reduction	40	100	29	33
Jon	[53, 54]	M	bilateral hpc volume reduction of 50%	19	114	45	41
Patient Mean (SD)		M = 7, F = 3		55 (16.9)	110 (12.1)	38.7 (6.8)	40.1 (4.1)
Control Mean (SD)		M = 60, F = 49		56 (8.7)	106 (10.3)	45.4 (3.1)	41.8 (3.9)

There were no significant differences between the patients and controls in age or IQ. None of the patients were reported to have any verbal or perceptual impairment. The following abbreviations were used: hpc, hippocampus; parahpc, parahippocampal gyrus; CA, cornu ammonis (subfields of the hippocampus); SD, standard deviation; IQ, full-scale IQ from the Wechsler Adult Intelligence Scale (revised version or version III [55]) or, for the controls, estimated from the National Adult Reading Test (2nd edition [42]).

volume correlates with poorer performance on the RMT words subtest, but not on the faces subtest [16].

This result is incompatible with declarative memory theory, which does not predict differential effects of hippocampal damage on recognition memory according to the nature of the test stimuli. Clearly, brain regions outside of the hippocampus are capable of retaining sufficient information on items of certain types (in this case, faces) to judge their prior occurrence.

According to dual-process theory, regions such as the perirhinal cortex in the medial temporal lobe support preserved recognition by retaining an enduring trace of the familiarity of previously presented items [17]. This familiarity trace solely concerns the characteristics of the items themselves [1–3], whereas a functioning hippocampus supports the additional contextual element of where and when the item was encountered ("recollection," "context-dependent" memory, or "episodic" memory [18]). Because words do not appear to be more intrinsically "contextual" than faces, we now consider other differences between these materials that might account for the pattern of data we report.

A key difference between the memoranda used in the two subtests of the RMT is the pre-experimental familiarity of the test items themselves. The words are all common, high-frequency words. By contrast, the faces are all male, of a similar age, and, most critically, unfamiliar to the participant. This could impact upon test performance in two ways. First, during the encoding phase of the RMT, participants are asked to decide whether each test item is "pleasant" or "unpleasant" (see Experimental Procedures). For words, this may trigger the retrieval of pre-existing associations with the word, providing a rich contextual memory to boost subsequent recognition memory for the item. Second, on the words subtest, the participant must judge which of two already "familiar" words was presented in the preceding study phase—in effect, make a simple source-memory judgment (see also [19]). Both of these context-dependent memory processes are generally agreed to rely on the hippocampus. In comparison, unknown faces have no pre-existing associations that can be activated (unless the face happens to resemble someone known to the participant), and pleasantness judgments are likely to be made on the basis of a perceptual analysis of the features. Furthermore, recognizing an unknown face as one of the previously presented targets compared with a never-seen-before foil can be achieved without retrieval of the source in which the face was presented. Therefore, normal face recognition memory as assessed by the RMT may not require hippocampally mediated memory processes under a dual-process model. There is some evidence that recognition memory for novel but not familiar items depends upon the entorhinal cortex [20].

An alternative to this "prior familiarity" explanation is simply that the hippocampus supports memory for some types of verbal material (words), but not for some types of nonverbal material (faces), whether familiar or unfamiliar. We cannot directly test this explanation because we do not know the effects of focal hippocampal damage on recognition memory for familiar faces and for novel words (nonwords) for comparison with the data in Figure 1. In partial support of this material-specific explanation is the finding that amnesics with mixed etiologies are impaired at recognizing novel "pseudowords" [21–23]. However, in these studies, it is unclear whether the impairment was due to extrahippocampal damage (in studies [21] and [22]) or because controls treated the pseudowords as paired associations of the short familiar words from which they were constructed (in study [23]).

By contrast, in support of the prior-familiarity explanation is the finding that recognition memory for novel words (i.e., nonwords) relies more on familiarity than recollection [24, 25]. Moreover, hippocampal involvement in recognition memory

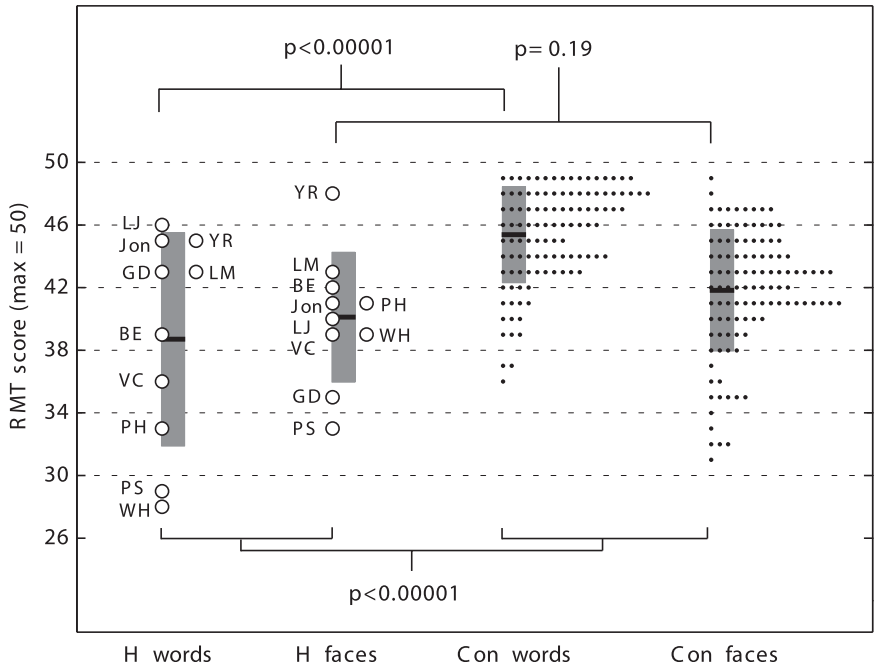

Figure 1. Differential Performance of the Hippocampal Patients on the Two Subtests of the Recognition Memory Test

The patients' scores on the two subtests of the RMT are shown on the left, controls' scores on the right. Data were analyzed with a repeated-measures analysis of variance (ANOVA), with subtest as the repeated factor and participant group as the between-subjects factor. The patients performed lower than the controls when both recognition tests were considered together (significant effect of group: $F [1, 117] = 22.9$, $p < 0.00001$). Importantly, there was a significant group-by-subtest interaction ($F [1, 117] = 8.4$, $p = 0.004$); the patients performed better on the faces than on the words subtest, whereas the controls showed the opposite pattern. Direct comparisons between the groups' performances on each subtest revealed a difference only on the words subtest (words: $t = 5.76$, degrees of freedom [df] = 117, $p < 0.00001$; faces: $t = 1.33$, $df = 117$, $p = 0.185$). The following abbreviations were used: H, hippocampal patients; Con, healthy controls. Individual patients' data points are labeled. Bold lines indicate mean group performance, and shaded bars indicate standard deviations.

for faces appears to increase with how well known the faces are to the participant ([26], see also [27–29]). These data are consistent with the prior-familiary explanation, given also that recognition-memory performance is better for familiar than unfamiliar faces [30] and that hippocampal activation is increased in items with more prior contextual associations [31]. Overall, the evidence is incomplete but nonetheless supportive of a hippocampal role in providing contextual support for the recollection of familiar stimuli.

The fact that recognition memory for words appears to involve the hippocampus exposes a limitation of the familiarity-based processing proposed by dual-process theory. It suggests that familiarity signals are not efficient for differentiating target items presented during the study phase from foil items newly presented during the test phase when the items concerned have been experienced prior to the experiment. It should also be noted that recognition of unfamiliar faces is impaired by hippocampal damage when the interval between study and test is increased to 24 hr [32]. This finding suggests that the familiarity signal decays with time since exposure (see also [33] and [34]), becoming less discriminating between targets and foils until performance may ultimately depend on hippocampally mediated recollection of the context of the previous presentation. Furthermore, even short-term representation of items that themselves resemble the contextual component of episodic memory, such as spatial layout or multimodal associations, require the hippocampus [11–15, 33, 35–37].

In sum, recognition impairments after hippocampal damage depend on the nature of the to-be-remembered stimuli. We suggest that a familiar item's pre-experimental associations serve to enrich the context of its presentation, aiding subsequent (hippocampally mediated) recollection, as expressed in some versions of dual-process theory. In addition, extrahippocampal familiarity traces created during the encoding phase may be relatively poor at discriminating between targets and foils when both items are already familiar. Furthermore, the familiarity trace may decay faster than representations supporting recollection during a delay between presentation and test. These considerations may explain why tasks with similar procedures that use different memoranda (words or unfamiliar faces) have found inconsistent evidence for a hippocampal role in item recognition memory [7, 15]. It may also explain why studies using delayed non-match-to-sample tasks with trial-unique stimuli show mild or no effect of hippocampal damage in nonhuman primates at short delays but impairments at longer delays [38, 39]. We predict that deficits would be seen at short delays if pre-experimentally familiar stimuli, e.g., pictures of faces familiar to them, were used.

Experimental Procedures

Isolated damage to the hippocampal formation in humans is very uncommon. This is problematic when attempting to conduct meaningful comparisons between patients with hippocampal damage and a healthy control population. To overcome this problem, we conducted a meta-analysis of amnesics' performances on Warrington's RMT [6]. The same method was used by Aggleton and Shaw [40] in an influential meta-analysis of recognition memory in patients of various etiologies. However, this study only included three focal hippocampal patients.

The RMT comprises two subtests. The verbal subtest uses short, high-frequency words. In the study phase, 50 words are presented individually with an orienting question (do you consider the item to be "pleasant or unpleasant"?). A two-alternative forced-choice test phase follows immediately after the study phase. Thus, in the test phase, 100 words are presented; the 50 words presented at study (targets) are paired with 50 new ones (foils). The left or right position of the target on the test stimulus is assigned randomly. The participant indicates which word he or she believes to have been present in the study list. The nonverbal subtest uses black-and-white photos of unfamiliar Caucasian males. The study and test phases, including the orientation question, are the same as for the verbal subtest.

Patients were selected according to similar criteria as those used by Aggleton and Shaw [40]. Thus, on the occasions that a person had been tested more than once on the RMT, we used the most recent score in order to reduce the effect of transient disruptions of memory in the acute phase of recovery. (However, it should noted that the main findings are unchanged if the score at first assessment is used.) Ten patients with relatively focal hippocampal lesions were identified, all of whom have been described in the literature as having discrete bilateral lesions to the hippocampal formation (see Table 1 for details and Supplemental Data for full case report). These patients were compared with a control group of healthy adults matched for age and IQ.

The population of healthy controls was taken from a study by Bird et al. [41]. They were neurologically healthy adults with no history of alcohol or substance abuse, nor any history of psychiatric illness requiring inpatient care. Individuals were only selected if they had been assessed on both subtests of the RMT, if they performed below ceiling on both subtests of the RMT (49/50 or below), and if they had an estimated IQ [42] of 120 or less. The latter requirement was included for ensuring that the group was well matched to the patients in terms of intellectual ability.

Supplemental Data

Supplemental Data include additional details about the patients and can be found with this article online at http://www.current-biology.com/supplemental/S0960-9822(08)01415-2.

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