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Under What Conditions Is Recognition Spared Relative to Recall After Selective Hippocampal Damage in Humans?

J.S. Holdstock,[1*] A.R. Mayes,[1] N. Roberts,[3]
E. Cezayirli,[3] C.L. Isaac,[2] R.C. O'Reilly,[4]
and K.A. Norman[4]

[1]*Department of Psychology, University of Liverpool, Liverpool, UK*
[2]*Section of Clinical Neurology, Division of Clinical Sciences, University of Sheffield, Royal Hallamshire Hospital, Sheffield, UK*
[3]*Magnetic Resonance and Image Analysis Research Centre, University of Liverpool, Liverpool, UK*
[4]*Department of Psychology, University of Colorado, Boulder, Colorado*

ABSTRACT: The claim that recognition memory is spared relative to recall after focal hippocampal damage has been disputed in the literature. We examined this claim by investigating object and object–location recall and recognition memory in a patient, YR, who has adult-onset selective hippocampal damage. Our aim was to identify the conditions under which recognition was spared relative to recall in this patient. She showed unimpaired forced-choice object recognition but clearly impaired recall, even when her control subjects found the object recognition task to be numerically harder than the object recall task. However, on two other recognition tests, YR's performance was not relatively spared. First, she was clearly impaired at an equivalently difficult yes/no object recognition task, but only when targets and foils were very similar. Second, YR was clearly impaired at forced-choice recognition of object–location associations. This impairment was also unrelated to difficulty because this task was no more difficult than the forced-choice object recognition task for control subjects. The clear impairment of yes/no, but not of forced-choice, object recognition after focal hippocampal damage, when targets and foils are very similar, is predicted by the neural network-based Complementary Learning Systems model of recognition. This model postulates that recognition is mediated by hippocampally dependent recollection and cortically dependent familiarity; thus hippocampal damage should not impair item familiarity. The model postulates that familiarity is ineffective when very similar targets and foils are shown one at a time and subjects have to identify which items are old (yes/no recognition). In contrast, familiarity is effective in discriminating which of similar targets and foils, seen together, is old (forced-choice recognition). Independent evidence from the remember/know procedure also indicates that YR's familiarity is normal. The Complementary Learning Systems model can also accommodate the clear impairment of forced-choice object–location recognition memory if it incorporates the view that the most complete convergence of spatial and object information, represented in different cortical regions, occurs in the hippocampus. *Hippocampus 2002;12:341–351.*

INTRODUCTION

One influential view concerning the role of the hippocampus in memory is that it is critically involved in both recall and recognition (Reed and Squire, 1997; Squire and Zola, 1998). This view therefore predicts that both types of memory will be impaired equally by selective hippocampal damage if tests are matched for difficulty.

An alternative view is that, although critical for recall, the hippocampus is not required for recognition memory decisions that can be made successfully on the basis of the familiarity of the material (Aggleton and Shaw, 1996; Aggleton and Brown, 1999). This proposed dissociation has received some support from a recent functional magnetic resonance imaging (MRI) study (Eldridge et al., 2000). This study used the remember/know procedure to tap recollection and familiarity, respectively, of recently studied words. It found that hippocampal activation, relative to a prestimulus baseline in which subjects fixated a cross-wire, was greater during remember responses than during know responses. However, evidence that know responding, and therefore familiarity, does not involve

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*Correspondence to: J.S. Holdstock, Department of Psychology, University of Liverpool, Eleanor Rathbone Building, P.O. Box 147, Liverpool, L69 3BS, UK. E-mail: j.holdstock@liverpool.ac.uk

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the hippocampus at all was less strong. Although relative hippocampal activation during know responses did not differ from the activation found when subjects correctly rejected new words or did not recognise studied words (misses), it remains to be determined whether these similar levels of activation reflect the same or different underlying hippocampal processes.

Aggleton and Brown's view predicts that recognition should sometimes be spared after hippocampal damage. Consistent with this prediction, Vargha-Khadem et al. (1997) found that hippocampal damage early in life impaired recall but spared the recognition of individual items (e.g., individual faces or words) and the recognition of associations between items of the same kind (e.g., word–word and face–face associations). However, Squire and colleagues have found impairments of both recall and item recognition in their patients with adult-onset, apparently selective, hippocampal damage (Manns and Squire, 1999). This finding has led them to attribute the pattern of memory performance shown by the young patients of Vargha-Khadem and colleagues to compensation occurring as a result of the early age of onset of their pathology.

AIMS OF THE STUDY

Aim 1: Comparison of YR's Forced-Choice Object Recognition and Object Recall

The present experiment examined the recall and recognition memory of a patient, YR, who has selective hippocampal damage. Like the patients described by Squire and colleagues, YR's hippocampal pathology occurred during adulthood; she is therefore unlikely to have differed from them with respect to compensation. The first aim of the study was to investigate whether YR's forced-choice object recognition and object recall dissociated when task difficulty was controlled. Previous testing of YR after the onset of her hippocampal pathology has shown that despite a deficit in recall, her performance has been unimpaired on 25 forced-choice item recognition tests (Mayes et al., 2002; see also Holdstock et al., 2000a; Mayes et al., 2001). For example, on the Recognition Memory Test (Warrington, 1984), her recognition of words was at the 75th percentile level (45 out of 50) and her recognition of faces was at greater than the 95th percentile level (48 out of 50). These findings suggest that a relative sparing of item recognition after hippocampal damage is not restricted to developmental cases. The relative difficulty of the recall and forced-choice recognition tests needs to be matched where possible. Only in this way can one be sure that dissociations have occurred because of specific processing differences between recall and recognition tests. In the present study a forced-choice object recognition task was developed that was as difficult for control subjects as an accompanying recall test when difficulty was measured by the accuracy of subjects' performance. As stated above, the first aim of the present experiment was, therefore, to determine whether YR's recall and forced-choice item recognition would dissociate when task difficulty was controlled.

Aim 2: Comparison of YR's Forced-Choice and Yes/No Object Recognition

Although forced-choice item recognition may be spared by YR's hippocampal damage, the neural network-based Complementary Learning Systems model of recognition (Norman, 2000; Norman and O'Reilly 2001; see also McClelland et al., 1995; O'Reilly and Rudy, 1999, for further discussion of the Complementary Learning Systems idea) predicts that under specific circumstances item recognition should be impaired by hippocampal damage. More specifically, it predicts that hippocampal damage should impair yes/no item recognition when targets and foils are similar to each other. By contrast, forced-choice item recognition should be relatively spared when targets are tested against foils similar to that target. The second aim of this article was to investigate this prediction.

The framework distinguishes between two specialised memory networks: The neocortex integrates information across episodes to arrive at a representation of what is generally true in the environment. It learns slowly, and assigns similar representations to similar stimuli, allowing it to generalise to novel stimuli based on their similarity to those that were previously encountered. The hippocampus stores specific patterns of cortical activity in a manner that supports subsequent recall based on partial cues ("pattern-completion"). The hippocampus assigns distinct representations to stimuli, and the use of relatively nonoverlapping ("pattern-separated") representations allows it to learn rapidly without suffering from catastrophic interference (see McClelland et al., 1995, for further discussion of these Complementary Learning Systems principles).

Other models have postulated similar processes in the hippocampus. For example, Rolls has written extensively about how the hippocampus could implement pattern completion and pattern separation (e.g., Rolls, 1989; Rolls and Treves, 1998; see also O'Reilly and McClelland, 1994). Also, Squire has argued that the hippocampus plays a critical role in binding together the features of episodes in a manner that supports recall based on partial cues (Squire, 1992).

According to the Complementary Learning Systems model of recognition, learning mediated by the medial temporal lobe cortices is too slow to support recall (recollection) of specific studied items after limited exposure. However, even limited exposure to a stimulus causes changes in the medial temporal lobe cortex such that studied (familiar) stimuli strongly activate a small number of medial temporal lobe cortical units, whereas unstudied (unfamiliar) stimuli weakly activate a large number of medial temporal lobe cortical units; this allows the item's familiarity to be read from its representation in medial temporal cortex. As a result, the medial temporal lobe cortices can support good recognition performance because studied items tend to trigger a stronger familiarity signal than do foils.

However, because the medial temporal lobe cortices assign similar representations to similar stimuli, targets and corresponding similar foils will trigger similar levels of medial temporal cortical familiarity output. So, if targets are quite different from each other but corresponding targets and foils are very similar, the foils corresponding to a highly familiar target may be more familiar than a target of low familiarity. This leads to extensive overlap in the distribution of familiarity for targets and foils. When overlap is high, it is not possible to place a familiarity threshold (criterion for accepting an item as familiar) without there being either a large number of foils above it or a large number of studied items below it. Consequently, many errors will be made when recognition is tested by a yes/no paradigm. When targets and foils are similar, successful performance on yes/no recognition would depend on the hippocampus, which, unlike the medial temporal lobe cortices, assigns relatively distinct representations to stimuli, thereby allowing it to respond differentially to similar targets and foils.

Although the familiarity distributions for targets and similar foils overlap, the model posits that the familiarity of a target will be reliably higher than that of foils related to that target. This familiarity difference (between targets and corresponding related foils) is reliable because there is considerable covariance in the familiarity scores associated with studied items and corresponding related foils (for discussion of this point, see Hintzman, 1988). Thus, if individuals with hippocampal damage are given a forced-choice recognition test in which they have to choose between targets and corresponding related foils, performance should be relatively spared.

In summary, when targets and foils are very similar, the model predicts that yes/no item recognition should be severely impaired by selective hippocampal damage; by contrast, performance should be relatively spared on a forced-choice test (so long as targets are paired with corresponding related foils as opposed to foils related to other targets). When targets and foils are not very similar, patients with selective hippocampal damage should perform well, regardless of test format.

Consistent with the Complementary Learning Systems model of recognition, YR has not shown a general impairment on yes/no relative to forced-choice visual and verbal item recognition tests (Mayes et al., 2002). The prediction that yes/no and forced-choice object recognition should dissociate when targets and foils are made very similar was investigated in the present article. To do this, the object recognition tasks were constructed so that their targets and corresponding foils were more difficult to discriminate than the targets and foils used in the other visual item recognition tests that YR had completed since her brain damage, and on which she was unimpaired (Holdstock et al., 2000a; Mayes et al, 2001, 2002). This was confirmed by a perceptual discrimination task.

Aim 3: Investigation of YR's Recall and Recognition of object–location Associations

The third aim of the study was to investigate how hippocampal damage affected recall and forced-choice recognition of associative information, in particular the associations between objects and their locations. Vargha-Khadem et al. (1997) reported that their young patients with hippocampal damage were impaired at recognising object–location associations despite unimpaired forced-choice item recognition. In the object–location association task used by Vargha-Khadem and colleagues each object was studied in a different circle of an array of circles presented on the computer monitor. At test, a circle in the array was illuminated and the subject chose which one of two studied objects had been presented in that position. These test objects were viewed at the side of the screen, rather than in the target position. As the entire studied configuration of object and location was not represented at test, this task may have depended to a larger extent on pattern completion and recollection than forced-choice item recognition tasks in which the entire studied item was viewed again at test. To avoid this potential difference between associative and item-recognition tasks, YR's object–location recognition was tested using a slightly different paradigm to that used by Vargha-Khadem and her colleagues. Our paradigm was developed to be as similar as possible to our paradigm for testing forced-choice item recognition. At test, a target object was viewed either in its studied location or in locations which had been occupied by other studied objects. The complete studied object–location configuration was therefore seen at test along with incorrect object–location pairings. YR's performance on this task relative to her performance on an equally difficult forced-choice object recognition task enabled us to address two questions: (1) whether forced-choice object recognition and forced-choice object–location associative recognition dissociated after adult-onset hippocampal damage; and (2) whether such a dissociation is found after controlling for task difficulty. If task difficulty had not been controlled, and the forced-choice object–location task had been more difficult for control subjects, then a relative deficit on it could have arisen merely because it was the harder task. Object–location recall was also examined to see whether this was more severely disrupted in YR than was forced-choice object–location associative recognition.

Summary of Aims

To summarise, the aims of the present article were (1) to determine whether, in a patient with adult-onset relatively selective hippocampal damage, forced-choice item recognition would be spared relative to recall when task difficulty was controlled; (2) to investigate the prediction arising from the Complementary Learning Systems model of recognition that forced-choice item recognition should be relatively spared but yes/no item recognition impaired after selective hippocampal damage when targets and foils are very similar; and (3) to investigate whether, in a patient with adult-onset hippocampal damage, both recall and forced-choice recognition of object–location associations would be impaired when the tasks used to test these forms of memory were no harder than the task used to test forced-choice object recognition.

METHOD

Subject

YR, a 61-year-old woman, has experienced memory loss for 13 years after administration of an opiate drug for the relief of severe back pain (Holdstock et al., 2000a,b; Mayes et al., 2001), which is thought to have resulted in an ischemic incident. To our knowledge, YR has never abused opiates or other drugs. Volumetric

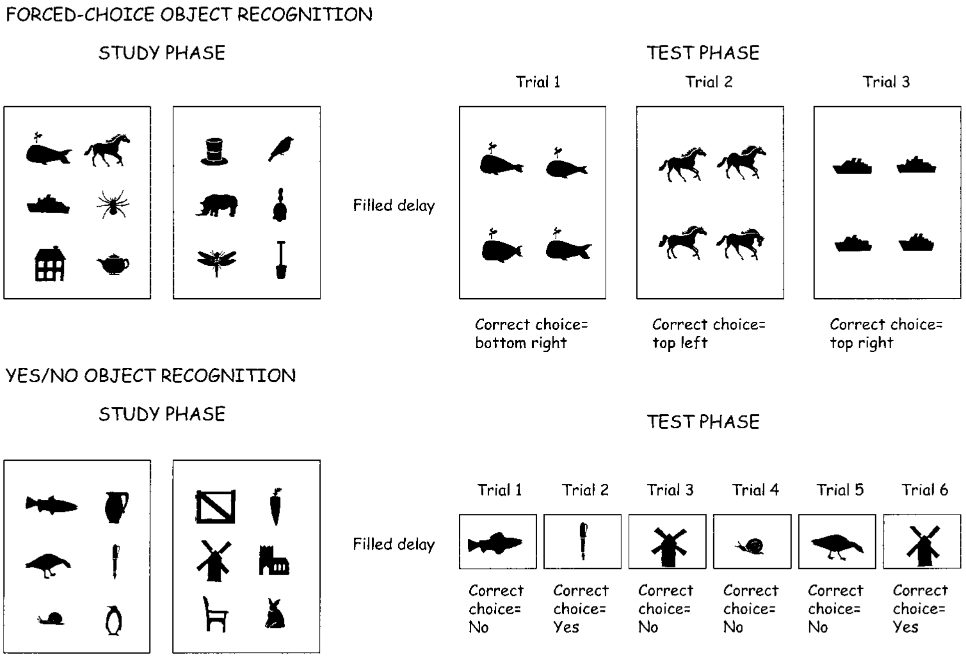


FIGURE 1. Schematic diagram illustrating the study and test phases for the forced-choice object recognition test (top half) and the yes/no object recognition test (lower half). For the forced-choice object recognition test a set of twelve study items are shown along with the stimuli presented on the first three test trials. The correct choice for each test trial is indicated in each case. For the yes/no object recognition test a set of twelve study items are shown along with the stimuli presented on the first six test trials. Again, the correct response is indicated for each test trial.

analysis of YR's structural MRI scan (see Holdstock et al., 2000b) showed pathological reduction in the volume of the hippocampus bilaterally throughout its length. There was no indication of significant volume reduction in other brain regions, including the medial temporal lobe cortices (defined here as perirhinal, parahippocampal, and entorhinal cortices). However, as we were unable to obtain a functional scan for YR, we cannot rule out the possibility that these nonhippocampal areas were functioning suboptimally despite their normal volume.

Standardised psychometric test performance (Holdstock et al. 2000a,b; Mayes et al., 2001) showed that YR's IQ was a little above average, with no evidence of a reduction from pre- to postmorbid IQ. Short-term memory and executive functions were unimpaired, as were spatial perception and reasoning. On standardised memory tests, YR's visual and verbal item recognition were unimpaired, but her recall was impaired. Her unimpaired item recognition memory has also been demonstrated on a range of other forced-choice and yes/no recognition memory tests (Holdstock et al., 2000a; Mayes et al., 2001, 2002).

YR's performance was compared with that of 10 female control subjects matched for age and IQ. For all tests except yes/no item recognition, the control group had a mean age of 58.8 years (SD = 3.8) (YR's age at test = 59 years), and a mean predicted full-scale NART-R IQ of 102.8 (SD = 6.29) (YR's WAIS-R IQ = 102). One subject was replaced for the yes/no item recognition test due to unavailability. The new control group had a mean age of 61.6 (SD = 3.7) (YR's age at test = 61 years), and a mean predicted full-scale NART-R IQ of 104.6 (SD = 7).

Design

Nine sets of 12 pictures of nameable natural and manmade objects were constructed for the memory tests. The experimental conditions are listed in Figure 2. Memory for the studied objects was tested using free recall (object recall), forced-choice recognition (forced-choice object recognition) and yes/no recognition (yes/no object recognition) paradigms. Memory for the tabletop locations in which specific objects were studied was tested by free recall (object–location recall) and forced-choice recognition tests (forced-choice object–location recognition). Memory was tested after a 40-s delay for all conditions and also after a 30-min delay for all but the yes/no object recognition test. A different set of pictures was used for each test.

Development of the Object Recognition Tests

For the object recognition tests, each of the 12 pictures allocated to a task was modified slightly three times. One of these pictures was selected to be the target (studied) picture. The others were foils (Fig. 1).

A discrimination task was used to obtain an objective measure of the perceptual target–foil similarity in these new object recognition tasks relative to the stimuli used in the other nonverbal item recognition tasks YR had completed since the onset of pathology and on which her performance has been found to be unimpaired (Mayes et al., 2002).

Two of the previous nonverbal item recognition tests that YR had completed were standardised memory tests: the Warrington Recognition Memory Test (Warrington, 1984) and the Doors and People Test (Baddeley et al., 1994). The other tasks were constructed either in our laboratory or by collaborators. These specially constructed tests used faces, abstract patterns, photographs of scenes and photographs of animals as stimuli. Subsets of these tests are reported in more detail elsewhere (Holdstock et al., 2000a; Mayes et al., 2001). For the purposes of the discrimination task, only those recognition tasks that had used delays of less than 24 h were considered. These tests had used twelve different sets of stimulus materials.

The discrimination task included the twelve sets of materials from the tests described above and the materials constructed for the forced-choice and yes/no object recognition tests reported in the present article. For the discrimination task, 12 stimuli, which were targets in the memory tests, were selected at random from each of these sets of materials. For each of these target items, a corresponding foil from the memory test was also selected (when a target had multiple foils in the memory test, one foil was selected at random).

A total of 28 healthy volunteers (5 male, 23 female, age range: 51–65 (mean 54.9 years)) were tested. Subjects viewed pairs of stimuli on a computer monitor and indicated (with yes/no button presses) whether the pictures were identical. On half the trials the pictures were identical (target–target), for the other trials target–foil pairs were presented. Two stimulus sets were constructed such that targets which had been used for target–target pairs in stimulus set one were presented with a foil in stimulus set two and vice versa. The set used alternated between subjects. Stimuli from the same memory task were blocked together and were preceded by four practice trials. The order in which these stimulus blocks were presented was counterbalanced using a latin square design.

Accuracy was emphasised over speed. Response time and number correct were recorded for target–target and target–foil pairs. Analyses focused on the data from the latter condition. Response time for correct decisions was considered only.

t-tests showed that there was no significant difference, in either successful discrimination time ($t = 1.539$, $df = 27$, $P > 0.05$) or number of discrimination errors ($t = 1.396$, $df = 27$, $P > 0.05$), between the sets of new stimuli which were constructed for the yes/no and forced-choice object recognition tests reported in the present article. The mean discrimination time for these stimuli (3030.6 ms) was 3.03 SD slower than the mean discrimination time for the stimuli used in the other nonverbal yes/no and forced-choice recognition tests YR had completed since the onset of pathology (mean = 1614.6 ms, SD = 467.8). Similarly, the mean number of discrimination errors (0.375) made for these new stimuli was 6.5 SD larger than the mean number of errors made or the stimuli from the other tests YR had completed (mean = 0.07, SD = 0.04).

Target–foil discrimination was therefore considerably more difficult for the object recognition tasks designed for the present experiment than for the other yes/no and forced-choice item recognition tasks YR had completed.

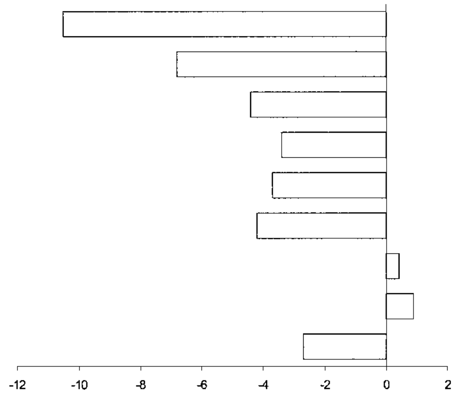
Procedure

The procedure for the forced-choice and yes/no object recognition tasks is shown schematically in Figure 1. In the forced-choice object recognition task, the object recall task and the yes/no object recognition task a set of 12 pictures was presented twice for 3 s per picture on each presentation. The pictures were presented on two A4 sheets, six pictures per sheet, and the experimenter directed the subject's attention to each stimulus in turn. A natural/manmade judgment was made on the first presentation (and the object named in the recall paradigm) and picture detail studied on the second. For the forced-choice recognition test, subjects selected the studied item from among three very similar foils. A practice example preceded the proper trials for each condition. For the free recall test, subjects listed as many of the 12 studied items as possible.

For the yes/no object recognition test the 12 studied pictures and 36 foils were randomly intermixed and presented individually. Subjects had to respond "yes" to studied pictures. To encourage subjects to make a decision about each test picture which was independent of their decisions concerning the preceding pictures in the test list, four of the studied (target) pictures occurred twice in the test list, and four occurred three times in the test list. Targets had to be detected each time they were presented at test, but only the subjects' response to the first occurrence of each target was scored and included in the analysis. The yes/no object recognition task was the last to be completed by the subjects. Potentially, this could have put the controls at an advantage over YR in that they would have had better memories for the high similarity of the targets and foils in the preceding recognition tests. To ensure that this was not a problem, YR and the control subjects completed two practice runs of the yes/no recognition tests (each of six study items and 30 test items) immediately before completing the proper yes/no recognition test. The pictures used for the practice were of the same style and used equally similar foils to those used in the main test. All subjects were therefore very familiar with the level of similarity of targets and foils before proper testing began.

In the object–location association tasks, 12 pictures were arranged in predetermined positions on a plain white circular table (90-cm diameter). Positions were selected so that the pictures were not arranged in a regular grid pattern. The experimenter directed the subject's attention to each picture in turn for three seconds (in a predetermined pseudo-random order) and the subject made a natural/manmade decision concerning the pictured object. The subject's attention was directed to each picture a second time for 3 s per picture and the subject studied the location of that picture. At test a circle of card (45-cm diameter) was used to represent the circular tabletop and the pictures of the objects were appropriately scaled down. In the recognition test, each circle of card showed a picture in its studied location and in three locations (foils) which had been occupied by other studied pictures. The studied location of that particular picture had to be selected. As the foils were recombinations of studied pictures and studied locations, memory for pictures or locations alone was insufficient for successful task performance. The remembered location of all 12 studied pictures was tested in this way. In the recall test, each of the studied pictures had to be placed in its studied location. Only one picture was placed down at a time, its location was recorded and the picture removed before the subject was handed the next picture to position. A practice example preceded the proper trials for each condition.

Memory Task	Test Order	Control mean*	YR's score*
40s object-location recall	S1c	3.14 (0.85)	12.07
30m object-location recall	S2d	4.83 (0.99)	11.54
40s object recall	S2c	8.5 (1.7)	1
30m object recall	S1d	6.1 (1.79)	0
40s forced-choice object-location recognition	S2a	2.72 (0.44)	1.06
30m forced-choice object-location recognition	S1b	2.21(0.59)	-0.25
40s forced-choice object recognition	S1a	1.34 (0.51)	1.55
30m forced-choice object recognition	S2b	1.6 (0.32)	1.88
40s yes/no object recognition	S3a	2.24 (0.48)	0.94



Number of standard deviations that YR's performance was above or below the control mean. (Negative values indicate worse performance than controls, not necessarily a numerically lower score.)

* object-location recall performance is shown as the distance between the recalled position and the studied position in centimeters; object recall performance is shown as the number correct out of a maximum of 12; d' scores are shown for recognition tests.

Key:
S1 = session 1
S2 = session 2
S3 = session 3

a = first test in the session
b = second test in the session
c = third test in the session
d = fourth test in the session

FIGURE 2. Performance of YR and the control group on the memory test battery. Each row of the figure tabulates the mean performance of the control group (standard deviation in parentheses) and YR's performance for a particular memory test, and also shows plotted as a bar graph the number of standard deviations that YR's performance fell above (+) or below (−) the control group mean. The order in which the tasks were completed is shown in the table. The performance measure for each task is indicated below.

Subjects completed the tests over three sessions in the order shown in Figure 2. The tests were developed with the aim of producing a forced-choice object recognition task that was no easier for control subjects than the yes/no object recognition test, the object recall test or the object–location recall and recognition tests. To determine whether this had been achieved, we obtained a measure of the difficulty of each task for control subjects. Difficulty was measured as a percentage score that indicated where between chance and a perfect score the control subjects' mean performance fell, so that a higher score corresponded to an easier test. The following equation was used:

$$\text{Difficulty} = \frac{s - c}{p - c} \times 100$$

where s is the control subjects' mean score, c is chance performance and p is a perfect score.

For the forced-choice object and object–location recognition tests perfect performance was 100% correct and chance was 25% correct. For the yes/no object recognition test, we subtracted the control subjects' mean false alarm rate from their mean hit rate. Therefore, for yes/no object recognition, perfect performance was a hit-false alarm difference of 100 and chance was zero. For the object–location recall test perfect performance was a placing error of zero. Chance performance on this task was determined by asking naïve subjects to place the objects used in the memory tasks on the board without giving them the opportunity to study the locations they should occupy (i.e., subjects had to guess where each object would have been presented in the memory test). Subjects placed the objects with a mean error of 17 cm away from the target location.

TABLE 1.

Difficulty, Measured as a Percentage Score Indicating Where Between Chance and a Perfect Score the Control Subjects' Mean Performance Fell for Each Task in the Battery

Task	40-s delay	30-min delay
Forced-choice object recognition	55.6	66.4
Yes/no object recognition	62	—
Object recall	70.8	50.8
Forced-choice object-location recognition	95.6	84.4
Object-location recall	81.6	71.7

As shown in Table 1, these measures confirmed that forced-choice object recognition task was no easier for YR's control subjects than the yes/no object recognition task, the forced-choice object–location recognition tasks and the object–location recall tasks.

The forced-choice object recognition task was numerically harder than these other tasks. Similarly, the 40s delayed forced-choice object recognition task was no easier for the control subjects than the 40-s delayed object free recall task. However, after the 30-min delay, the forced-choice object recognition task was significantly easier than the object recall task ($t = 3.008$, $df = 9$, $P < 0.05$).

RESULTS

Figure 2 displays YR's performance and the mean performance of the control group for each task. Performance is expressed as d' for the recognition tests (Green and Swets, 1966; Macmillan and Creelman, 1991).

For object recall the performance measure is number correct (maximum 12) and for spatial recall the performance measure is the mean distance between recalled location and actual studied location. The number of standard deviations (SDs) that YR's performance fell above or below the control group mean is displayed graphically.

YR's performance was considered impaired if it was >1.96 SD worse than the control mean (type 1 error probability of 0.05, 2-tailed). Using this criterion of impairment, YR's free recall of studied objects was impaired after delays of both 40 s and 30 min. In contrast, on the forced-choice object recognition task YR performed (nonsignificantly) above the control group mean at both delays. However, YR's yes/no object recognition was impaired. This latter impairment resulted from YR producing a large number of false alarms (0.96 hits and 0.80 false alarms). The mean proportion of hits and false alarms made by controls was 0.93 ($SD = 0.05$) and 0.26 ($SD = 0.1$), respectively. When memory for the studied locations of objects was tested, YR's performance was clearly impaired, after 40 second and 30 minute delays, both when memory was tested by free recall and by forced-choice recognition.

DISCUSSION

Our results demonstrate that YR's hippocampal damage resulted in a severe impairment in the recall of both objects and object–location spatial associations. In contrast, the data show that, at least for our patient, nonhippocampal regions, such as the medial temporal lobe cortices, are sufficient to support good performance on some, but not all kinds of recognition test. Our findings showed that YR's hippocampal damage did not impair forced-choice object recognition even when targets and foils were very similar. It did, however, impair performance on an equally difficult yes/no object recognition test, which used very similar targets and foils. YR's forced-choice recognition of object–location associations was also impaired even though for control subjects this task was no harder than the forced-choice object recognition task at which she was unimpaired. YR's pattern of memory performance reveals three theoretically important dissociations.

Dissociation Between YR's Free Recall and Forced-Choice Object Recognition

The first dissociation is between her impaired object free recall, but unimpaired forced-choice object recognition. YR's spared forced-choice object recognition contrasts with the impaired performance on this task of patients with more extensive medial temporal lobe damage and patients with Korsakoff's syndrome (unpublished data). In a forgetting rate study, it was necessary to give such amnesic patients four or more times the amount of exposure received by control subjects in order to match their forced-choice object recognition to that of the control group mean after a filled 40-s delay (JS Holdstock, AR Mayes, D Montaldi, unpublished observations).

A similar dissociation to that shown by YR, between impaired recall and relatively normal item recognition, was shown by the patients reported by Vargha-Khadem et al. (1997), who suffered relatively selective hippocampal damage early in life. Our data indicate that such a pattern can also be found after adult-onset selective hippocampal damage, which, unlike childhood-onset hippocampal damage, cannot be easily explained by the development of compensatory mechanisms. Further, our data show that such a pattern is found even when the object recall task is numerically easier for control subjects than the object recognition test (40-s delayed test). This indicates that YR's pattern of memory performance cannot be explained simply in terms of impairments on the tasks which control subjects find more difficult.

Our finding that YR's object recall is more impaired than her forced-choice object recognition, which appears to be relatively or completely normal, is consistent with far more extensive data on recall and item recognition in this patient (see Mayes et al., 2002). However, other patients in whom adult-onset hippocampal damage seems to be relatively selective have shown clear item recognition deficits (e.g., Reed and Squire, 1997; Manns and Squire, 1999). The discrepancy between YR's pattern of memory impairment and that of these other patients is unlikely to be explained by task differences because it is found even when their performance is compared on identical tests. For example, on the Doors and People Test (Baddeley et al., 1994) the patients described by Squire and his colleagues were impaired on both recall and recognition subtests (Manns and Squire, 1999) whereas Jon (Baddeley et al., 2001) and YR were impaired at recall, but within the normal range on the item recognition subtests (see Mayes et al., 2002). It is, therefore, more likely that differences in the neuropathology of the hippocampus and/or other brain regions will explain the differences in the patterns of memory deficits shown by YR and the patients described by Squire and colleagues (for a full discussion of these issues see Mayes et al, 2002).

Dissociation Between YR's Forced-Choice and Yes/No Object Recognition

The second dissociation is between YR's unimpaired forced-choice object recognition but impaired yes/no object recognition only when targets and foils were similar. This dissociation has not been previously reported. It is therefore important to rule out the possibility that confounding factors may explain the finding. A confound in the present study was task order. This was unavoidable because the memory of a single patient was investigated and so the tasks needed to be run in the same order for the control subjects and for the patient. The yes/no object recognition test was the last to be completed. It could therefore be argued that YR's impairment on this, but not the earlier forced-choice object recognition tests, was due to a difference in the extent to which YR and control subjects remembered how difficult the discrimination between targets and foils had been in the forced-choice object recognition tests. However, this is an unlikely explanation of YR's deficit on the yes/no object recognition test for two reasons. First, the use of two practice sequences gave both YR and the control subjects experience of the difficulty of the target/foil discriminations immediately before the proper yes/no recognition test. Second, control subjects' forced-choice item recognition did not benefit more than YR's from prior experience of discriminations of similar difficulty. YR performed numerically better than controls on both the first (40-s delayed test) and second (30m delayed test) forced-choice object recognition tests which were about 1 week apart.

Another possible explanation for the dissociation between YR's performance on the yes/no and forced-choice object recognition tests is that this resulted from YR having a bias to respond "yes" in yes/no recognition tests. YR showed such a bias in the present experiment (c for YR was : -1.3; mean c for controls was -0.45 ($SD = 0.23$)), making a high number of hits but also a lot of false alarms. However, on other yes/no tests of recognition, which have used less similar targets and foils than the present experiment, she showed no more of a "yes" bias than control subjects. Therefore, YR does not show a general tendency to respond "yes" on yes/no recognition tests; rather, this pattern of responding is specific to the task reported in the present article, which used very similar targets and foils. As discussed in the Introduction, such a pattern of responses on this particular task is consistent with the predictions from the Complementary Learning Systems model of recognition (Norman, 2000; Norman and O'Reilly, 2001; see also McClelland et al., 1995; O'Reilly and Rudy, 1999 for further discussion of the Complementary Learning systems idea). According to the model, YR's recognition responses are made on the basis of familiarity because hippocampal recollection is disrupted by her brain damage.

When the distributions of the familiarity of targets and foils overlap to a large extent, as would have been the case in the present experiment, it is not possible to place a familiarity threshold (criterion for accepting an item as familiar) in a yes/no task without there being either a large number of foils above it or a large number of studied items below it. As a result, when targets and their corresponding foils are very similar, a large number of errors (misses or false alarms) will be made in yes/no recognition tasks when decisions are based on familiarity alone. If a lenient criterion is used, the errors produced would be primarily false alarms.

Although the Complementary Learning Systems model of recognition predicted that after selective hippocampal damage there should be a dissociation between unimpaired forced-choice object recognition but impaired yes/no object recognition only when targets and foils were difficult to discriminate, this dissociation was not predicted by other models of memory.

The Complementary Learning Systems model is the only mechanistic model of recognition memory that predicts the aforementioned dissociation, whereby yes/no recognition with similar targets and foils should be impaired after selective hippocampal damage, but performance on forced-choice recognition tests with similar targets and corresponding foils and performance on yes/no, as well as forced-choice recognition tests with unrelated targets and foils should be relatively spared.

Other mechanistic models of recognition memory (e.g., REM: Shiffrin and Steyvers, 1997; SAM: Gillund and Shiffrin, 1984; and MINERVA 2: Hintzman, 1988) differ from the Complementary Learning Systems model insofar as they are abstract mathematical systems that do not incorporate specific claims about how recognition is implemented by the brain. As a result, these models do not make specific predictions concerning the effect of hippocampal damage on recognition memory under different task conditions. The Complementary Learning Systems model is the only predictive mechanistic model that makes claims about how recognition is implemented by the brain.

However, several nonmechanistic theoretical frameworks have been proposed that make claims about how the hippocampus and neocortex contribute to memory (e.g., Squire and Zola, 1998; Aggleton and Brown, 1999). These models make qualitative rather than quantitative predictions.

The view held by Squire and colleagues is that the hippocampus and all regions of the medial temporal lobe cortices are critical for both recall and recognition (Reed and Squire, 1997; Squire and Zola, 1998). This predicts that hippocampal damage should impair recognition irrespective of task paradigm or how similar foils are to targets. Our finding that YR's performance on yes/no and forced-choice object recognition tests dissociated after selective hippocampal damage when targets and foils were very similar is, therefore, inconsistent with this view. The dissociation is consistent, however, with the framework put forward by Aggleton and Brown (1999). Like the Complementary Learning Systems model, the Aggleton and Brown view holds that (1) the hippocampus is completely essential for recall (recollection) of studied stimuli, after limited exposure to those stimuli, and (2) the medial temporal lobe cortices implement a familiarity process that can, in some circumstances, support good discrimination of studied items from unstudied items. However, because this framework does not provide a mechanistic account of how recollection and familiarity are mediated by the hippocampus and medial temporal lobe cortices, unlike the Complementary Learning Systems model, it does not make specific predictions about how a task manipulation will affect memory performance after hippocampal damage. Consequently, the Aggleton and Brown framework does not specifically predict that selective hippocampal damage should impair yes/no object recognition but leave forced-choice object recognition unimpaired when targets and foils are similar.

As far as we are aware, therefore, the Complementary Learning Systems model is the only model to predict YR's pattern of item recognition performance. As the Complementary Learning Systems model postulates that hippocampal lesions impair recollection but leave item familiarity completely normal, YR's data provide indirect evidence that she has normal item familiarity. This view of YR's preserved memory abilities is also supported by evidence from the Remember/Know procedure. "Know" responses provide a direct means of assessing the frequency of item familiarity memory.

Estimates of familiarity using the Remember/Know procedure depend on whether one assumes a relationship of redundancy, stochastic independence, or exclusivity between recollection and familiarity. Although Knowlton (1998) has argued that the relationship is one of redundancy, it has been more frequently argued that there is an independence relationship (Mandler, 1980; Jacoby, 1991; Yonelinas and Jacoby, 1995). There is little evidence favouring an exclusivity relationship. In our view, it is most likely that the relationship lies closer to independence than redundancy and depends to some extent on the task conditions.

Remember/know item recognition tests have been administered to YR on eight occasions (YR's recognition performance on these tasks is described by Mayes et al. (2002), but her familiarity d' scores are unpublished). By considering her worst and best performance on these tests we show that her familiarity is probably normal. If one assumes a redundancy relationship, then YR's familiarity d' score is the same as her recognition d' score. Assuming redundancy, YR's d' score ranges from 2.6 SD below the control mean to 1.9 SD better than the control mean. Assuming independence, it ranges from being identical to the control mean to 2.05 SD better than the control mean. Assuming exclusivity, her d' score ranges from 0.3 SD to 4.9 SD better than the control mean. Even if one assumes complete redundancy, across the eight tasks, YR's mean familiarity d' lies only 0.17 SD below the mean of her control group and if one assumes either independence or exclusivity, it will lie clearly above the control mean (and above 0 for each of the eight tests). It is therefore plausible to assume that YR's familiarity is unimpaired. This clear impression from the "Remember/Know" procedure of normal familiarity in YR is consistent with observations of her memory in daily life, which showed that her recall was poor, but that after she had encountered objects and other items (e.g., peoples faces) subsequent encounters produced a clear sense of familiarity.

Although the Complementary Learning Systems model posits that familiarity, mediated by the medial temporal lobe cortices, can support good performance on item recognition tests, the model does not predict that patients with focal hippocampal damage will necessarily show completely normal performance on these tests. This is because hippocampal recollection can also support good performance on item recognition tests in control subjects. If both familiarity and recollection contribute to control subject performance, and their contributions are not fully redundant, then lesions that impair hippocampal recollection should result in below normal levels of item recognition memory. However, a recollection deficit is likely to disrupt item recognition only slightly as long as familiarity provides an effective basis for recognition judgements. Such a small reduction in performance may not be detected as a significant item recognition impairment in a single patient but it would produce consistent below control level performance in a group of such individuals. Therefore, further patients need to be tested to determine whether the mean item recognition performance of a population of patients with selective hippocampal damage is (1) at the control mean, as predicted by a redundancy relationship; (2) slightly below the control mean, like YR's mean item recognition performance on 43 tests (Mayes et al., 2002); or (c) clearly impaired, like the patients described by Reed and Squire (1997).

Dissociation Between YR's Forced-Choice Recognition of Objects and Her Recall and Forced-Choice Recognition of Object–Location Associations

The third dissociation of interest in this article was that between YR's impaired forced-choice recognition of associations between objects and their locations and her unimpaired forced-choice object recognition. This dissociation was found even though control subjects found the latter task slightly harder than the former; therefore, it cannot be explained simply in terms of YR having a deficit on tasks which are more difficult for control subjects. YR's deficit on the forced-choice object–location association task must relate to the type of information that has to be remembered in that task. Her deficit in recognising the associations between objects and their locations could be due to the spatial nature of the task as others have proposed that the hippocampus plays a special, and critical, role in spatial memory (e.g., O'Keefe and Nadel, 1978). In a classic study, Smith and Milner (1984) found that after right temporal lobectomy patients were impaired at recalling the positions of objects under incidental task instructions only if they had extensive damage to the hippocampus. The critical role of the right hippocampus for recalling object–location associations, which Smith and Milner's findings suggest, is supported by YR's impairment on the object–location recall task, which also highlights the role of this region in intentional as well as incidental spatial memory. YR's spatial recognition impairment is consistent with earlier reports of a disproportionate intentional spatial recognition deficit in medial temporal lobe amnesia (e.g., Mayes et al.,1991). Others have argued, however, that disproportionate deficits in spatial recognition only occur, after medial temporal lobe damage, under incidental task instructions (Chalfonte et al., 1996). Additional testing has suggested that YR's impairment on the forced-choice object–location recognition test may reflect a more general associative memory deficit. YR has also been found to be impaired at recognising the temporal order of words and pictures (Mayes et al., 2001), and at recognising associations between faces and voices, words and meanings, and pictures and occupations (Mayes et al., 1999; Holdstock et al., in press). In contrast, and like the young patients of Vargha-Khadem and her colleagues, YR has been found to be relatively normal at recognising associations between items of the same kind. For example, she recognises word pairs relatively well

(Mayes et al., 2001). These findings suggest that YR's deficit on the object–location recognition test most likely reflects a more general deficit of holding in memory associations between information of different kinds.

YR's deficit in forced-choice recognition of object–location associations is not predicted by the key postulates of the Complementary Learning Systems model (for a full description of the predictions of the model see Norman and O'Reilly, 2001). However, the model can accommodate this deficit by incorporating the view, based on the anatomy of the medial temporal lobe, that spatial and object information converge most completely in the hippocampus (e.g., Mishkin et al., 1998). Some, but less complete, convergence of different processing streams (e.g., visual object and visuospatial processing streams) may also occur in the medial temporal lobe cortices, which would allow some residual object–location recognition after hippocampal damage. This may explain why YR's object–location recognition performance was above chance levels at the 40-s delay. However, after a 30-min delay, her performance on this task was at chance. YR's impairment on the forced-choice object–location recognition test was of similar severity to her impairment in object recall but appeared less severe than her impairment of object–location recall. Caution is needed, however, in comparing the severity of her performance on the recall and recognition object–location memory tests. The object–location recall test may be more sensitive than the recognition test because on that test there are more SD units between the control mean and chance.

If memory representations for object–location associations depend mainly on the hippocampus, then hippocampal lesions should also disrupt priming of these associations. Preliminary support for this prediction has been found by Chun and Phelps (1999), who showed that repetition priming for spatial arrays was disrupted in patients with medial temporal lobe lesions. However, the specificity of their patients' lesions was not fully assessed and so it is uncertain whether the deficit was due to hippocampal damage or to damage to the medial temporal lobe cortices. In contrast, the hippocampus and medial temporal lobe cortices may not be required for the representation in memory and the priming of associations that link together information that converges in the neocortex, outside the medial temporal lobes. The evidence concerning this prediction is controversial. Priming of associations between unrelated words has been reported to be preserved in amnesics (including patients with large medial temporal lobe lesions) in the face of impaired recognition of these associations (Moscovitch et al., 1986; Gabrieli et al., 1997; Goshen-Gottstein et al., 2000). However, this finding has been challenged by Gooding et al.'s (2000) meta-analysis of novel item and novel associative priming in amnesics, which showed that, across studies, there was a significant impairment. Pace Goschen-Gottstein and colleagues, it still remains to be determined whether there are kinds of associative priming that are mediated by domain-specific perceptual representation systems, localised solely in the neocortex, which are consequently preserved in amnesics. However, the findings that both YR (Mayes et al., 2001; Grigor, 2001) and the young patients described by Vargha-Khadem and her colleagues (1997) showed relatively spared recognition not only of word–word associations, but also of face–face associations, despite their hippocampal damage, suggest that the representation of such domain-specific associations may not require the hippocampus. These data therefore predict that selective hippocampal damage should not impair priming for associations of this kind.

SUMMARY OF FINDINGS

After controlling task difficulty we have shown, at least for our patient YR, that adult-onset selective hippocampal damage spared forced-choice object recognition despite a clear impairment in object recall. Strikingly, we have also shown that YR's hippocampal damage impaired her yes/no object recognition when targets and foils were very similar. In addition, YR's recall and forced-choice recognition of object–location associations was impaired. These findings suggest separable contributions to memory of the hippocampus and medial temporal lobe cortices such as those postulated by the neural network-based Complementary Learning Systems model.

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