Memory Encoding Following Complete Callosotomy

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Abstract

■ Three patients with complete resection of the corpus callosum were tested in a series of memory tasks to determine the effects of callosotomy on the encoding and retrieval of information in memory. Verbal and pictorial conjunction tests were administered to measure patients' ability to consolidate the elements of a stimulus into an accurate composite memory. Patients were also tested in a paired-associate learning task to determine the consequences of callosotomy on the encoding and retrieval of associations between stimuli. Although callosotomy patients were unimpaired in the verbal conjunction task, results from both the pictorial conjunction task and the paired-associate learning task suggest that the absence of callosal cross-talk impairs encoding in these patients. In addition, the pattern of results in the paired-associate learning task suggests that callosotomy impairs retrieval processes. The role of the callosum in the formation of memory traces for nonverbal material and associations between verbal stimuli is discussed. ■

INTRODUCTION

Although special hemispheric contributions to mnemonic processing have long been recognized (Gazzaniga, Risse, Springer, Clark, & Wilson, 1975; Milner, 1968; Phelps & Gazzaniga, 1992; Zaidel & Sperry, 1973, 1974; Tulving, Markowitsch, Kapur, Habib, & Houle, 1994; Zaidel, 1990), there is a paucity of knowledge about the types of mnemonic processes that are most benefited by the integration of information across the callosum. In the present set of experiments, callosotomy patients were tested on a variety of tasks to determine the effect of a complete disconnection of the two cerebral hemispheres on the ability to encode verbal and pictorial information under full field free viewing conditions. The behavioral profile of these patients is compared with the performance of young and age-matched controls, and previously tested patients with focal brain lesions known to affect memory.

There has been a long-standing disagreement about the effect of callosotomy on memory performance. One of the earliest reports on memory function following callosotomy comes from Zaidel and Sperry (1973, 1974). They reported that patients with section of both the corpus callosum and the anterior commissure do not have normal performance on standardized memory tests. Their patients were particularly poor on nonverbal tasks, on "hard" word associations, and on short story passages. However, LeDoux, Risse, Springer, Wilson, and Gazzaniga (1977) reported, in detail, a patient whose memory was normal following callosotomy, as measured by a number of both standard and specialized tests. These early studies, however, were primarily concerned with tests of immediate memory and, although they both examined memory in callosotomy patients, they did not completely overlap in focus and set in motion a field of theoretical and experimental inquiry.

Phelps, Hirst, and Gazzaniga (1991) examined memory performance in patients with partial and complete callosotomy to determine if damage to the hippocampal commissure and other callosal fibers connecting the hippocampi resulted in memory deficits that were not observed when callosotomy spared these connections. They concluded that when the posterior fibers of the callosum were resected, memory performance was impaired. Specifically, they reported that recall was more impaired in patients with resection of posterior callosal fibers than recognition performance because posterior callosotomy disrupted the encoding of information into long-term memory. This encoding, they suggested, may normally occur via the integration of information from the right and left hippocampal systems (see also Milner, Taylor, & Jones-Gotman, 1990).

Perhaps the dissociation between recall and recognition performance in the Phelps et al. study resulted from recall being more sensitive to multiple representations of an event than recognition (e.g., Milner et al., 1990; Paivio, 1971, 1990; see also Phelps, Phillips, & Gazzaniga, 1994). For example, when a memory trace involves encoding both verbal and imagery elements instead of either alone, recall performance may be disproportionately impaired relative to recognition. That is, accurate recall performance may require more integration of these facets than does recognition performance. In addition, recall is highly sensitive to elaboration and organization of to-be-remembered stimuli (Bransford & Johnson, 1972). If there is specificity in the type of information stored and processed in each hemisphere that necessitates interhemispheric integration for such elaborative and organization processes, then disconnecting the communication between the representations would be particularly harmful for recall performance.

One approach taken to investigate differential memory performance for such tasks in callosotomy patients is to determine the specialized character of memory in each cerebral hemisphere. Metcalfe, Funnell, and Gazzaniga (1995) investigated such hemispheric differences in a callosotomy patient by lateralizing stimulus presentation. They concluded that there is a right hemisphere superiority for rote memorization and that the right hemisphere is better able to reject distractors, both verbal and nonverbal, that are similar to the originally presented materials. While the right hemisphere is a more veridical encoder, the left hemisphere interprets and integrates incoming information with existing schemata making it available to semantic processing but losing some precision in retrieval.

The overall goal of the present study is to compare the different types of encoding that may be differentially affected by callosotomy. First, we investigate the performance of callosotomy patients on three different tasks in order to characterize which types of memory processes rely most heavily on callosal integration. The tasks employed here are: verbal conjunction memory, pictorial conjunction memory, and paired-associate learning. Each of these tasks tests a different type of encoding mechanism. The verbal conjunction task requires the binding of verbal elements (e.g., morphemes, phonemes, or syllables) into whole words.[1] During memory encoding for the word, correct binding of these elements is necessary for the later recognition of the correct word and rejection of distractors composed of "old" elements, whereas the pictorial conjunction task requires proper encoding and binding of pictorial elements into a complete pictorial whole. The paired-associate learning task requires both encoding individual words and encoding the association between arbitrarily paired words.

Second, the performance of callosotomy patients on these tasks is compared to the performance of patients with unilateral and bilateral lesions in the hippocampal system.[2] The hippocampal system is known to be involved in the encoding of information into long-term memory (Cohen & Eichenbaum, 1993; Milner, 1971). Comparing the performance of callosotomy patients with hippocampal lesion patients on identical tasks allows for a test of the hypothesis that callosotomy impairs the types of encoding that require integration of information from both intact hippocampal structures.

EXPERIMENT 1

Moscovitch (1994) has suggested that "cohesion" is an early component of the process of memory consolidation. The function of cohesion is to "bind" or "glue" aspects of incoming information into separately retrievable engrams (e.g., Chalfonte & Johnson, 1996; Johnson & Chalfonte, 1994; Metcalfe, Cottrell, & Mencl, 1992; Wickelgren, 1979) and the hippocampal system is believed to be intimately involved in such binding (Cohen & Eichenbaum, 1993, pp. 286–288; Eichenbaum & Bunsey, 1995; Eichenbaum, Otto, & Cohen, 1994). Recently Kroll, Knight, Metcalfe, Wolf, and Tulving (1996) demonstrated that patients with damage to the hippocampal system are also impaired in their capacity to bind the constituent parts of an individual stimulus into its complete "Gestalt." Patients with hippocampal lesions were more likely than control subjects to falsely recognize as old, new stimuli that consist of components of the original, studied stimuli.

In particular, Kroll et al. (1996, Experiment 1) utilized two-syllable words in a continuous recognition paradigm and found that patients with lesions in their left hippocampal system were much more likely than were control subjects or patients with right hippocampal lesions to false alarm to new words made up of components of recently presented words (e.g., MENACE . . . BRUTAL . . . MENTAL). We repeated this experiment with the callosotomy patients with the expectation that, unlike the patients with left hippocampal damage, their performance on the verbal task would be relatively normal. That is, the "disconnection" of the right hippocampal system in the callosotomy patients should not interfere with their performance in this verbal task because verbal information and word form systems tend to be primarily in the left hemisphere (Baynes, Tramo, & Gazzaniga, 1992; Dejeurine, 1892; Gazzaniga, Nass, Reeves, & Roberts, 1984; but cf. Coslett & Saffran, 1989). Therefore, the binding of these elementary verbal units should not be impaired. This tendency for left hemisphere language may also explain why patients with right hippocampal lesions did not show an increased false alarm rate to distractors made up of previously presented components (Kroll et al., 1996).

Results

The results are presented in Table 1. The overall pattern of results did not change with different retention intervals and, consequently, the data were collapsed over all retention intervals.

As can be seen in the table, in this task, the callosotomy patients compare favorably with the normal, older adults. Only the patients with left hippocampal lesions

Table 1. Average percentage of "old" responses for each of the groups in each of the conditions in Experiment 1. (Data hippocampal patients and control subjects from Kroll et al., 1996, Table 3.)

Group	N	True Repetition (Hit)	Conjunction 1 Word Lag	Single Syllable Repetition	First Word (New)
Callosotomy Patients	**3**	**81.5**	**9.3**	**5.6**	**4.3**
JW		88.9	5.6	16.7	2.9
VP		88.9	22.2	0.0	7.4
DR		66.7	9.3	5.6	4.3
Aged-Matched Controls	18	78.9	14.5	7.7	9.5
Students	18	88.4	9.7	4.0	4.6
Patients with Hippocampal Lesion					
Right	8	83.9	12.0	8.3	2.9
Left	7	84.7	41.3	16.3	7.6
Bilateral	1	88.9	52.8	24.0	4.9

Note: The experiment also included a 5-Word Lag Conjunction condition, but this condition did not reliably distinguish among the groups—see Kroll et al. 1996, for a more complete discussion of the differences between lags.

(including the bilateral patient) show a disproportionately high rate of false alarms to the conjunction words, that is, lures constructed out of components of previously presented words. In the one-word lag conjunction condition, patients with left hippocampal lesions were significantly worse than the callosotomy patients [$t(9) = 2.794$, $MS_e = 11.97$, $p < 0.05$]. The scores of the callosotomy patients, like the patients with right hippocampus lesions, in this condition are virtually identical to those of the two normal groups.

Discussion

The normal performance of the callosotomy patients on this task indicates that they are accurately binding word segments into word units. Because stimuli are presented free field, either hemisphere could be responsible for good performance, although each hemisphere must be assumed to be working in isolation. However, using verbal responses generally favors the language dominant left hemisphere even in those callosotomy patients with some right hemisphere speech (Gazzaniga, Eliassen, Nisenson, Wessinger, Fendrich, & Baynes, 1996). Moreover, the poor performance of patients with left hippocampal lesions indicates that the intact right hemisphere cannot adequately complete the task. The converging evidence from callosotomy and hippocampal patients suggest that the left hemisphere is capable of independently mediating this binding procedure.

The left hemisphere word form system appears to operate rapidly and automatically. Its influence on perceptual tasks such as letter recognition has long been acknowledged (Reicher, 1969). The advantage conferred on letter strings that form a real-word may be the key factor that permits the automatic accurate binding of these word fragments. Although there is evidence of a word form system in the right hemisphere of some callosotomy patients, its characteristics appear to be different from the left hemisphere system (Reuter-Lorenz & Baynes, 1992) and it may not support these binding procedures.

Current neuropsychological models of reading recognize both a lexical route that processes whole words and possibly root morphemes (Funnell, 1983; McCarthy & Warrington, 1986) and a sublexical route that processes graphemes or possibly syllable length segments (Hillis & Caramazza, 1995). The results from Experiment 1 suggest that this paradigm uses the lexical route that results in stronger activation of lexical units than of recombined sublexical units. However, it is unclear if this result is due to the special status of word units within the language system. Is the left hemisphere recognition system also capable of performing visual, nonverbal binding in the absence of right hemisphere input. Experiment 2 will compare the callosotomy patients to the same hippocampal patients and control subjects in tasks where nonverbal visual composites must be formed.

EXPERIMENT 2

Patients with damage only to their right hippocampal system (Kroll et al., 1996) did not give high false alarm rates to verbal distractors constructed from components of previously seen words. However these patients were impaired when the stimuli were pictures that were not easy to fully characterize through verbalization. In their second experiment, subjects studied abstract pictures (Fig. 1) and faces (Fig. 2) and were then tested for their ability to recognize old, studied stimuli and to reject new stimuli. They found that damage to either side of the

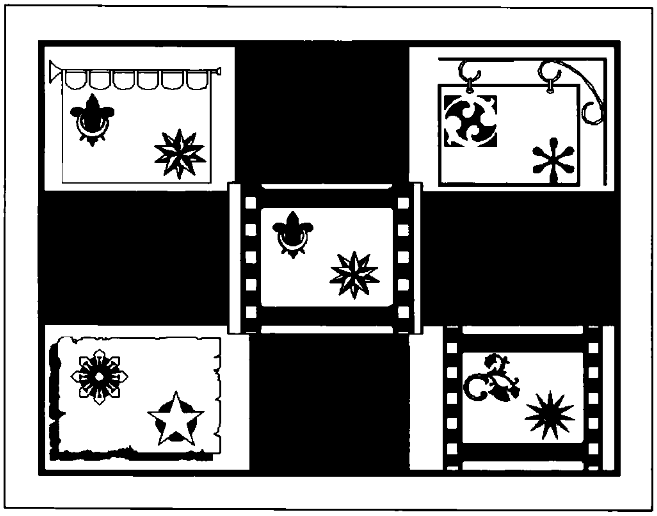


Figure 1. Example of a perceptual test trial, with the abstract figures. The four study figures are in the four corners, and a test figure is in the middle. In this example, the test figure is a *conjunction* of the upper left and lower right study figures.

hippocampal system tended to result in an increased likelihood of falsely recognizing new faces constructed from the components of previously seen faces.

We repeated the nonverbal, pictorial experiment of Kroll et al. (1996) with the callosotomy patients to see if they would be impaired on this task. Based on the results of Experiment 1, there are at least two alternative predictions. If binding is a generalized left hemisphere capacity regardless of stimulus domain, then callosotomy patients should be unimpaired on this nonverbal task. Alternatively, if nonverbal binding is subserved by the right hemisphere, or requires both hemispheres, then callosotomy patients will be impaired in this task. Our goal was to resolve these alternative explanations and to better characterize the nature of nonverbal binding.

In addition, we report data on a slightly different version of this task, using pictorial elements that are more easily placed into semantic relations, that is, pictures containing a house and a vehicle (Fig. 3). With these pictures, subjects reported an ease of establishing a meaningful relationship between the kinds of houses and kinds of vehicles shown together. Many subjects, for example, reported imagining the kind of people who would choose such homes and vehicles.

Results

Abstract Figures

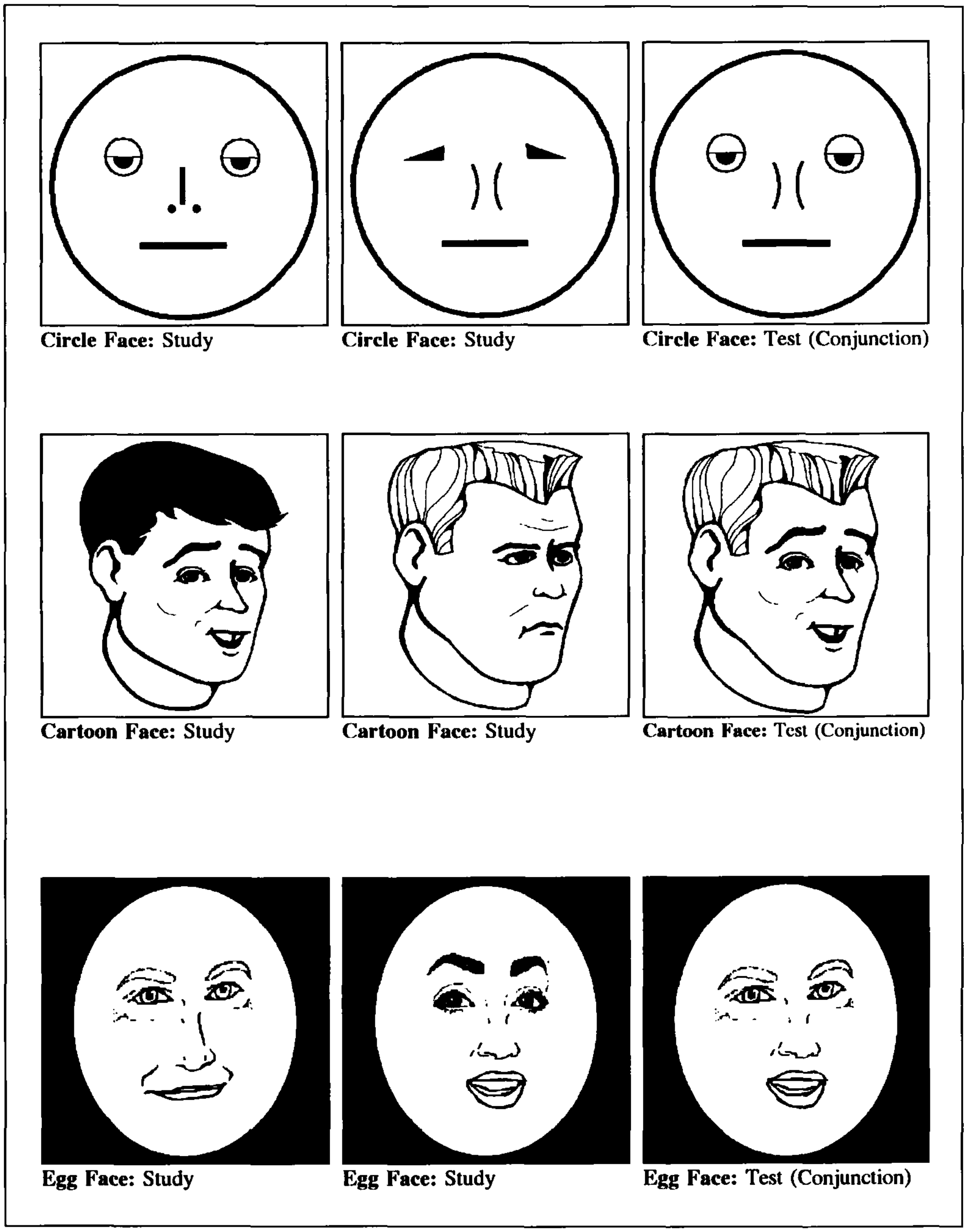
The results of the practice tasks with the pictorial stimuli are presented in Table 2. "Same" stimuli were exact copies of the original, studied figures, "Conjunction" stimuli were made up of components of studied figures, and "Feature" stimuli were composed of one component of a studied figure and one component that was new. In order to use the same stimuli in the memory task, where only the target stimuli were presented before test, and in the perceptual task, where both targets and distractors were presented simultaneously, the memory task was given first. Then, the exact same figures were used in the perception task to measure the subject's ability to make the required distinctions between target and distractors.

The callosotomy patients had no difficulty at all with the perception task (where study pictures are present while test stimuli are shown). On the other hand, their performance on the memory task was very similar to that of the patients with hippocampal lesions; that is, they had a very high false alarm rate to the conjunction stimuli. From their performance on the perception test,

Table 2. Average percentage of "old" responses for each group in each condition of the memory and perception tests using the abstract figures. (Data from hippocampal patients and normal control subjects from Kroll et al., 1996, Table 4.)

		Memory Test			*Perception Test*		
Group	*N*	*Same*	*Conjunction*	*Feature*	*Same*	*Conjunction*	*Feature*
Callosotomy Patients	**3**	**58.3**	**58.3**	**16.7**	**100.0**	**0.0**	**0.0**
JW		50.0	50.0	50.0	100.0	0.0	0.0
VP		50.0	50.0	0.0	100.0	0.0	0.0
DR		75.0	75.0	0.0	100.0	0.0	0.0
Aged-Matched Controls	18	72.2	33.3	5.6	98.6	2.8	2.8
Students	18	86.1	18.1	5.6	100.0	0.0	0.0
Patients with Hippocampal Lesions							
Right	8	65.6	46.9	18.8	96.9	6.3	6.3
Left	7	78.6	46.4	17.9	96.4	32.1	7.1
Bilateral	1	100.0	100.0	50.0	100.0	0.0	0.0

Figure 2. Examples from three of the face sets.



however, it appears that they were able to perceive the differences among even these complex figures and able to make the required judgments.

Face Tests

In order to reduce the amount of noise inherent in a single test with few items, the five face tests, which were approximately all of the same level of difficulty, were averaged together. These average scores are presented in Table 3.

Student subjects discriminated almost perfectly (Table 3). Both hippocampal and callosotomy patients, however, gave high percentages of false alarms to the test faces, which were conjunctions of features they had seen in the study faces. A comparison of the three callosotomy patients with the eighteen normal, older adults finds that the callosotomy patients made significantly more false alarms to the conjunction faces than did the control subjects, $t(19) = 3.309$, $MS_e = 13.66$, $p < 0.01$. Thus, although the data from Experiment 1 are consistent with the hypothesis that the callosotomy patients do not perform like patients with left hippocampal damage (i.e., their performance does not seem to lead to inferior binding of the memory traces of individual word stimuli), this experiment finds callosotomy patients, like

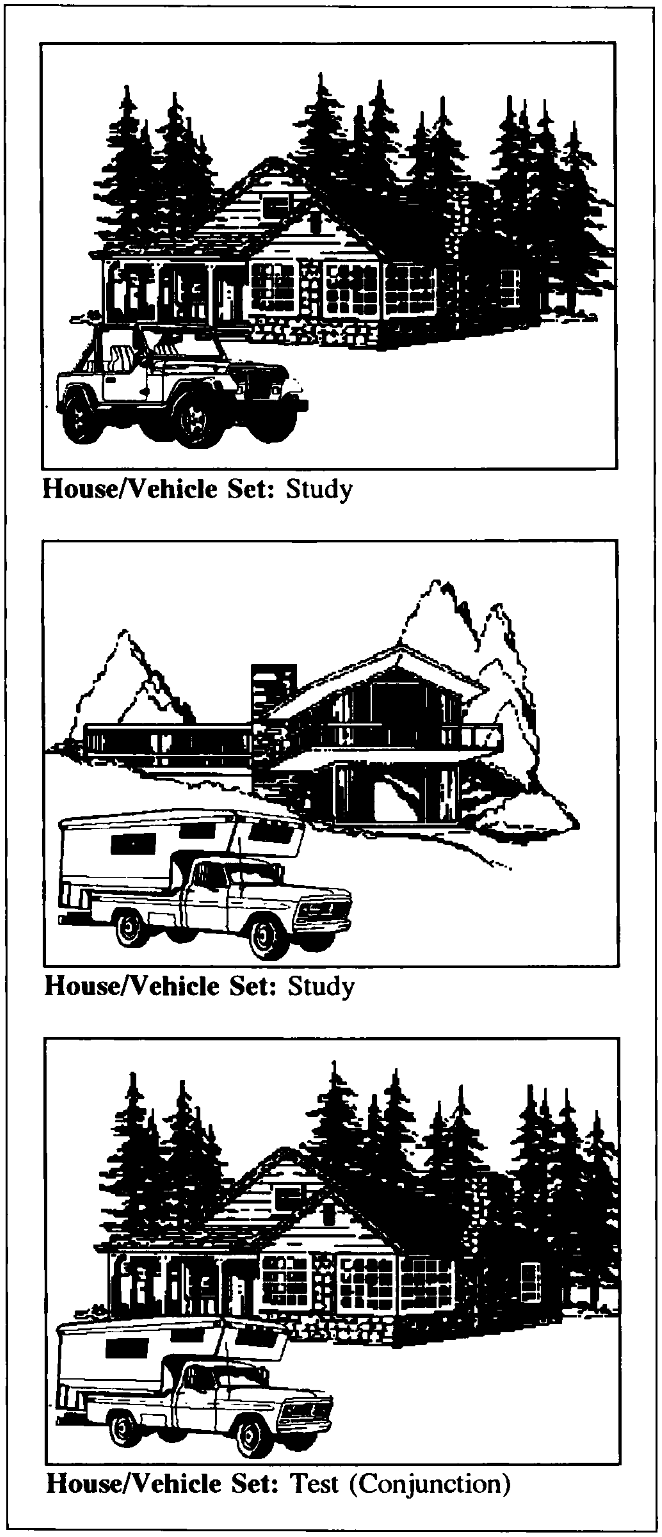


Figure 3. Examples from the House/Vehicle set.

Table 3. Average percentage of "old" responses for each group in each condition of the Faces Tests. (Data from hippocampal patients and normal controls from Kroll et al., 1996, Table 6.)

Group	*N*	*Same*	*Conjunction*	*Feature*	*New*
Callosotomy Patients	**3**	**100.0**	**75.7**	**11.8**	**0.0**
JW		100.0	81.3	6.3	0.0
VP		100.0	87.5	25.0	0.0
DR		100.0	58.3	4.2	0.0
Aged-Matched Controls	18	96.7	30.5	6.1	0.0
Students	18	95.6	7.2	0.6	2.5
Patients with Hippocampal Lesions					
Right	8	100.0	58.4	12.5	1.3
Left	7	100.0	56.4	10.7	7.2
Bilateral†	1	100.0	100.0	25.0	0.0

† Although all other subjects had a 10 min retention interval between study and test with the Cartoon Faces, the Bilateral Hippocampal patient was tested immediately after his study phase with all faces.

patients with damage to either their left or right hippocampal systems, to be impaired at binding of the memory traces of visual/spatial information.

House/Vehicle Test

The results of the memory test involving the house/vehicle pictures are presented in Table 4. In this version of the test, even though the stimuli were still pictorial, semantic relationships are easily developed to relate the elements of the pictures. With these types of pictures, only the patients with left hippocampal lesions exhibited any difficulty. In fact, one of the callosotomy patients (JW) was retested on these materials a week following the initial learning and testing session and again obtained a perfect score, recognizing both of the targets and rejecting all of the distractors.

Discussion

In contrast to their accurate performance in Experiment 1, callosotomy patients were unable to reject the visual conjunctions in Experiment 2 when the relationships among the components were not easy to verbalize. For both abstract figures and faces they had a false alarm rate comparable to hippocampal patients. Their accurate performance on the perception task indicates that they had no difficulty understanding the task or perceiving the discriminating differences, but were nonetheless unable to accurately make the required discriminations when

Table 4. Average percentage of "old" responses for each group in each condition of the house/vehicle test.

Group	*N*	*Same*	*Conjunction*	*Feature*	*New*
Callosotomy Patients	**3**	**100.0**	**0.0**	**0.0**	**0.0**
JW		100.0	0.0	0.0	0.0
VP		100.0	0.0	0.0	0.0
DR		100.0	0.0	0.0	0.0
Aged-Matched Controls	14	100.0	7.1	0.0	0.0
Students	16	100.0	0.0	0.0	0.0
Patients with Hippocampal Lesions					
Right	5	70.0	10.0	20.0	0.0
Left	4	100.0	62.5	12.5	0.0
Bilateral	1	100.0	100.0	.50	0.0

the task involved a memory component. This suggests that they were unable to bind visual features into a unified whole. These results further suggest that nonverbal binding processes cannot be accomplished by an isolated hemisphere. The integrity of the right hippocampal system alone is not sufficient to adequately bind visual features for retrieval as a unified whole. One codicil to this statement is needed. The dominance of the verbal left hemisphere in responding may have hampered the full expression of right hemisphere competence on this task. However, since both patients with damage only to their left hippocampus *and* patients with damage only to their right hippocampus have difficulty with nonverbal binding, it is likely that both hemispheres are necessary to perform well when stimuli are primarily nonverbal in nature. On the other hand, when it was easy to develop semantic relationships and verbal descriptions among the components of the visual stimuli, the callosotomy patients no longer exhibited any difficulty.

Hillger and Koenig (1991) conducted a series of face processing experiments with normal subjects using divided visual field presentations. On the basis of these experiments, they concluded that both hemispheres are involved in face processing, with right hemispheric processing being superior for holistic processing (already discussed by Milner as early as 1968) and left hemispheric processing being superior for the analysis of individual components. It is not surprising, then, that the callosotomy patients have difficulty with a visual task. However, it remains possible that the nonverbal binding tasks were more complex or required a greater number of steps than the verbal binding task, which might account for the need for cross-hemispheric communication. Therefore, we sought to investigate the associative properties of a primarily verbal but more difficult task.

EXPERIMENT 3

Previous experiments have demonstrated that callosotomy patients perform poorly on paired-associate learning (PAL) tasks (e.g., Milner et al., 1990; Zaidel & Sperry, 1973, 1974). The PAL task, however, is a complex task that can be difficult for a number of reasons. Indeed, a number of different patient groups have difficulty with this task. Here we used a version of this task, adapted from one used by Shimamura, Jurica, Mangels, Gershberg, and Knight (1995), which allows for a separation of some of the component processes involved in the task. We will also compare the callosotomy patients not only with normal controls but also with hippocampal patients and the frontal lobe patients of Shimamura et al. (1995).

In the paired-associate learning task employed here, cue and response words were manipulated to increase interference across two study lists. The first task involved an initial learning of the association between a cue word and a response word; then a second task involved associating a cue word presented in the first task with a different response word. This is typically referred to as a PAL A-B; A-C interference task and is used to study proactive interference; that is, the increased difficulty in learning the second list as a result of having learned the first list. In addition, it can be used to study retroactive interference in the memory for the first list, that is, the increased difficulty in remembering the first list as a result of having learned the second list. Shimamura et al. (1995) used this task to demonstrate impaired source monitoring in frontal lobe patients. We are using the same task in order to assess the ability of callosotomy patients to learn two associates in separate blocks, as well as to determine their ability to keep the first associate from interfering with the second, and to be able to remember both sets of response words at the end of the experiment.

Results

Table 5 presents the average number of correct responses made on each test trial for each of the subject groups. The data were evaluated by a 4×2 mixed-design analysis of variance, with subject group (Callosotomy vs. Right Hippocampal vs. Left Hippocampal System vs. the Normal controls) and the list set (A-B vs. A-C) as independent variables. Note that the age-matched controls in our task have an overall level of performance lower than that of the patient controls in Shimamura et al. (1995)—perhaps indicating that minor procedural differences made the task somewhat more difficult than theirs—but that the *pattern* of results is the same for the two normal groups.

Table 5. Average number of correct responses made by each of the subject groups for each of the three test trials for each of the two lists.

		List					
		A-B *Trials*			A-C *Trials*		
Group	*N*	*1*	*2*	*3*	*1*	*2*	*3*
Callosotomy Patients	**3**	**7.33**	**9.67**	**11.00**	**6.00**	**7.67**	**10.00**
JW		8	9	12	6	8	9
VP		5	9	9	6	6	9
DR		9	11	12	6	9	12
Kroll, Dobbins, Jha, Knight, and Tulving (in preparation)							
Aged-Matched Controls	18	9.50	11.22	11.83	9.39	11.33	11.83
Patients with Hippocampal Lesions							
Left & Bilateral	5	1.80	2.40	3.20	0.80	1.60	3.40
Right	5	5.40	8.40	9.20	3.80	7.00	8.00
Shimamura et al. (1995)							
Control Patients	12	10.44	11.88	12.00	10.20	11.76	12.00
Frontal Patients	6	9.48	11.04	12.00	7.56	9.12	11.04

In comparing patient controls and patients with frontal lobe lesions, Shimamura et al. (1995) found both a significant effect of subjects (with frontal lobe patients doing more poorly than control subjects) and a significant interaction (with frontal lobe patients showing greater proactive interference, i.e., dropping more on the A-C list). We also found a significant effect of group [$F(3, 23) = 39.3, MS_e = 31.53, p < 0.001$] and an effect of list [$F(3, 23) = 9.4, MS_e = 1.11, p < 0.001$], but not the interaction between group and list ($p > 0.05$). (Although the interaction effect is significant [$F(1, 29) = 5.2, MS_e = 1.04, p < 0.05$] if the patients are compared as a group against the control subjects.)

We also compared the callosotomy patients with each of the other groups in separate analyses and found that they performed significantly better than the patients with left hippocampal lesions [$F(1, 6) = 120.9, MS_e = 12.96, p < 0.001$] and significantly worse than the control subjects [$F(1, 19) = 6.5, MS_e = 21.02, p < 0.025$], but not significantly different from the patients with right hippocampal lesions ($p > 0.10$). In none of these separate analyses was the interaction significant ($p > 0.05$).

Table 6 presents the average number of correct responses made during the final recall test for each of the subject groups. The data were evaluated by a 4×2 analysis of variance, with subject group and the list set as independent variables. This overall analysis found a significant effect of group [$F(3, 27) = 43.6, MS_e = 3.68, p < 0.001$] and also found that the A-C list was remembered significantly better than the A-B list [$F(1, 27) = 9.1, MS_e = 3.19, p < 0.01$], but the interaction was not significant ($p > 0.10$). Separate analyses comparing the callosotomy patients with each of the other groups again found that they remembered less than the normal subjects [$F(1, 19) = 42.2, MS_e = 1.59, p < 0.001$] and more than the patients with left hippocampal lesions [$F(1, 6) = 166.0, MS_e = 0.82, p < 0.001$] and were not significantly different from the patients with right hippocampal lesions ($p > 0.10$). The interaction of list and group effects was significant only for the comparison with the patients with left hippocampal lesions [$F(1, 6) = 20.5, MS_e = 0.49, p < 0.001$]. Inspection of the table suggests that this interaction is caused by the patients with left hippocampal lesions remembering very little from either list, whereas the other patient groups remembered more from the second list than from the first.

Shimamura et al. (1995) also reported intrusion errors, that is, responding with a word from the first list during the learning of the second list. This is another method in which to assess memory interference effects. The average number of intrusions per trial are also presented in Table 6. Age-matched controls made relatively few intrusion errors. Patients with left hippocampal lesions made even fewer intrusion errors—probably because they remembered very little from the first list. The other patients, however, exhibited considerably more intrusion errors. An analysis of variance found a significant group effect across the four groups [$F(3, 27) = 21.0, MS_e = 0.12, p < 0.01$]. This effect remains significant even if the patients with left hippocampal lesions are left out of the error term because of their lower variability [$F(3, 23) = 17.9, MS_e = 0.14, p < 0.01$]. Tukey's pairwise comparison test, using the larger MS_e, found the callosotomy patients had significantly more intrusions than the patients with

Table 6. Number of correct responses in the final recall test and the number of intrusions from the first list while trying to learn the second.

Group	*N*	*Number Correct Final Recall*		*First List Responses during Second List Learning (Intrusions)*
		B	*C*	
Callosotomy Patients	**3**	**6.00**	**9.67**	**1.33**
JW		6	9	1.67
VP		6	9	1.33
DR		6	11	1.00
Kroll et al. (1996)				
Aged-Matched Controls	18	11.00	11.89	0.20
Patients with Hippocampal Lesions				
Left & Bilateral	5	1.60	2.00	0.07
Right	5	6.40	8.20	1.40
Shimamura et al. (1995)				
Control Patients	12	11.76	12.00	0.17
Frontal Patients	6	9.24	11.04	1.67

left hippocampal lesions ($p < 0.01$) and more intrusions than the age-matched controls ($p < 0.01$), but their number of intrusions did not significantly differ from those of the patients with right hippocampal lesions ($p > 0.10$). The patients with right hippocampal lesions similarly differed from patients with left hippocampal lesions ($p < 0.01$) and controls ($p < 0.01$). The performance of patients with left hippocampal lesions did not differ from the performance of control subjects ($p < 0.10$).

Discussion

The performance observed in callosotomy patients on the PAL task appears most similar to that of the performance of the patients with right hippocampal lesions. Their original learning scores on the first list tend to be somewhat higher than the scores of patients with right hippocampal lesions and lower than those of control subjects and patients with frontal lesions. On the second list, learning performance drops for both the frontal patients and the callosotomy patients. The final recall scores of the callosotomy patients are essentially equivalent to those of the right hippocampal patients. The callosotomy patients' pattern is different from the pattern observed in patients with frontal lobe lesions; that is, their learning and memory scores are lower, but they do not appear to make as many intrusion errors. This reduces the possibility that the memory performance deficits of the callosotomy patients is, like the frontal lobe patients, primarily the result of impaired on-line monitoring of information.

For the callosotomy patients, right hemispheric processing would be unavailable because the callosal transfer of this information cannot take place. It may be that the verbal system adequately supports the learning of the first list, but that right hippocampal processing is needed to uniquely identify and consolidate the word pairs. The right hippocampal patients, on the other hand, have impaired performance for both the first and second associates because the area of the right hippocampal system involved in forming these associations is damaged.

Gazzaniga et al. (1975) presented a group of total and partial commissurotomy patients with a paired-associate learning task in two conditions. In the first condition, the word pairs were simply presented for them to remember with no instruction. In the second condition, a visual imagery strategy was suggested as a memory aid. Of the patients tested, one had a complete section of the corpus callosum and anterior commissure. This patient was unable to do the task under either condition. Two of the remaining patients had all or partial sparing of the splenium and the fourth patient had only the splenium sectioned. All three of the latter patients were able to benefit from the imagery strategy, improving their performance from 10–20% of the pairs recalled to 60–70% of the pairs recalled. This finding indicates that cross-hemispheric integration can greatly improve performance on a similar task and underlines the importance of visual strategies in improving performance on this task. However, Milner et al. (1990) *were* able to improve the learning performance of callosotomy patients using visual imagery, but found that these results were shortlived, with the performance advantage from imagery instructions dropping off over a two-hour retention interval.

These results suggest that on a verbal task that requires new associations, as opposed to single word registration, and recall, as opposed to recognition, the left hemisphere word form system is not adequate for normal encoding and/or retrieval. It does provide some foundation for the learning, allowing callosotomy patients to approach normal levels while learning the first list (compared with hippocampal patients). However, when a second list is introduced, the prior list interferes with the new learning and contributes to intrusive errors. By the final recall trial, the callosotomy patients are no more able to recall these initial items than were right hippocampal patients. It appears that both hemispheres are necessary for normal paired-associate learning to occur.

GENERAL DISCUSSION

There is growing evidence about the brain systems responsible for different aspects of memory (Squire & Knowlton, 1994; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). Encoding processes, for example, have been localized to medial temporal structures, such as the hippocampal formation (Eichenbaum et al., 1994; Zola-Morgan, Squire, & Ramus, 1994). A bulk of this evidence comes from patients with medial temporal lesions, who suffer from anterograde amnesia suggesting that they are unable to encode new episodic information. Recently, a study by Kroll and colleagues (1996) characterized one type of encoding process that is impaired in hippocampal patients. The results from their testing of patients with unilateral and bilateral lesions to the hippocampal system suggest that the hippocampal system is critical for the encoding and binding of elements that comprise a memory trace. Additionally, this work suggests that this binding process is lateralized such that the encoding of verbal material is most seriously impaired when the lesion is in the left hippocampal system. On the other hand, the encoding of pictorial information seems to require the integrity of both the left and right hippocampal structures (see also Hillger & Koenig, 1991).

Experiments 1 and 2 investigated the effects of callosotomy on the binding of elements during the encoding of words and pictures. The results from the verbal conjunction task suggest that callosotomy does not impair the binding of word elements into the memory for a particular word. Given that callosotomy patients were unimpaired on this task, it appears that the left hemisphere, dominant for verbal response generation and output from the visual word form areas (Baynes et al., 1992; Gazzaniga, Smylie, Baynes, Hirst, & McCleary, 1984), is capable of processing verbal information. Thus, it does not require integrating this information with the right hemisphere in order to form a word trace that lasts at least over the brief retention intervals involved in this experiment. This may represent an advantage conferred by the lexical processing route of the visual word form system. Patients with lesions in their right hippocampal system are also unimpaired at the verbal conjunction task, a result consistent with the view that the encoding of a whole word resulting from the consolidation of verbal elements does not require right hippocampal structures. Note, however, that this task requires only word registration. No new associations need be formed. In addition, performance is measured by means of a recognition response that may, for the left hippocampal patients at least, be mediated mainly by familiarity, as opposed to recollection, processes.

The results from the pictorial conjunction task suggest that callosal integration is essential for the encoding into memory or the retrieval from memory of pictorial stimuli. Callosotomy patients are severely impaired at this task when it requires a memory component but not when it requires only a perceptual discrimination—their ability to make discriminations when the comparison stimuli were both visible was unimpaired. One explanation for their poor performance in this task is that, once the callosal fibers have been resected, the left hemisphere is unable to use the information from the right hippocampal system to make discriminations between true repeats and distractors constructed out of the components of the studied faces. However, the results of hippocampal patients do not support this hypothesis. Both the patients with lesions only to the right *and* those with lesions only to the left hippocampal system are impaired at this task. This suggests that the integrity of *both* hippocampal structures is required for normal encoding of pictorial elements. Callosotomy patients reveal another important requirement for the normal encoding of pictorial stimuli, the callosal transfer of information.

Perhaps each hemisphere not only has specialized processing requirements (Metcalfe et al., 1995), but is also responsible for inhibiting processing occurring in the other hemisphere. McNaughton and Morris (1994; see also Hiscock & Kinsbourne, 1987) have suggested that in normal subjects, mutual inhibition of the hemispheres prevents specialized processing for a single hemisphere from running out of control. This inhibitory checking may be the kind that enables an elimination of inappropriate alternatives (Kroll et al., 1996). Hippocampal damage may leave this inhibitory process nonoperational, resulting in excessive binding of conjunctions. That is, both elements that did occur together as well as combinations that did not occur may become encoded in memory.

An alternative explanation for the poor performance of callosotomy and hippocampal patients on this task is that normal encoding of pictorial information may require the integration of processing subserved by each hemisphere in the creation of a complete memory trace for a pictorial stimulus. If processing is disturbed by a hippocampal lesion, all of the components required for a complete memory trace will not be created. Thus, integration of information from both hemispheres will be incomplete and unable to carry the proper trace for a particular stimulus. Similarly, if processing within each hemisphere is normal but integration is not possible, due to the absence of a callosum, the requisite memory trace for proper encoding of the stimulus will not be formed. In both cases, there will be a resultant memory impairment for pictorial stimuli (Hillger & Koenig, 1991).

Converging evidence from callosotomy and hippocampal patients allows for a resolution to the alternative explanations for deficits in pictorial encoding observed in these patients. The hemispheric inhibition hypothesis predicts that patients with left hippocampal lesions may be impaired because of both the inhibition of left hemisphere processing by the right hemisphere and the reduced ability to encode verbal information within the left hemisphere. This hypothesis, however, also predicts that right hippocampal damage should result in impaired performance in the verbal conjunction task. If the right hippocampus is damaged it will be unable to adequately inhibit excessive left hemisphere binding.

For callosotomy patients, the inhibitory hypothesis predicts that callosotomy will impair performance on the verbal conjunction task, because the disconnection of the two hemispheres prohibits inhibition of excessive binding of verbal elements to be carried out by the right hemisphere. Since both patient groups, right hippocampal lesion patients and callosotomy patients, were not significantly different from normal subjects on the verbal conjunction memory task, the inhibition hypothesis is not supported. More likely is the explanation that a complete memory trace, or the most optimal memory trace, is one that combines information from both hemispheres during the binding of pictorial elements into a complete "Gestalt."

The results from Experiment 3 suggest that optimal performance on the paired-associate learning interference task may require the integration of information from both hemispheres as well. Although callosotomy patients were unimpaired in the verbal conjunction task, they performed below normal subjects in the initial learning of the word pairs in the paired-associate learning task. This impairment suggests that the encoding of associations between words is unlike the binding of conjunction elements into a word, perhaps because the individual word stimulus is a previously well-learned Gestalt. Words must be available to recombine freely into sentences to provide the generative power of language. Word and root morpheme units, however, are more fixed and therefore have more perceptual integrity to aid in encoding and retrieval. The encoding of word pairs appears to require the integrity of both hippocampal structures. This is evidenced by the poor performance of both groups of unilateral hippocampal patients on this task. Like the hippocampal patients, callosotomy patients are characterized as having *encoding* deficits during this task, that is, both are impaired during the initial learning of the word pairs. In contrast, the memory deficit seen in patients with frontal lesions seems to *not* be primarily caused by encoding deficits (their learning of the first list was essentially normal) but rather by retrieval and monitoring deficits (Shimamura et al., 1995). However, the possibility cannot be ruled out that the callosotomy patients may also suffer from some degree of deficit in their retrieval and/or monitoring processes and that this may be a cause of the relatively large number of first list intrusions into their learning of the second list. It is also difficult to differentiate between encoding and retrieval deficits in callosotomy patients when assigning blame for their rapid loss of information over time (Experiment 3, final recall; and also in other experiments, e.g., Milner et al., 1990). That is, is encoding so poor that there is not much to retrieve after even brief intervals, or is the encoding relatively intact but retrieval/monitoring processes so weakened by separation from the right hemisphere that the memory is not available? The pattern of results seen in Experiment 3 suggest that it is most likely that both encoding and retrieval mechanisms are weakened by the callosotomy. That is, initial learning is slower for callosotomy patients than for control subjects, which, together with the results from Experiments 1 and 2, suggest primarily an encoding deficit. On the other hand, after even the short retention interval employed here, their recall scores drop to almost the level of the performance of right hippocampal patients.

The frontal lobes are thought to be involved in the on-line monitoring of information as it gets encoded into memory and involved in creating strategies for the retrieval of this information (Gershberg & Shimamura, 1995; Schacter, 1987; Shallice, Fletcher, Frith, Grasby, Frackowiak, & Dolan, 1994; Shimamura et al., 1995; Shimamura, 1995). Lesions to the frontal lobes typically result in interference effects, as patients are unable to successfully retrieve the encoded information. Patients with frontal lobe lesions are relatively unimpaired during the initial encoding of information in the paired-associate learning task but are impaired during the learning of a second associate, typically due to large amounts of interference from the words presented during the first pairing. This strong proactive interference that characterizes the deficits observed in these patients is different from the type of impairments shared by both hippocampal and callosotomy patients who show at least some deficit already while learning List 1.

One explanation for this encoding impairment seen in the callosotomy patients in the PAL task is that the encoding of associations between pairs of words will benefit more by many representations of the association between the words in the pair than by only a few. For example, if the association between two words is remembered both verbally and pictorially, the memory trace for the association between these words may be stronger than if only a verbal representation occurs. Since callosotomy prevents the transfer of information from one hemisphere to another, it is possible that during this verbal task, only the verbal encoding of the associations is accessible. This logic is similar to the multiple representation idea proposed by Paivio (1971) for recall processes.

Another possibility is that the encoding of any association benefits from the involvement of both hippocampal structures (Phelps et al., 1994). If information from both hippocampal structures is unavailable, memory for the pair of words, as an associative unit, is impaired. This hypothesis is supported by the result that patients with unilateral right and left lesions of the hippocampus are impaired on this task. Again, callosotomy patients may be impaired because the verbal, dominant left hemisphere is unable to access the processing occurring in the right hemisphere.

Both Gazzaniga et al. (1975) and Milner et al. (1990) studied the effect of instructing callosotomy patients to use a visual mnemonic in a basic PAL task. Gazzaniga et al. found that imagery helped patients with partial callosotomy but did not help their patient with a complete callosotomy. Milner et al., on the other hand, found that visual imagery did improve performance in their callosotomy patients during the learning of the task—but that their performance was still much below that of control subjects and also that the improvement dropped precipitously over a two-hour retention interval. Thus, the benefit they received from visual imagery did not seem to carry over to a long-term memory benefit.

The performance of callosotomy patients on the three tasks reported here was remarkably similar to that of patients with damage to their right hippocampal system. The present set of experiments, thus, suggest that callosotomy impairs the types of encoding that require callosal integration from the left and right hippocampal structures. The performance of these patients on the verbal conjunction task did not differ from age-matched control subjects. However, the results from both the pictorial conjunction task and the paired-associate learning task support this hypothesis, with callosotomy patients performing significantly below normal subjects and not significantly different from hippocampal patients. This dissociation between tasks on which callosotomy patients perform normally versus tasks on which they are impaired reveals that callosal integration serves many purposes during the encoding of information. More speculatively, the boost that the verbal left hemisphere appears to provide for pictorial material suggests that the development of language-related abilities strengthens memory encoding and hence enhances behavior based upon memory of prior experience—even when that memory does not directly involve verbal components.

Table 7. Standardized Test Scores for Callosotomy Patients.

Tests	*Patients* J.W.	D.R.	V.P.
WMS-R			
Subtest Scores			
Orientation	13	13	14
Mental Control	6	3	4
Logical Memory I	17	35	18
Logical Memory II	5	31	13
Verbal Paired Associates I	12	21	16
Verbal Paired Associates II	7	3	7
Digit Span	18	15	15
Visual Memory Span	14	12	13
Visual Paired Associates I	14	13	13
Visual Paired Associates II	6	3	6
Visual Reproduction I	29	23	31
Visual Reproduction II	25	16	27
Figural Memory	2	4	8
Indexes			
Verbal Memory	79	121	83
Visual Memory	83	76	94
General Memory	79	100	84
Attention/Concentration	102	87	75
Delayed Recall	80	83	88
WAIS-R			
FSIQ	96	89	91
Verbal	97	105	95
Performance	95	72	88

Subjects

Three callosotomy patients served in all three experiments. Magnetic resonance (MR) brain scans of all three of these subjects are presented elsewhere (Gazzaniga, Holtzman, Deck, & Lee, 1985; Phelps et al., 1991). The standardized test score results from all three callosotomy patients are reported in Table 7.

Experiments 1 and 2 report the data from seven patients with lesions to their left hippocampal system, four resulting from strokes and three from lobectomy, eight patients with lesions to their right hippocampal system, five resulting from strokes and three from temporal lobectomy, and one patient with a bilateral hippocampal lesion resulting from anoxia. The lobectomy patients were not available for testing with the house/vehicle pictures in Experiment 2 nor for testing in Experiment 3. All strokes were due to infarction of the posterior cerebral artery from embolus or atherosclerotic occlusion except for one patient whose stroke was due to vasospasm after a subarachnoid hemorrhage. The patient with a bilateral lesion resulting from anoxia would not be expected to have any parahippocampal damage and, based on postmortem data from other patients, should have predominantly CA1 damage. There may, however, be cellular damage in other regions of the brain in addition to the CA1 region in the posthypoxic patients that eludes quantification. The hippocampal stroke patients all have parahippocampal in addition to hippocampal damage. All of the hippocampal patients suffered from variable degrees of anterograde amnesia. The bilateral hippocampal patient presented the most severe anterograde amnesia and the left hippocampal patients tended to show more severe anterograde amnesia symptoms than the right hippocampal patients. Aside from these memory problems, all patients were capable of understanding complicated instructions and of carrying on intelligent conversations with the examiner. However the patients with the more severe symptoms were unlikely to remember these conversations a short time later. The patients with infarcts all had variable degrees of homonoymous field defects due to calcarine damage. Two of the left hippocampal patients also suffered some damage to their splenium resulting in some degree of alexia without agraphia. These patients were asked to look at the screen while the words were read to them. Their results mirrored that of the other patients and thus they were included in the overall analysis. Computerized reconstructions of computed tomography (CT) or MR brain scans of the patients are presented in Kroll et al. (1996).

The ages and sex ratios of control patients and the patients with hippocampal lesions resulting from strokes are presented in Table 8.

Table 8. Comparison Subjects.

Group	*Female/ Male*	*Age*	*Age Range*
Age-Matched Controls	11 / 7	56.7	40–70
Students	7 / 11	20.3	18–25
Patients with Hippocampal Lesions			
Right	1 / 4	59.2	43–72
Left/Bilateral	0 / 5	70.2	62–78

For more details on these subjects, see Kroll et al. (1996).

Callosotomy Patient Histories

JW is a 42-year-old right-handed man who has had intractable epilepsy since the age of 19. Although there was no known family history of neurologic disorder and his developmental milestones were appropriately achieved, JW began experiencing brief absence spells at the age of 13 years after a concussive head injury. These absence spells were not treated. He graduated from high school at 18 years and experienced a major motor seizure one year later. After this seizure, a complete neurologic evaluation revealed normal blood chemistries, brain scan, skull films, and lumbar puncture. However, EEG revealed irregular polyspike and high voltage repetitive 3 cps spike and wave bursts during sleep. JW was placed on antiepileptic medication. During the next 7 years in spite of adequate serum levels, EEGs continued to reveal irregular polyspike activity. In 1979, JW underwent a two-stage microneurosurgical section of his corpus callosum. Eight months after his surgery, he appeared alert and able to converse easily about the past and present. Results from neurologic examination from that period appeared were normal. Although he appeared to have normal "everyday memory" following his callosotomy, JW and his family members are quite aware of his memory problems. For example, when asked about specific events in the recent past, several retrieval cues are necessary before he describes the event. His mother describes this phenomenon by saying "he has a lazy memory." JW has been studied extensively over the past 14 years on a variety of perceptual, cognitive, and attentional tests (e.g., Gazzaniga, 1989).

VP is a 44-year-old right-handed woman. Like JW she has no family history of neurologic disorder, and she reached developmental landmarks normally. At the age of 9 years she experienced seizures following febrile illness. Medication controlled the seizure activity and she was able to graduate from high school. By 1976, she was experiencing periods of blank staring lasting for seconds. EEG recordings from this period revealed bilateral 4 cps spike and slow-wave activity, and sharp activity with left temporal predominance. In 1979, while on medication, she experienced major motor, absence, and myoclonic seizures. She underwent partial anterior callosal section in early April 1979, and the resection was complete in a second operation 7 weeks later. Following the surgery, the neurologic exam revealed no focal findings. Her Weschler IQ scores were in the normal range.

DR is a 52-year-old right-handed woman. Though there is no family history of neurologic disorder and her developmental milestones were appropriately achieved, she began experiencing brief episodes of altered consciousness, which involved unpleasant olfactory hallucinations, motor automatisms, abdominal discomfort, and emotional outbursts. Anticonvulsant drugs were able to abolish these secondary effects, however, she continued to have several complex partial seizures per day. DR not only graduated from high school but went on to get a Bachelor of Science in accounting. She was employed as an accountant until her mid-thirties when her seizures impaired her job performance. In 1983, she underwent a single stage callosotomy for these intractable primary complex partial seizures. Eleven years since callosotomy, she continues to experience complex partial seizures though no generalized convulsions have occurred.

EXPERIMENT 1 METHOD

Design

Two lists of common two-syllable nouns were constructed such that each word presented fell into one of the following four categories:

First: this is the first time this word or either of its syllables appeared in the list.

Syllable-Repeat: this is the second time that *one* of the syllables appeared in the list.

True-Repetition: this is the second time that this exact word appeared in the list.

Conjunction: this is the second time for *each* of the syllables, but the first time that they appeared together.

Consider, for example, the series: EMPTY FICTION MUSTARD BUCKLE EMPTY FICKLE MUSTANG. *First* words would include FICTION, MUSTARD, BUCKLE, and the first EMPTY; MUSTANG would be a *Syllable-Repeat* (repeating 'MUS'); the second EMPTY would be a *True-Repetition;* and FICKLE would be a *Conjunction* (repeating 'FIC' from FICTION and 'KLE' from BUCKLE).

A *Conjunction* set consisted of the two initial words containing the key syllables and the test word. The "lag" of a *Conjunction* set was the number of words between the two initial words. In this experiment, the lag was either one (i.e., one word intervened between the first and second initial words) or five. The "retention interval" of a *Conjunction* set was the number of words between the second of the initial words and the test word. This is also the definition of the retention interval for *True-Repetition* and *Syllable-Repeat* sets. The retention intervals in this experiment varied between five and forty words. There were a minimum of six *Conjunction* sets of each lag/retention interval combination and an equal number of *True-Repetition* and *Syllable-Repeat* sets tested at each retention interval. In addition, the number of *Conjunction* sets in which the first syllable of the test word was presented before the second was equal to the number of sets in which the second syllable was presented before the first for each lag and retention interval. Across the *Syllable-Repeat* sets, the first and second syllables were equally often chosen to be the syllable repeated.

Syllables were not repeated within or across lists unless the design required it. In order to best compare different groups of subjects, all subjects received the exact same lists (i.e., the words were not counterbalanced across conditions). Including filler words, there were 99 words in the first list and 109 in the second. (Note: the comparison groups are discussed in Kroll et al., 1996. Some of these comparison groups received a third list.)

One of the callosotomy patients had been tested 18 months previously, but, at that time, had responded "old" to practically all stimuli—this may have been the result of his being somewhat overwhelmed by the number of experiments in which he was participating at the time (i.e., he may have been suffering from an induced "source amnesia" where the words seemed familiar from other experiments). The data reported here includes only his most recent test.

Procedure

A continuous recognition paradigm was employed. The words were presented sequentially in the center of a computer monitor. The subject read aloud the word on the screen and judged whether the word was "old" (i.e., had occurred previously in the list) or "new" (i.e., is occurring for the first time in the list). Note that in this experiment, saying "old" to the second member of a *True-Repetition* pair is a "hit" and saying "old" to any other word is a "false alarm."

The subjects proceeded through the list at their own speed, which averaged 1.59, 1.74, 1.65, and 1.47 seconds per word for the callosotomy patients, hippocampal patients, normal adults, and students, respectively. After completing the first list, subjects were given several visual memory tests (see Experiment 2), and then reminded of the instructions before receiving list 2.

EXPERIMENT 2 METHOD

Design

Seven sets of visual stimuli were used: a set of abstract figures that were used in the practice trials, five sets of faces, referred to as circle faces, cartoon faces, egg faces, simple drawings of female faces, and simple drawings of male faces,[3] and a set of house-vehicle pairs. Examples of these figures are presented in Figures 1 through 3. The face sets were made to appear as different from one another as possible in order to reduce the possibility that subjects would confuse components across sets.

The abstract figures each consisted of two designs inside of a frame. These were used to teach the tasks to the subjects and to measure their ability to understand the instructions and to perceive conjunction errors. The face sets were used for the measurement of the face conjunction effect. The house/vehicle set was used to test their ability to deal with visual stimuli when the relationships were relatively easy to express.

Each of the face sets was composed of a study-subset and a test-subset. All of the faces within a study subset were different, but the eight test faces were related to the study faces in the following ways: two of the test faces were identical to two of the study faces, two test faces were "conjunctions" of the features of two of the study faces (e.g., one of the conjunction circle faces had the eyes of one of the study faces and the nose of another), two test faces had one of the features of a study face and one feature that had not appeared on any of the study faces, and two test faces were completely new. All subjects received the exact same set of stimuli in the exact same order, but the orderings of the relationships were different across the different face sets. See Kroll et al. (1996) for more details.

The house/vehicle study set was composed of five pairs of houses and vehicles. Two of the test pairs were identical to two of the study pairs, two were conjunctions of the features of two of the study pairs (i.e., with the house from one study pair and the vehicle from another), two test pairs had one feature from a study pair (one the house, the other the vehicle) with the other feature being new, and two test pairs were completely new.

For the abstract (practice) figures, the two internal designs constituted one feature set and the border the other feature. Only four study figures were used, but twelve test figures were created—four sames, four conjunctions, and four feature repetitions.

Procedure

Each subject began with the practice tasks with the Abstract figures—first a memory task, then a perceptual task. Subjects were instructed that a test stimulus was to be designated as "old" only if both features were repeated *and* paired as they had been in the study set. In the practice memory task, all four of the study figures appeared together on the screen for 30 seconds. Then the test figures appeared sequentially and subjects judged each test figure as "new" or "old."

Immediately after the memory task, the same figures were used in the perception task. Here, the same four study figures remained in the four corners of the monitor screen throughout the test, while the test figures appeared sequentially in the middle of the screen. The subject's task was to judge if the center figure was identical to any of the corner figures. The primary purpose of this part of the procedure was to train the subject how to do the task and how to look for mis-pairings of old components, but it also served as a measure of a subject's ability to perceive the figures.

After the perceptual task, subjects began the facial memory tests. Each of the face tests consisted of a study phase and a test phase. Before each study phase, subjects were warned to pay close attention to how the components of the faces were put together and were shown examples of a "new" test face that consisted of components of "old" study faces. In the study phase, subjects saw the current set of faces three times. The faces were shown for ten seconds per face during the first trial block, then five seconds each during the second and third trial blocks.

The circle faces were tested immediately after the third study trial. Immediately following the testing of the circle faces, the subject received study phase of the cartoon faces. This was followed by the first list from the verbal experiment (lasting approximately ten minutes) before presentation of the test of the cartoon faces. This was followed by the second list from the verbal conjunction experiment. The remaining three face tests and the house/vehicle test were given in later sessions. These remaining three face tests were separated from one another by other, verbal tasks. In all three, the test phase occurred immediately after the study phase.

EXPERIMENT 3 METHOD

Stimuli and Design

The experiment used the same two lists of 12 moderately associated paired-associates (e.g., LION-CIRCUS, BABY-SPOON) used by Shimamura et al. (1995, Experiment 1). The first (cue) word of the pairs was the same across lists, but the second (response) word was different (e.g., BABY-SPOON, BABY-FOOD).

Procedure

Following Shimamura et al. (1995), subjects received three study-test trial blocks of each paired-associate list. In the study phase, subjects were shown the word pairs and instructed to remember them. Each word pair was presented for 4 sec in the center of the screen and, while it was on the screen, the experimenter read the pair twice to the subject. In the test phase, only the cue word was presented on the screen. The experimenter read the cue word and asked the subject for the response word. Subjects were encouraged to guess if the correct word could not be retrieved. Study pairs and test cues were presented in a different random order in each block of trials.

Following the three study-test trial blocks for the first list, the three study-test trial blocks for the second list were presented. Subjects were warned that the second list would contain the same cue words but have different response words. After both sets of study-test trial blocks, the sequential list of 12 cue words were again presented and the subjects were asked to report both of the responses for each cue. They were encouraged to guess and told that they could report the response words in either order.

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Notes

1. In this paper, we use the term "binding" to refer to an early component of memory consolidation—similar to perceptual binding (e.g., Treisman & Gelade, 1980), but occurring *after* the act of perception with its product being a coherent engram of the perceived event. Perceptual binding may be essential for memory binding but does not guarantee it.
2. By using the term "hippocampal system," as opposed to "hippocampus" per se, we mean to refer to the same area designated by Eichenbaum, Otto, and Cohen (1994, pp. 450-451). A description of the lesions of the hippocampal patients discussed in the present paper is given in the Subjects section and reported in more detail in Kroll et al. (1996).
3. A sixth set of faces was also administered but not included. This set was the same as that used by Reinitz, Lammers, and Cochran (1992), but was not included in the analysis because its level of difficulty is such that even many students had a considerable difficulty in differentiating new from old faces.

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