A demonstration that the hippocampus supports both recollection and familiarity

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Recognition memory is thought to depend on two distinct processes: recollection and familiarity. There is debate as to whether damage to the hippocampus selectively impairs recollection or whether it impairs both recollection and familiarity. If hippocampal damage selectively impairs recollection but leaves familiarity intact, then patients with circumscribed hippocampal lesions should exhibit the full normal range of low-confidence and high-confidence familiarity-based recognition. High-confidence, familiarity-based decisions are ordinarily accompanied by successful recollection (when memory is intact). However, patients with hippocampal lesions, if recollection is impaired, should frequently experience high-confidence, familiarity-based recognition in the absence of recollection, and this circumstance (termed the "butcher-on-the-bus" phenomenon) should occur more often in patients than in healthy controls. We tested five patients with circumscribed hippocampal damage, asking them to recognize recently studied words as well as to remember the context in which the items were studied. Relative to controls, the patients exhibited no increased tendency to experience the butcher-on-the-bus phenomenon. The simplest explanation of the results is that hippocampal damage impairs familiarity as well as recollection. The same conclusion was suggested when two competing models of recognition memory were used to analyze the data.

amnesia | recognition | source memory

The ability to accurately recognize a previously encountered item is generally thought to be based on two processes: recollection and familiarity. Recollection involves remembering the source of a prior encounter, whereas familiarity involves simply knowing that the item was previously encountered despite the absence of any information about its source. The following anecdote, offered by Mandler (1), illustrates these two processes:

> Consider seeing a man on a bus whom you are sure that you have seen before; you "know" him in that sense. Such a recognition is usually followed by a search process asking, in effect, Where could I know him from? Who is he? The search process generates likely contexts (Do I know him from work; is he a movie star, a TV commentator, the milkman?). Eventually the search may end with the insight, That's the butcher from the supermarket! (pp 252–253)

The initial sense of familiarity reflects strong recognition of the item itself, whereas the subsequent experience of recollection (if it occurs) reflects the retrieval of source information associated with that item. A pure, familiarity-based experience of strong recognition in the absence of source recollection has come to be known as the "butcher-on-the-bus" phenomenon (2–4).

An issue of considerable interest is how the structures of the medial temporal lobe support recollection and familiarity. According to one view, recollection depends on the hippocampus, whereas familiarity depends on the adjacent perirhinal cortex (5, 6). Alternatively, it has been proposed that the functional differences between the hippocampus and the perirhinal cortex that have been described do not correspond to the distinction between recollection and familiarity (7, 8). Instead, both structures contribute to these memory processes.

If recollection were selectively impaired after hippocampal lesions, the experience of high-confidence, familiarity-based recognition in the absence of source recollection (i.e., the butcher-on-the-bus phenomenon) should be especially common (Fig. 1). Specifically, after hippocampal lesions, the experience of familiarity should be intact across the full range of confidence. When high-confidence, familiarity-based recognition occurs in intact individuals, recollection is often successful. In patients, high-confidence, familiarity-based recognition should be just as common as in intact individuals, but recollection should be less successful. Accordingly, if the hippocampus selectively subserves the recollection process, then patients with selective hippocampal lesions should experience the butcher-on-the-bus phenomenon *more often* than healthy controls. This counterintuitive prediction has not been widely appreciated and has never been tested.

Five memory-impaired patients (H-25) and seven controls (C-25) studied a list of 25 words (adjectives) three times in succession and in one of two contexts (source A or source B; Fig. 2). To match patient performance, a second control group (C-100) studied 100 words once using the same two-context procedure. Memory for the words (item memory) was then tested in an old/new recognition memory test with a 6-point confidence scale (1 = sure new, 6 = sure old). For items endorsed as old, participants were asked what context the study word appeared in (source memory) and again gave a 6-point confidence rating (1 = sure source A, 6 = sure source B). Old decisions made with high confidence but in the absence of successful source recollection would correspond to the butcher-on-the-bus phenomenon. The question of interest was whether patients with hippocampal lesions experience that phenomenon more often than controls.

Results

On the Old/New portion of the recognition test, the performance of patients with hippocampal lesions (H-25) was impaired relative to controls (C-25; Fig. 3*A*). Controls who studied a longer list (C-100) were also impaired relative to the C-25 group but performed similarly to the patients. The same pattern was obtained for the source memory judgments made to targets that had been correctly recognized as old (Fig. 3*B*). In addition, in all three groups, the accuracy of the Old decisions (Fig. 4*A*) and the accuracy of the source memory judgments (Fig. 4*B*) increased as confidence in each decision increased.

Of particular interest are the targets that received a high-confidence Old decision (i.e., targets that received a rating of "Old-6") (Fig. 4*A*). When an item received a rating of Old-6, participants were usually correct in their Old/New judgment (H-25, 0.84; C-100, 0.91; C-25, 0.99). In its classic formulation (1), the butcher-on-the-bus phenomenon involves having high con-

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Target Item Number	Item Memory Confidence When Based Only on Item Familiarity	Source Recollection in Healthy Controls	Butcher-on-the-Bus Phenomenon
1	2		
2	5		
3	4	✓	
4	6		*
5	4		
6	6	✓	(*)
7	3		
8	5	✓	
9	6	✓	(*)
10	3		

Fig. 1. A hypothetical illustration of the status of item recognition and source memory after studying 10 target words. *Item recognition* refers to the ability to discriminate old, previously studied items from new items. *Source memory* refers to the ability to recollect information about the context in which the item was studied. On the recognition test, each item will be associated with some level of familiarity that, even on the basis of familiarity alone, would be sufficient to support some level of confidence rating on a rating scale of 1–6 (second column). In healthy controls, some target words would also be associated with successful source recollection (indicated by a checkmark in the third column). Target items that are so strongly familiar that they receive a confidence rating of 6 but are not accompanied by source recollection illustrate the butcher-on-the-bus phenomenon (as indicated by an asterisk for item 4 in the fourth column). If source recollection were impaired, and familiarity preserved, as has been proposed to be the case after hippocampal lesions, then additional target items should be associated with source memory failure, and the butcher-on-the-bus phenomenon should occur with high frequency [i.e., source memory failure despite strong item memory (confidence rating = 6), as indicated by the additional asterisks in parentheses for items 6 and 9]. In short, if the hippocampus selectively supports recollection, then patients with hippocampal lesions should experience the butcher-on-the-bus phenomenon more often than controls.

fidence that an item is Old ("Consider seeing a man on a bus whom you are *sure* that you have seen before") but low confidence that the source is known ("Do I know him from work; is he a movie star, a TV commentator, the milkman?"). In our study, Old-6 decisions accompanied by a high-confidence source

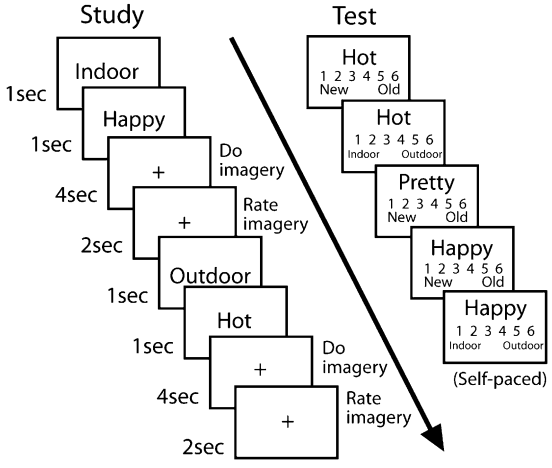

Fig. 2. Task procedure. Participants learned a list of words by imagining an indoor or outdoor scene associated with each word. At study, participants were shown a cue (indoor/outdoor) for 1 s, a study word for 1 s, and then had 4 s to form an indoor or outdoor image as they viewed a fixation cross. Participants then rated (2 s) how successfully they created a mental image. At test (1 to 2 min later), participants made old/new decisions for the studied words and the novel foils on a 6-point confidence scale (1= "sure new", 6 = "sure old"). For words endorsed as "old," participants also made source judgments (indoor or outdoor) on a 6-point scale (1 = "sure source A", 6 = "sure source B").

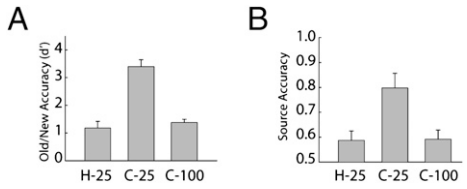

Fig. 3. Recognition memory performance for patients with hippocampal lesions (H-25) and controls (C-25) who studied 25 words three times in succession, as well as controls (C-100) who studied 100 words once. (*A*) On the Old/New portion of the test, overall recognition accuracy (*d'*) exceeded chance for each group ($P < 0.005$, one-tailed *t* tests). For the C-25 group, performance was better than performance for the other two groups ($P < 0.05$). Performance was similar for the H-25 and C-100 groups. (*B*) Overall source accuracy scores (proportion correct) exceeded chance for each group ($P < 0.05$, one-tailed *t* tests), and performance for the C-25 group was better than in the other two groups (all $P < 0.05$, two-sample *t* tests). Performance was similar for the H-25 and C-100 groups. Error bars show standard errors.

judgment occurred much less often in the H-25 group than in the C-25 group (Fig. 5*A*). This finding is consistent with the idea that recollection is impaired by hippocampal lesions. In the C-100 group, performance was similar to that in the H-25 group, suggesting that long study lists reduce recollection as well. A similar pattern, although less pronounced, was evident for Old-6 decisions associated with medium source confidence (Fig. 5*B*).

Of most interest were Old-6 decisions that were associated with low-confidence source judgments, because this condition illustrates the butcher-on-the-bus phenomenon (Fig. 5*C*). The percentage of targets falling into that category did not differ significantly across groups and occurred numerically less often (not more often) in the H-25 and C-100 groups than in the C-25 group. This finding is inconsistent with the idea that hippocampal lesions (or long study lists) impair recognition memory in such a way that leaves familiarity intact while impairing recollection. If familiarity were fully intact in the H-25 group, and recollection impaired, there should have been more instances of high-confidence Old/New responses associated with low source confidence. The simplest explanation of this pattern of results is that both familiarity and recollection were impaired.

Next, we estimated the percentage of targets that received an Old-6 decision accompanied by successful source recollection and the percentage of targets that received an Old-6 decision but unaccompanied by source recollection. To do so, the obtained source accuracy scores were first corrected for guessing because, even in the absence of source recollection, participants have a 50% chance of correctly identifying the source. For example, consider a participant who correctly recollects the source of 50% of the targets rated Old-6 (i.e., true recollection = 0.50) and who

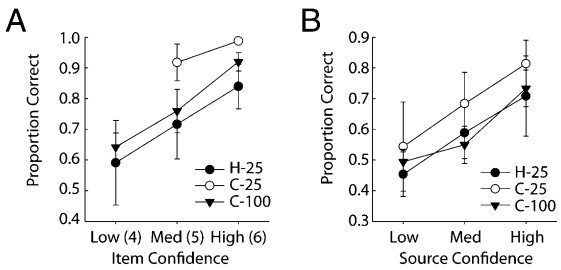

Fig. 4. Relationship between confidence and accuracy. (*A*) For each group, accuracy in the Old-New decision increased as confidence in that decision increased (participants in the C-25 group made too few low-confidence ratings to compute an accuracy score for ratings of 4). (*B*) For each group, accuracy in the source memory decision also increased as confidence in that decision increased. Error bars show standard errors.

NEUROSCIENCE

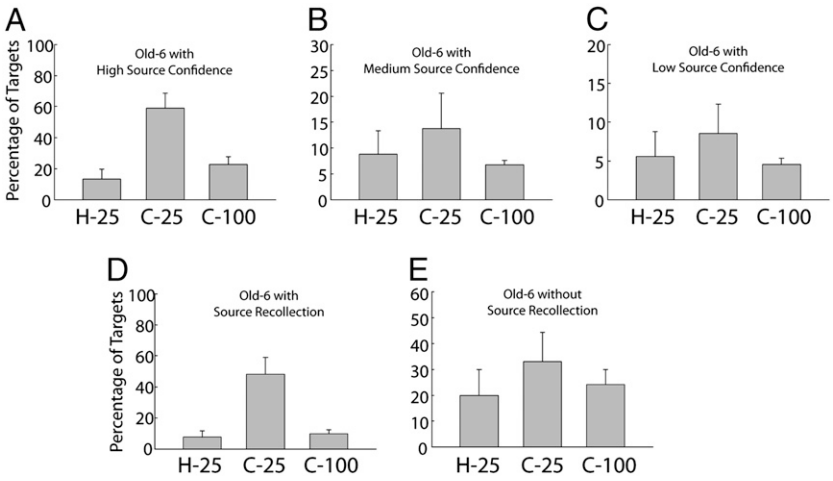

Fig. 5. High-confidence Old decisions (Old-6) as a function of high, medium, and low source confidence (*A*–*C*) and as a function of source accuracy (*D* and *E*). (*A*) The percentage of target items associated with an Old-6 decision and a high-confidence source decision was significantly higher for the C-25 group than for the H-25 and C-100 groups. Performance was similar for the latter two groups. (*B*) The percentage of target items associated with an Old-6 decision and medium confidence in the source decision did not differ significantly across groups. (*C*) The percentage of target items associated with an Old-6 decision and low confidence in the source decision (which corresponds to the subjective experience known as the butcher-on-the-bus phenomenon) also did not differ significantly across groups and was numerically highest for the C-25 group. (*D*) The percentage of target items associated with an Old-6 decision and successful source recollection was significantly higher for the C-25 group than for the H-25 and C-100 groups. The proportion of items associated with successful source recollection was computed using a standard correction-for-guessing formula that assumes that recollection is a discrete (i.e., present or absent) phenomenon (see text). (*E*) The percentage of target items associated with an Old-6 decision and unsuccessful source recollection did not differ significantly across groups and was numerically highest for the C-25 group.

guesses for the remaining 50%, with approximately half of those guesses being correct due to chance alone. The obtained source accuracy score for this participant would be 0.75, but the corrected score would be 0.50 (for correction formula, see *SI Materials and Methods*).

Using the corrected source accuracy scores, we found that the percentage of targets that received an Old-6 decision accompanied by successful source recollection was much higher in the C-25 group than in the other two groups (Fig. 5*D*). This finding is again consistent with the idea that hippocampal lesions (and long study lists) impair source recollection. However, the percentage of targets that received a rating of Old-6 in the absence of source recollection did not differ significantly across groups and was numerically lower (not higher) for the H-25 and C-100 groups than for the C-25 group (Fig. 5*E*). Again, this finding is inconsistent with the idea that hippocampal lesions (or long study lists) impair recollection while leaving familiarity intact. Instead, the results suggest that familiarity, as well as recollection, is impaired for the H-25 and C-100 groups.

A participant's decision as to whether to rate a test item as being Old with high confidence (i.e., to rate it as Old-6) depends on whether the memory strength of that item exceeds a criterion value. If the criterion used for making high-confidence Old decisions differed for the H-25, C-25, and C-100 groups, this circumstance would complicate the effort to compare the frequency of the butcher-on-the-bus experience across groups. For example, if hippocampal patients were reluctant to express high confidence in an Old decision, even when the familiarity of a test item was high enough that a healthy control would express high confidence, then the measured frequency of the butcher-on-the-bus phenomenon for the H-25 group might be reduced for that reason alone. However, as described next, the patients were more inclined than controls (not less inclined) to express high confidence in Old decisions for a given level of familiarity. As such, if anything, the estimated frequency of high-confidence Old decisions and low-confidence source decisions (the butcher-on-the-bus phenomenon) for the H-25 group (Fig. 5 *C* and *E*) was overestimated.

Specifically, the C-25 participants used a more stringent Old-6 criterion than the patients. As a result, for the C-25 group only a small proportion of foils was incorrectly rated Old-6 (0.01 ± 0.01). By contrast, the H-25 group used a less-stringent criterion and incorrectly rated a higher proportion of foils as Old-6 (0.10 ± 0.06). In addition to inflating the Old-6 false alarm rate, the use of a less-stringent Old-6 criterion by the H-25 group would necessarily admit additional (comparatively weak) *target* memories into the Old-6 category than would be admitted by the C-25 group. This effect would serve to inflate the estimated percentage of high-confidence targets associated with weak source memory (i.e., it would inflate the frequency of the butcher-on-the-bus phenomenon in the H-25 group relative to the C-25 group). Yet, even with this influence operating, the H-25 group did not exhibit the butcher-on-the-bus phenomenon to a greater extent than was observed in the C-25 group (Fig. 5 *C* and *E*).

We also constructed receiver operating characteristic (ROC) curves from the confidence ratings for Old/New decisions and analyzed the data using two prominent models: the traditional unequal-variance signal detection model (9) and the high-threshold/signal detection model (10) (*SI Materials and Methods*). A ROC is a plot of the hit rate vs. the false-alarm rate associated with different levels of confidence, and these two models have often been used to interpret ROC data. The goodness of fit statistics for the unequal-variance signal detection model [$\chi^2(3) = 6.49$, 12.84, and 7.14 for the H-25, C-100, and C-25 groups, respectively] were lower than the corresponding values for the high-threshold/signal detection model [$\chi^2(3) = 6.60$, 27.69, and 8.34, respectively]. Thus, the unequal-variance signal-detection model provided a better fit of the ROC data for all three groups, a result that is consistent with many prior individual and group ROC analyses (11–16).

The unequal-variance, signal-detection model assumes that the memory strengths of the target and foils on an Old/New recognition test are normally distributed, such that the mean and variance of the target distribution are greater than the mean and variance of the foil distribution. Interpreted in terms of this model, our ROC results suggest that hippocampal lesions (and

long study lists) reduce both the mean and variance of the memory strengths associated with the target items compared with the C-25 group (*SI Materials and Methods*). If the memory strength of each target item is a joint function of a recollection process and a familiarity process, as required by some models (15, 17) and as recent evidence suggests (15), then the simplest interpretation of our findings is that hippocampal lesions and long study lists weaken both recollection and familiarity. Accordingly, hippocampal lesions do not create a circumstance whereby strong familiarity regularly occurs in the absence of recollection (i.e., the butcher-on-the-bus phenomenon does not commonly occur).

The alternative, high-threshold/signal detection model (10) suggests a similar interpretation. Unlike the unequal-variance model, the high-threshold model yields quantitative estimates of recollection and familiarity. In addition, its estimate of recollection includes both source recollection (i.e., indoor or outdoor) and any other recollection that might occur (e.g., recollection of unrelated thoughts about the item that occurred at presentation). The results of this analysis (*SI Materials and Methods*) suggest that recollection was markedly impaired for the H-25 and C-100 groups relative to the C-25 group (Fig. 6*A*) and that familiarity was impaired in these two groups as well (Fig. 6*B*). The impairment in familiarity was such that the estimated frequency of the butcher-on-the-bus phenomenon for the H-25 group was very small and approximately the same as for the C-25 group (for the calculations, see *SI Materials and Methods*).

Discussion

Recognition memory is generally thought to be subserved by two processes: recollection and familiarity (1). In everyday experience, the familiarity process is perhaps best illustrated when one has certain knowledge that an item has been previously encountered even though the source (or context) of the prior encounter cannot be recollected (the so-called butcher-on-the-bus phenomenon) (1). Some accounts hold that the hippocampus selectively subserves recollection and is not involved in the familiarity process (5, 6). If so, then the butcher-on-the-bus phenomenologic experience should occur commonly after bilateral lesions limited to the hippocampus. This should occur because, if familiarity is preserved, then patients with hippocampal lesions should experience the butcher-on-the-bus phenomenon for items that in healthy individuals would have been accompanied by source recollection. As a result, despite having weaker memory overall, patients with hippocampal lesions should experience the butcher-on-the-bus phenomenon more often than controls given similar study conditions (Fig. 1).

Our results did not support this prediction. We tested patients with well-characterized, bilateral hippocampal lesions and no detectable pathology outside of this structure. When these patients (H-25 group) expressed high confidence that a target item was old, the frequency of low-confidence source judgments (Fig. 5*C*) was no greater than for controls (C-25 group) who were given the same study conditions or for controls matched for overall memory strength (C-100 group). In addition, when the H-25 group expressed high confidence that a target item was old, the frequency with which these high-confidence Old responses were unaccompanied by source recollection (Fig. 5*E*) was no greater for controls given the same study conditions (C-25 group) or for controls matched for overall memory strength. Indeed, if anything, Fig. 5*C* and Fig. 5*E* show that the patients exhibited the butcher-on-the-bus phenomenon less often (not more often) than controls given the same study conditions (C-25 group).

Experimental studies of the familiarity process in patients with hippocampal lesions have not previously considered the idea that these patients might be especially prone to experiencing high-confidence recognition in the absence of source recollection. Studies that have come closest to doing so used the Remember/Know procedure in which participants declare each "Old" decision as being based either on recollection ("Remember") or on familiarity ("Know"). Standard instructions for this procedure include the stipulation that the Know judgments should be made only when the participant is sure that the item was previously encountered, even though no source details can be recollected. If these instructions are followed correctly, Know judgments should correspond to the butcher-on-the-bus experience. Accordingly, if recollection were selectively impaired, Know judgments should be especially common after hippocampal lesions. In such studies, amnesic patients have sometimes (18, 19), but not always (20, 21), exhibited a higher frequency of Know judgments than controls (as if they experience the butcher-on-the-bus phenomenon more often than controls). However, in recent years, much evidence has accumulated showing that, despite receiving standard instructions, participants usually make Know judgments for Old decisions that are associated with low-to-medium confidence, not high confidence (22–24). Thus, Know judgments reflect relatively weak memory (as well as weak source recollection), not strong memory in the absence of source recollection. Accordingly, it is not surprising that hippocampal patients sometimes make more Know judgments than controls.

Similarly, in our study, the H-25 group gave low- and medium-confidence Old/New ratings (4 and 5) to a higher percentage of targets (42.0% ± 11.7%) than did the C-25 group (6.3% ± 1.7%). If Know judgments reflect relatively low confidence, then the fact that hippocampal patients make more Know judgments than controls simply means that they have more weak memories than controls, not that they exhibit intact familiarity in the absence of recollection. A stronger and less theory-dependent test of the idea that recollection is selectively impaired (either by an experimental manipulation or by hippocampal lesions) is to measure the frequency of the butcher-on-the-bus phenomenon, as we have done in the present study. Hippocampal lesions did not result in an absolute increase in that phenomenon (as would be expected if recollection were selectively impaired), and we are unaware of any experimental manipulation that has demonstrated that effect.

In two recent reports, the high-threshold/signal-detection model (10) was fit to ROC data from rats, and the results suggested that hippocampal lesions impair recollection while preserving familiarity (25, 26). Given the considerable human literature raising questions about the high-threshold/signal-detection model (17, 27–29), these results could mean either that the hippocampus selectively subserves recollection in rats (even though this does not seem to be the case in humans) or that the novel method used to generate ROC data in rats violated standard assumptions that underlie ROC analysis (30). In any case, our findings suggest that hippocampal lesions in humans

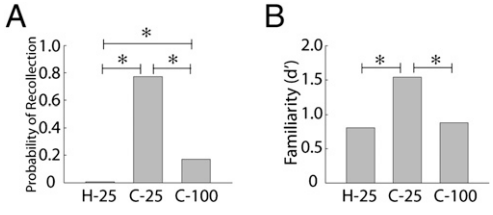

Fig. 6. Recollection and familiarity parameter estimates based on the maximum likelihood fit of the high-threshold/signal-detection model (10) to the Old/New group ROC data for the H-25, C-25, and C-100 groups. (*A*) The recollection parameter was significantly higher for the C-25 group than for the H-25 and C-100 groups. The recollection parameter for the C-100 group was also significantly higher than that for the H-25 group. (*B*) The familiarity parameter (*d'*) was significantly higher for the C-25 group relative to the H-25 and C-100 groups. *$P < 0.05$.

impair both recollection-based and familiarity-based recognition memory. Patients with hippocampal lesions do not experience the butcher-on-the-bus phenomenon more often than unimpaired controls, as is required by the view that the hippocampus supports recollection but not familiarity. Our findings conform to our impressions over the years that patients with hippocampal lesions are not commonly in a state where they recognize as fully familiar a recently encountered person, place, or object but cannot recollect when or where the encounter occurred.

Materials and Methods

Participants. Five memory-impaired patients participated (four male) (*SI Text*). All five patients have bilateral lesions thought to be limited to the hippocampus (CA fields, dentate gyrus, plus subicular complex).

K.E. became amnesic in 2004 after an episode of ischemia associated with kidney failure and toxic shock syndrome. L.J. became amnesic in 1988 during a 6-month period, with no known precipitating event. Her memory impairment has been stable since that time. Patients G.W. and R.S. became amnesic in 2001 and 1998, respectively, after a drug overdose and associated respiratory failure. J.R.W. became amnesic in 1990 after cardiac arrest. Estimates of medial temporal damage were based on quantitative analysis of magnetic resonance (MR) images compared with data for 19 controls (for the 4 male patients) and 11 controls (for L.J.) (31, 32). K.E., L.J., R.S., G.W., and J.R.W. have an average bilateral reduction in hippocampal volume of 49%, 46%, 33%, 48%, and 44%, respectively (31, 33). On the basis of histologic analysis of two other patients who also had reductions in hippocampal volume of approximately 40% (34), it seems likely that a volume reduction in this range indicates a nearly complete loss of hippocampal neurons. The volume of the parahippocampal gyrus is reduced by 17%, −8%, 1%, 12%, and 6%, respectively (all values within 2 SDs of the control means). Nine coronal MR images for the patients, together with detailed descriptions of the lesions, and multiple, quantitative measurements outside the medial temporal lobe are presented in *SI Text*.

Sixteen age- and education-matched controls (11 male; mean age, 62.9 ± 2.6 years; education, 14.9 ± 0.5 years) also participated (7 in the C-25 group and 9 in the C-100 group).

Materials and Procedure. The procedure was similar to one used previously (35) (Fig. 2). Four lists of 50 words were constructed from a pool of 200 adjectives (mean frequency of 55 per million; range, 10–500). Half the words in each list (targets) were presented during both study and test. The other half (foils) were presented only at test. Target/foil assignment was counterbalanced across participants, and the four lists of 50 words were equally likely to be used. Five patients (H-25) and seven controls (C-25) studied 25 target words three times in succession. For each target word, participants first saw a cue (indoor/outdoor) followed by the target word (e.g., happy) and were asked to form an image of an indoor or outdoor scene that was associated with the target word. A fixation cross then appeared for 4 s, during which time participants formed their image. Across participants, each of the target words was equally likely to be presented with indoor or outdoor imagery instructions. Participants were asked to remember the target words for a subsequent memory test but were not asked to remember either the cue or the image they formed.

One to two minutes after the third presentation of the study list, a recognition memory test was given (25 target words and 25 foils). For each word, participants first made an Old/New recognition confidence judgment (the item question) on a 6-point scale (1 = "sure new", 2 = "probably new", 3 = "guess new", 4 = "guess old", 5 = "probably old", and 6 = "sure old"). In cases in which the participant indicated that the word was old (Old/New responses 4, 5, and 6), they were next asked whether the word was learned in association with an indoor or outdoor image (the source question), and they reported their confidence for their indoor/outdoor decision (1 = "sure indoor", 2 = "probably indoor", 3 = "guess indoor", 4 = "guess outdoor", 5 = "probably outdoor", 6 = "sure outdoor"). The patients (but not the controls) were also tested again at least 4 h later with a second set of words.

A second group of nine controls (C-100) studied 100 words once and were then tested with 200 words (100 targets, 100 foils), following the same procedure as just described. In this way, it was possible to ask whether patients and controls with similar item memory performance (patients in the H-25 group and controls in the C-100 group) would also exhibit similar source memory performance.

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