Short Title

MEMORY AND THE MEDIAL TEMPORAL REGION OF THE BRAIN

by

Philip M. Corsi

Ph.D. Psychology

Philip M. Corsi

HUMAN MEMORY AND THE MEDIAL TEMPORAL REGION OF THE BRAIN

A clear double dissociation between the effects of left and right temporal-lobe excisions was demonstrated for two identically-designed learning tasks that utilized different memoranda. Patients with left temporal-lobe lesions showed a deficit for the verbal task and normal performance for the non-verbal analogue, whereas the converse was evident for patients with right temporal-lobe lesions. Again, on two formally similar tests of short-term recall with interpolated activity, this same pattern of dissociation was observed for the retention of verbal as compared with non-verbal information. For both pairs of experiments, the severity of the material-specific learning and retention deficits was directly related to the extent of surgical encroachment upon the hippocampal zone of the affected hemisphere. These studies implicate the hippocampal region in the crucial transfer of experience from a temporary storage system (primary memory) to more permanent long-term storage (secondary memory).

HUMAN MEMORY AND THE MEDIAL TEMPORAL REGION OF THE BRAIN

by

Philip M. Corsi

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Department of Psychology
McGill University
Montreal

April 26, 1972

Preface

The chief finding here is that the medial temporal region of the brain, including the hippocampus and parahippocampal gyrus, is vital for several aspects of human learning. In particular, with unilateral left temporal lobectomy in the dominant hemisphere for speech, the learning and retention of elementary verbal information (letters and numbers) is impaired. If the left medial temporal region is also excised, then the verbal memory defect is exacerbated. Yet, the retention of non-verbal information such as spatial location and spatial sequence remains intact. Conversely, after surgical removal of the right temporal lobe, the learning and retention of spatial location and sequence — tasks which normally are mediated without verbal strategies — are more difficult, although the recall of simple verbal elements proceeds normally. The severity of this material-specific memory impairment is directly related to the extent of surgical encroachment upon the hippocampal zone in the right, nondominant, hemisphere. With bilateral damage to the medial temporal region, a more global memory disturbance results. Although the anterograde amnesia is not complete, it is emergent with respect to the memory defects observed after left and right hippocampectomy.

I am indebted to the patients at the Montreal Neurological Institute who permitted me to perform these studies of them. I am grateful to Dr. Theodore Rasmussen, Dr. Charles Branch, and Dr. William Feindel for referring their patients to me. Special thanks are offered to Miss Marcelle Provencher who, with great patience and care, transformed my handwritten draft into this finished manuscript.

This work was supported by the Medical Research Council of Canada through Grant M-2624 to Dr. Brenda Milner.

Table of Contents

It is now known that in man bilateral lesions of the medial temporal regions of the brain, involving both hippocampi and parahippocampal gyri, are associated with a generalized, severe, and lasting memory disturbance (Penfield & Milner, 1958; Scoville & Milner, 1957). Milner (1970) describes this disturbance:

> "Patients with these lesions show no loss of previously acquired knowledge or skill; nor do they have any perceptual difficulty. The immediate registration of new information appears to take place normally, provided the information does not exceed the span of immediate memory. Yet these patients seem largely incapable of adding new information to the long-term store."

This picture is supported by evidence from several experimental studies, many of which are based on observations of a single, important case. Intensive study of the patient H.M. who underwent bilateral resection of the hippocampal zone for the relief of intractable seizures (Scoville, 1968) has revealed much about the nature of the anterograde amnesia which follows damage to this area of the brain. Milner (1970) has shown that this patient is capable of remembering subspan verbal information for several minutes; however, as soon as his attention is diverted he forgets. This finding is consistent with the suggestion of Drachman and Ommaya (1964) that amnesic patients can hold a simple memorandum for long intervals in the absence of distracting activity. Further studies (Drachman & Arbit, 1966) have demonstrated that patients with bilateral lesions of the medial temporal region have normal immediate memory, but are unable to learn a series of digits or a sequence of light positions which exceed their immediate memory span.

It seems that as long as these people can verbally rehearse the material-to-be-remembered, their retention is intact. However, if the memoranda cannot be easily verbalized, then the opportunity for rehearsing the material without distraction does not benefit the amnesic subject. L. H. Prisko (1963) has used the delayed paired-comparison method of Konorski (1959) to show patient H.M.'s rapid forgetting of simple perceptual information which could not be verbally encoded. H.M. was unable to match clicks, tones, shades of red, light flashes, and nonsense patterns after short delays up to 60 seconds, whereas normal subjects showed no decrement in performance over the same intervals. Using a delayed matching-to-sample technique, Sidman, Stoddard & Mohr (1968) have confirmed Prisko's initial findings. They observed a sharp deterioration in H.M.'s recognition of non-verbal material (ellipses) over retention intervals of less than 30 seconds. At 32 second delays, the sample stimulus ceased to exert any control over H.M.'s matching choice, while for normal subjects accurate matching has been observed for delays of 40 seconds or longer. In both of these studies, a severe retention deficit was evident regardless of whether the patient was distracted during the intratrial interval. Most recently Milner & Taylor (1972) have investigated the retention of somesthetic information for patient H.M. In their experimental task, the subject was required to palpate an irregular wire shape and then, after varying delays, to select the sample shape again, by touch, from a group of four similar ones. H.M. was able to match the shapes at zero delay and showed normal intermanual transfer, yet his recognition declined sharply as soon as a delay was introduced, and fell to chance beyond 30 seconds. Control patients with unilateral cortical excisions showed errorless matching with intratrial intervals of several minutes.

The experimental studies of global memory dysfunction after bilateral lesions of the hippocampal zone, reinforce one's clinical impressions of patients with such lesions. For these people, the ongoing events of daily life seem to be forgotten as soon as the focus of attention shifts to other occurrences and so, for the most part, they seem to live from moment to moment. Yet, it has recently been shown that the memory loss in amnesic patients is not as complete as either their behavior in everyday life or in some formal learning experiments would suggest. Moreover, it has been proposed (Milner, 1968) that certain kinds of learning might even occur at a normal rate. Milner, Corkin & Teuber (1968) have demonstrated that patient H.M. was capable of some learning on simple visual and tactual maze problems with intensive practice. This patient was able to retain the solution of a visual maze up to one week after training to a strict criterion and when tested two years later on the same problem (Milner, 1970) he showed considerable savings (75 per cent), even though he had forgotten that he had previously learned the maze. Warrington & Weiskrantz (1968) have shown that amnesic subjects can learn to recognize fragmented drawings of words and common objects, and that they retain this form of perceptual learning for several weeks. This finding has been confirmed by Milner, Corkin & Teuber (1968) for the patient H.M., who learned to recognize incomplete pictures normally and demonstrated a high degree of retention after four months.

The most striking example of sparing of learning and memory after bilateral hippocampal damage occurs with respect to motor skills. Milner (1962) was the first to suggest that the acquisition of motor habits might be unaffected by hippocampal lesions. Following this suggestion, Corkin (1968) investigated the performance of patient H.M. on several manual tracking and manual coordination tasks. H.M. showed learning and retention of motor skills over several days of testing, although his initial performance was inferior to that of normal control subjects. This finding, in contrast to the evidence of severe deficits on many other learning tasks for this patient, is consonant with studies in normal subjects which have established differences between kinesthetic memory and memory for words or visual location (Posner, 1966; Posner & Konick, 1966; Williams, Beaver, Spence & Rundell, 1969).

To date, efforts to reproduce the hippocampal amnesic syndrome in monkeys have proved largely unsuccessful. It has been demonstrated that analogous bilateral lesions of the medial temporal region in monkeys do not produce deficits of the severity and permanence reported for man (Orbach, Milner & Rasmussen, 1960; Drachman & Ommaya, 1964; Cordeau & Mahut, 1964; Correll & Scoville, 1965). The most consistent and reproducible effect, although not invariable (Dorff, 1964; Waxler & Rosvold, 1970), is a selective impairment on spatial delayed-alternation but not on delayed-response tasks (Mahut & Cordeau, 1963; Correll & Scoville, 1967; Mahut, 1971). In addition, a general defect in visual discrimination learning has been found to be associated with bilateral inferotemporal lesions in the monkey (Mishkin, 1954; Mishkin & Pribram, 1954). Further experiments (Iwai & Mishkin, 1968; Iwai & Mishkin, 1969) have revealed that the impairment produced by large infero-temporal lesions involves at least two distinct components; with posterior damage to this area, a loss in visual pattern perception has been observed, whereas more anterior lesions have resulted in defects of visual learning and retention. Recently, Iversen & Weiskrantz (1970) have shown that hippo-campal lesions aggravate the deficit in pattern and object discrimination learning after bilateral inferotemporal damage. These authors have proposed in line with Iwai & Mishkin (1969) that in the monkey, the posterior inferotemporal cortex is concerned with perceptual analysis, whereas the anterior temporal cortex, including the medial structures, mediates the encoding of new information; and they further suggest that for man these mechanisms have evolved to process verbal in addition to non-verbal events. Still it is evident that although some learning defects have been found for monkeys, they have not been of the magnitude or kind observed in patients with bilateral hippocampal lesions, and these findings suggest an evolutionary discontinuity between monkey and man in the function of the medial temporal structures.

In contrast to the global memory disturbance produced in man by bilateral lesions in the hippocampal zone, the effects of unilateral lesions of the temporal lobe are far less severe and specifically related to the nature of the information presented to the patient. Although rare instances of persistent amnesia have been reported after unilateral temporal lobectomy, these are usually seen only in patients with electrographic or radiological evidence of additional damage to the opposite temporal lobe (Milner, 1966). In general, people with left temporal-lobe lesions in the dominant hemisphere for speech typically show impairment on verbal learning and verbal memory tasks (Meyer & Yates, 1955; Milner, 1958). This deficit is observed irrespective of whether the verbal material to be remembered is heard or read (Milner, 1967; Blakemore & Falconer, 1967). Further, it is not dependent on the specific method by which verbal retention is assessed (Milner, 1958; Milner & Kimura, 1964; Milner & Teuber, 1968). With corresponding lesions of the right, nondominant hemisphere, verbal memory remains normal; however, the retention of "non-verbal" information, such as complex visual or auditory patterns, is selectively impaired (Kimura, 1963; Prisko, 1963; Milner, 1968; Shankweiler, 1966; Warrington & James, 1967). People with right temporal lobectomies also show a learning deficit for both visual and proprioceptive maze problems (Corkin, 1965; Milner, 1965). The performance of patients with left temporal lobectomies is intact for all of these non-verbal tasks.

Within the large group of patients at the Montreal Neurological Institute who have undergone unilateral temporal lobectomy for the relief of focal epilepsy, there is a wide variation in the severity of these material-specific retention deficits. Since the surgical removals usually involve the hippocampus and parahippocampal gyrus as well as the lateral neocortex, it is important to the understanding of cerebral organization of function and critical on clinical grounds to find out whether the severity of the memory disturbance is related to the degree of damage to these medial structures. Milner (1967) has tentatively suggested that left hippocampectomy may increase the verbal learning impairment seen after removal of the left temporal lobe. Furthermore, it has been shown that following right temporal lobectomy, a deficit in maze learning occurs, if and only if the bulk of the hippocampus is removed on the right side (Milner, 1965; Corkin, 1965), and there is some indication that the same is true for the impairment in recognition of unfamiliar photographed faces (Milner, 1968).

The Present Investigation

The studies to be reported here were specifically designed to bring out the role of unilateral hippocampal lesions in material-specific memory disturbances. The tasks used to assess mnemonic function were tests of short-term retention and learning with interpolated activity. In addition to groups of normal subjects and patients with unilateral temporal-lobe excisions, the well-known patient H.M., with bilateral hippocampal damage was also examined. This man's performance provides a reference from which to evaluate the extent of the memory disturbances following unilateral temporal-lobe surgery.

Subjects

The people who were studied were patients at the Montreal Neurological Institute. All of these patients underwent unilateral temporal lobectomy for the relief of focal cerebral seizures. The cause of the seizures in most of these people was focal cerebral atrophy dating from birth or early life, although a few cases of adult head injury were also included. Patients with evidence of diffuse cerebral damage, or with epilepsy of unknown origin, were excluded, as were cases of intracranial tumor. Moreover, Wechsler Intelligence and memory quotients were known for all patients, and it was possible to eliminate those with an I.Q. rating below 70. Altogether 39 patients who underwent left temporal lobectomies and 39 patients with right temporal-lobe removals were studied. These two groups included only people with speech representation in the left hemisphere (as demonstrated by cortical stimulation and, in some cases, by the Wada (1949) technique of intracarotid injection of sodium Amytal). The majority of patients were tested in long-term (1-10 years) follow-up, although 19 patients in the right temporal-lobe group and 15 patients in the left temporal-lobe group were tested three weeks after operation. Most of the patients were on small doses of barbiturates, and there were no systematic group differences with respect to the nature or amount of this anti-convulsant medication.

In order to investigate the special role of the medial temporal-lobe structures in material-specific retention disorders, the right and left temporal-lobe groups were each divided into four sub-groups depending on how much of the medial temporal region was removed. A classification system suggested by Dr. Theodore Rasmussen was utilized in making this subdivision, and the hippocampus served as the brain-mark for delineating the extent of medial temporal-lobe excision. The surgeon's measurement of excised tissue at the time of operation was used in assigning a patient to a specific sub-group.

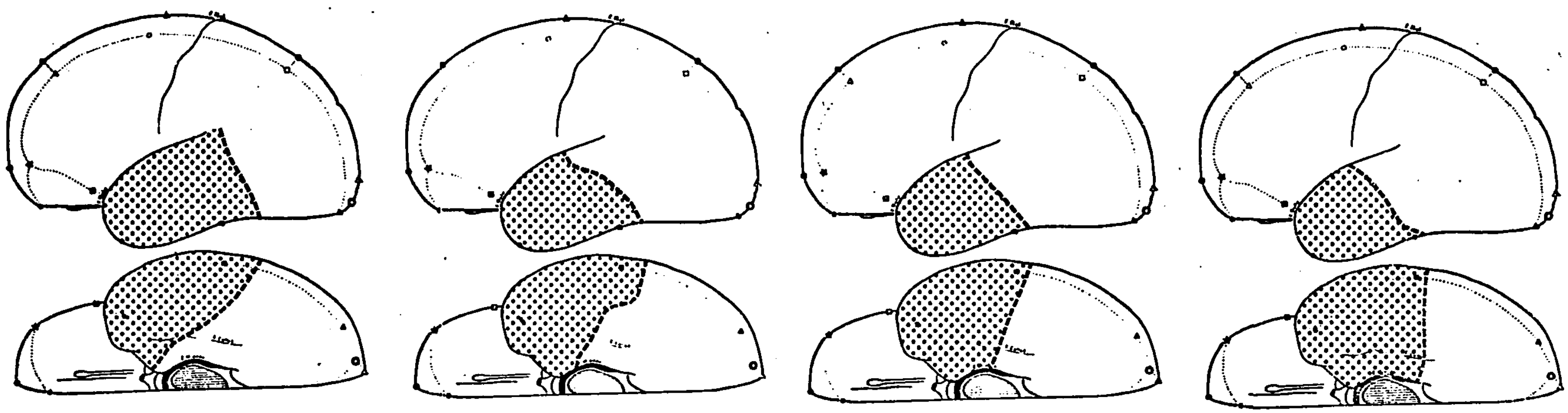
The four left temporal sub-groups are illustrated by representative cases in Figure 1. Figure 2 presents the analogous information for the right temporal group. The removals in every case included the uncus and amygdaloid nucleus, but the extent of removal of the hippocampal complex (hippocampus, parahippocampal gyrus, and fusiform gyrus) varied

Figure 1

REPRESENTATIVE LEFT-TEMPORAL LOBECTOMIES

EXTENT OF MESIAL REMOVAL

GROUP 1	GROUP 2	GROUP 3	GROUP 4
Hippocampus Spared	Pes Hippocampi Excised	Pes Hippocampi and approximately 1 cm. of Body Excised	Radical Excision of Hippocampus

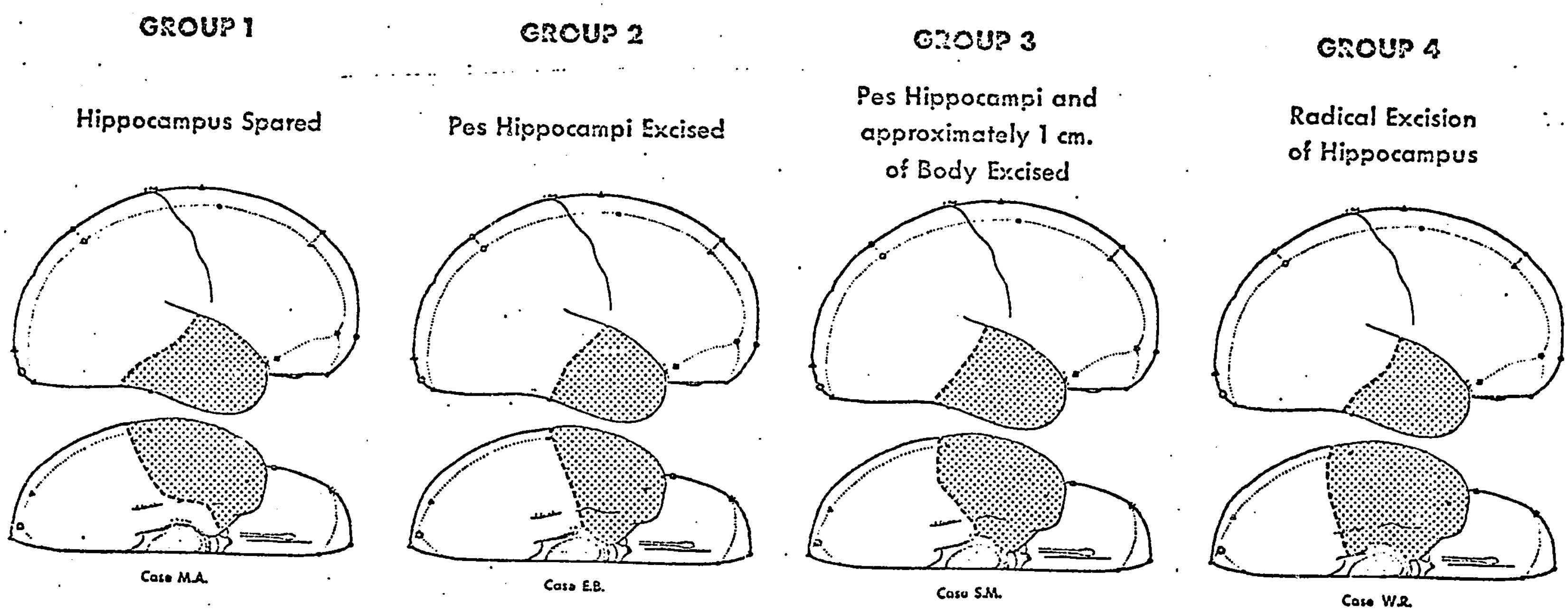


Case T.H.	Case R.S.	Case J.W.	Case M.O.

Note - Brain maps based on the surgeon's drawings at the time of operation, showing representative left temporal lobectomies in four groups of patients, classed according to the extent of hippocampal destruction (Lateral surface above; medial surface below. Stippled area indicates extent of cortical excision.)

Figure 2

REPRESENTATIVE RIGHT-TEMPORAL LOBECTOMIES
EXTENT OF MESIAL REMOVAL



Note - Brain maps based on the surgeon's drawings at the time of operation, showing representative right temporal lobectomies in four groups of patients, classed according to the extent of hippocampal destruction (Lateral surface above; medial surface below. Stippled area indicates extent of cortical excision.)

considerably from patient to patient. As indicated by the figures, Group I for each series consists of patients in whom the medial aspect of the temporal lobe was entirely spared. In Group II, the pes hippocampi was removed, but the body of the hippocampus was left intact. Group III is composed of patients with medial removals that include the pes hippocampi and one additional centimetre of the body of the hippocampus. The patients in Group IV underwent radical removal of the hippocampal zone. The medial excision in these cases was carried back lateral to the brain stem.

The extent of lateral cortical removal (measured at the Sylvian fissure and the base of the temporal lobe respectively) for the different lesion groups is presented in Table 1. Across the left temporal-lobe sub-groups no significant variation in terms of the lateral extent of removal at the Sylvian Fissure ($F = 1.39$, $p > .25$) or at the base of the temporal lobe ($F = 0.26$, $p > .25$) was observed. Similarly, no significant variation was found for the right temporal sub-groups, for removal along the Sylvian fissure ($F = 1.52$, $p > .25$) or along the base of the temporal lobe ($F = 0.69$, $p > .25$).

Age and intelligence-test data for the various patient sub-groups are given in Table 1. As indicated, 20 normal control subjects (student nurses and technicians) were also tested, and there was no significant variation for the right and left temporal groups and the control group with respect to age ($F = 1.24$, $p > .25$). In addition, the temporal-lobe groups did not differ significantly with reference to Wechsler-

Table 1

Age, Lateral Extent of Removal, and Follow-up I.Q. of Different Lesion Group

Group	N	Mean Age	Mean Lateral Removal (cm)		Mean Wechsler I.Q.
			Sylvian Fissure	Base of Temporal Lobe	
Normal Control	20	28.1	—	—	Not Tested
Left Temporal	39	30.9	5.2	5.9	104.1
Left Temporal					
Sub-Groups I	9	29.6	5.6	5.9	103.7
II	10	28.3	5.1	5.9	106.7
III	11	30.8	5.4	6.1	104.0
IV	9	35.2	4.7	5.7	101.7
Right Temporal	39	26.5	5.7	6.6	105.5
Right Temporal					
Sub-Groups I	7	21.3	6.2	7.3	102.7
II	14	30.1	5.6	6.6	107.1
III	7	22.1	6.3	6.9	106.4
IV	11	26.1	5.5	6.2	104.9

Bellevue Intelligence test scores (F = 0.11, p >.25). It should be noted that because the research reported here was conceived progressively, there is some minor variation in the composition of the different patient groups for the retention studies that follow. In all cases this variation is insignificant and Table 1 thus serves as an overall summary of the indicated variables across these studies.

In addition to the unilateral cases, the patient H.M. (Scoville, 1968) who underwent a radical bilateral medial temporal-lobe resection for the relief of generalized seizures was also studied. In H.M., the surgical removal was said to extend posteriorly along the medial aspect of the temporal lobes for a distance of 8 centimetres from the temporal tips, thus destroying bilaterally the anterior two-thirds of the hippocampi and parahippocampal gyri, as well as the unci and amygdalae, but sparing the lateral neocortex. At the time of testing, 15 years after operation, this man was 42 years old with a Wechsler I.Q. of 118. In order to highlight the special nature of this patient's memory disturbance, his performance will be considered separately from the group data.

The Experiments

Altogether, four short-term retention studies were carried out. Two of these tasks required the recall of verbal information and the other two required the recall of non-verbal information.

Verbal Studies

Recall of consonant trigrams. This verbal memory task, which is a simplified version of the Peterson and Peterson (1959) technique, required the recall of individually presented, consonant trigrams. The trigrams were selected to be of equal, low association-value (Witmer, 1935). On any given trial, a trigram followed by a 3-digit number (e.g. "DFX357") was read aloud to the patient at the rate of one letter (or number) per second. His task was to repeat the number immediately after hearing it and then to count backwards from it as quickly as possible until he was signalled by the onset of a red light to stop counting and recall the consonant trigram that preceded the number (e.g. "DFX"). The patient was given 15 seconds in which to recall the letters and then a new trial began. In this design, the counting served as a device to keep the subject from rehearsing the 3 consonant letters. Pilot studies had demonstrated that the original distractor task employed by Peterson and Peterson (1959) in their study of normal college students (counting backwards by three in time to a metronome) was too stressful for the present patient population, and therefore the patients were simply requested to count backwards as rapidly as possible. They were also told that the counting was just as important as remembering the letters.

There were 6 conditions in the experiment, the variable being the length of the retention interval, namely, 3, 6, 9, 12, 15 or 18 seconds. Altogether 24 trials were conducted for each subject, with 4 trials occurring at each of the 6 retention intervals. The score was the total number of letters correctly recalled for the 24 trials.

With normal control subjects the decline in correct recall for this task becomes quite marked as the retention interval gets longer (Figure 3). Analysis of variance on recall scores for the combined normal-control, left-temporal, and right-temporal groups yielded an F-ratio of 48.91 ($p < .001$). As illustrated in Figure 4, the left temporal patients were impaired relative to the right temporal patients ($t = 8.26$, $p < .001$), whose performance did not differ from that of the control subjects ($t = 0.13$). Mean per cent correct-recall scores for the various groups are given in Table 2 and are plotted in Figure 5 as a function of the retention interval.

Analysis of the performance of the 4 left temporal sub-groups, which is summarized in Figure 6, revealed significant variation across these groups ($F = 25.59$, $p < .001$). Those patients with the hippocampus spared (Group I) recalled significantly more letters than patients in Group II ($t = 3.98$, $p < .001$) who, in turn, were superior to the patients with more extensive medial removals in Group III ($t = 3.10$, $p < .005$). The scores for Groups III and IV did not differ statistically ($t = 1.55$, $p > .05$), although the patients with radical hippocampal removals tended to show the most severe impairment of verbal recall. The performance of patients in Group I was superior to that of the other left temporal groups; these people were nevertheless impaired relative to patients with right temporal-lobe excisions ($t = 1.83$, $p < .05$, one tail test).

The patients with right temporal-lobe lesions had also been

Figure 3

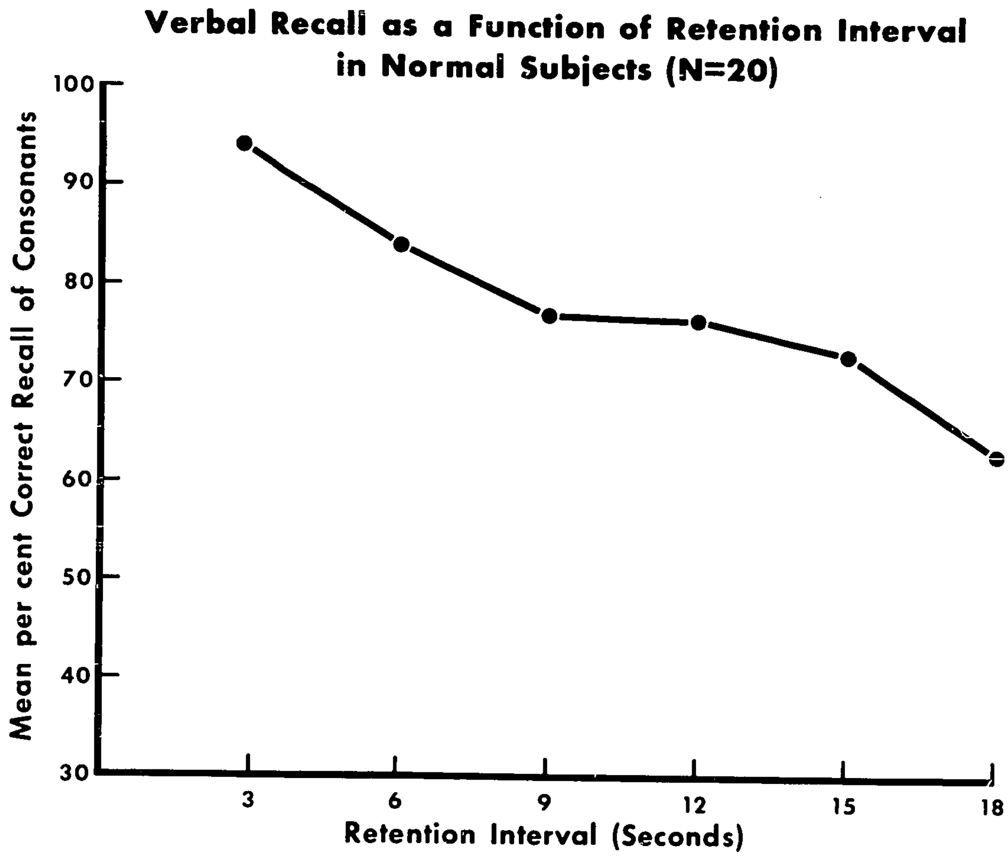

Verbal Recall as a Function of Retention Interval
in Normal Subjects (N=20)
Mean per cent Correct Recall of Consonants
100
90
80
70
60
50
40
30
3
6
9
12
15
18
Retention Interval (Seconds)

Figure 4

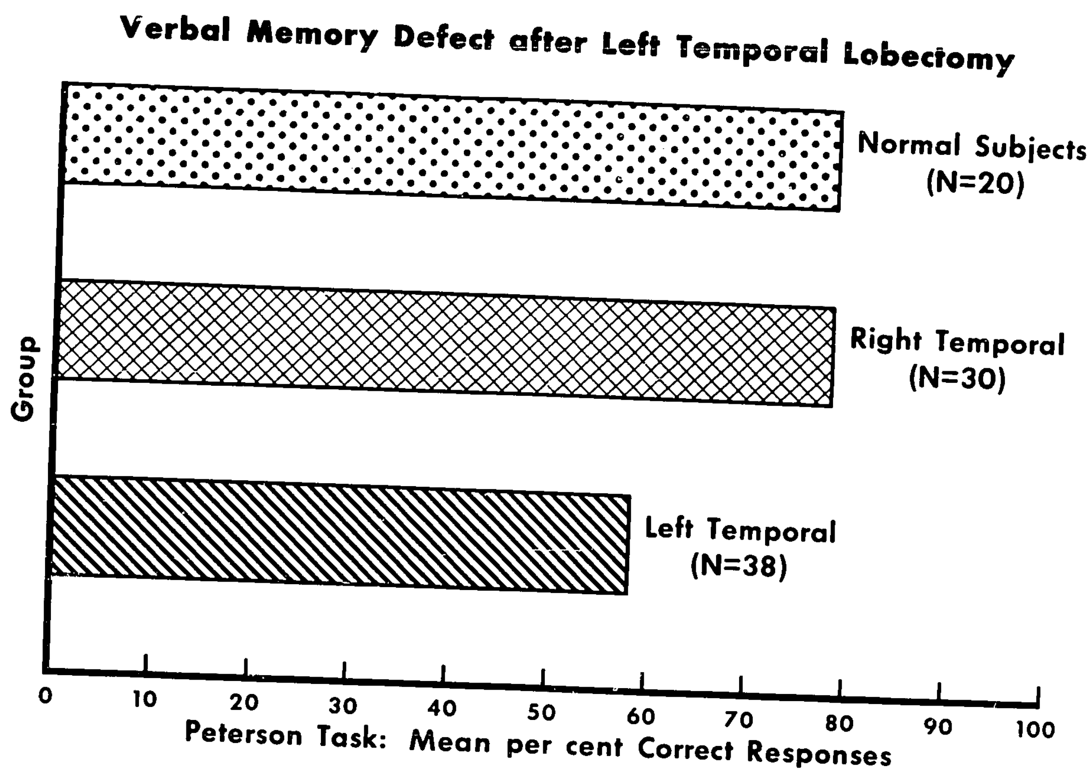

Verbal Memory Defect after Left Temporal Lobectomy
Normal Subjects (N=20)
Right Temporal (N=30)
Left Temporal (N=38)
Group
0
10
20
30
40
50
60
70
80
90
100
Peterson Task: Mean per cent Correct Responses

Table 2

Recall of Consonant Trigrams for Different Lesion Groups

Group	N	Mean % Correct Recall
Normal Control	20	77.8
Right Temporal	30	78.1
Left Temporal	38	58.3
Sub-Groups		
I	9	72.5
II	10	60.4
III	10	52.4
IV	9	47.7

Figure 5

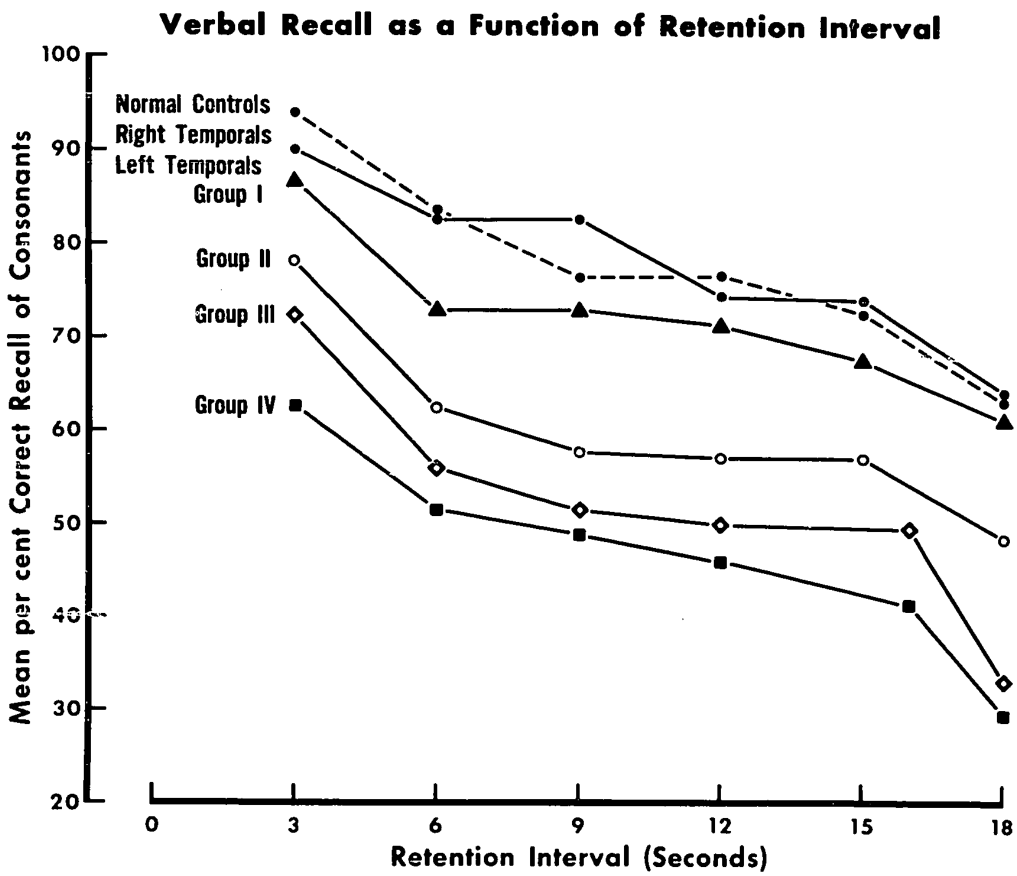
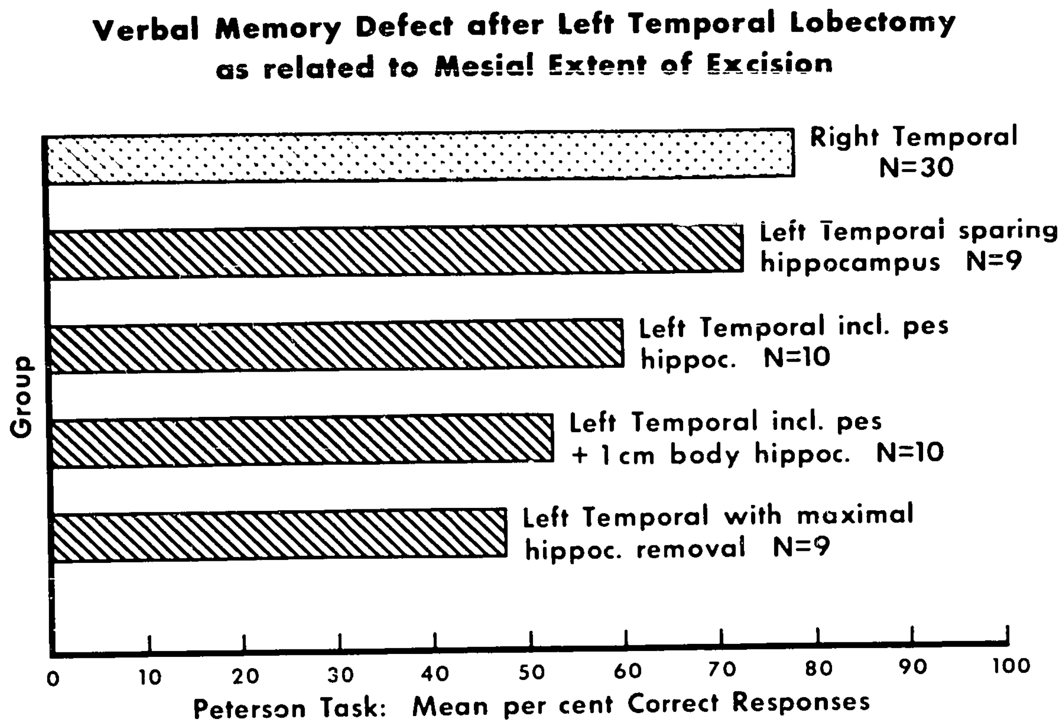

Verbal Recall as a Function of Retention Interval
Mean per cent Correct Recall of Consonants
100
90
80
70
60
50
40
30
20
Normal Controls
Right Temporals
Left Temporals
Group I
Group II
Group III
Group IV
0
3
6
9
12
15
18
Retention Interval (Seconds)

Figure 6


Verbal Memory Defect after Left Temporal Lobectomy
as related to Mesial Extent of Excision
Right Temporal
N=30
Left Temporal sparing
hippocampus N=9
Left Temporal incl. pes
hippoc. N=10
Left Temporal incl. pes
+ 1 cm body hippoc. N=10
Left Temporal with maximal
hippoc. removal N=9
Group
0
10
20
30
40
50
60
70
80
90
100
Peterson Task: Mean per cent Correct Responses

subdivided into 4 groups depending on the extent of medial temporal removal, using the same criteria as for left temporal classification. However, no significant variation was found across the four right-temporal sub-groups ($F = 0.83$, $p > .50$) on this verbal task.

The severity of the verbal memory deficit in this experiment was found to be directly related to the extent of the encroachment upon the hippocampal zone in the dominant hemisphere for speech. For patients sustaining extensive surgical removals of the medial temporal-lobe structures in the left hemisphere, there is an impairment in the ability to hold verbal inputs for even very short intervals when the opportunities for rehearsal are restricted. From this study, there appear to be no sharp discontinuities between the performance of people with large medial temporal-lobe excisions and that of normal control subjects (see Figure 5). Even though the verbal recall of left temporal patients in Groups III and IV is quite impoverished relative to other groups, the retention curves obtained for the various groups run roughly parallel to each other.

Hebb's recurring digits task. This next experiment was a further attempt to understand the nature of the verbal memory impairment which results after lesions of the hippocampal zone in the dominant hemisphere for speech. The design of this task follows from an experiment originally conducted by Hebb (1961). In the present study, the immediate memory span for digits was first ascertained for all subjects by the method of Wechsler (1944). The subject was next presented with 24 sequences of digits, one sequence at a time. Each sequence was one digit in excess of the patient's immediate memory span. So, for example, if a person was able to recall 7 digits in correct order immediately after hearing them, then he was presented with 24 sequences of 8 digits each. The sequences were read aloud at the rate of one digit per second, with a 15-second interval between sequences. The subject was simply instructed to repeat each sequence immediately, in the exact order of presentation. For this task, there was one special feature about which the patient was not informed: on every third trial (3rd, 6th, 9th . . . . 24th) the same series of digits was repeated, whereas the other intervening sequences occurred only once. Two performance scores were obtained for this task. The first score was the number of recurring sequences which were recalled in correct order (7 maximum) and the second was the number of non-recurring sequences correctly recalled (17 maximum). In scoring, the first presentation of the repeated sequence was treated as a non-recurring sequence.

With normal subjects, Hebb (1961) has shown and Melton (1963) has confirmed that recall of the recurring sequences improves progressively over repetitions, whereas no significant cumulative improvement occurs for the non-repeated sequences. In 1961, this finding convinced Hebb that some "structural trace" may be established very early in the memory process. It is of interest to analyse the performance of patients with dominant, left temporal lobectomies on this task because it provides a nice method for following the course of verbal learning and, presumably, the course of consolidation of memory traces over a short series of trials.

To date, 33 patients who have undergone right temporal lobectomy, 39 patients with left temporal-lobe removals and 17 normal control subjects have been examined on this task. These groups are comparable with regard to age, intelligence and immediate memory span for digits ($F = 1.06$, $p > .25$). The mean digit span for the three groups was as follows: normal control subjects 6.7; right temporal patients 6.5; left temporal patients 6.3. In addition, no significant variation was observed for this variable across the four left temporal sub-groups ($F = 0.01$, $p > .50$).

Analysis of variance for the combined left temporal, right temporal, and normal groups yielded an F-ratio of 19.93 ($p < .001$) for the recurrent-sequence scores and 3.31 ($p < .05$) for the non-recurrent sequence scores. As indicated in Figure 7, the patients with left temporal-lobe removals show an impairment on this verbal task when compared to the right temporal patients (recurrent sequence, $t = 5.40$, $p < .001$; non-recurrent sequence, $t = 1.99$, $p < .05$) whose performance did not differ from that of the control subjects (recurrent sequence, $t = 0.14$, $p > .50$; non-recurrent sequence $t = 0.41$, $p > .50$).

Scores expressed as mean per cent correct digit-sequences for the left temporal sub-groups are given in Table 3 and are plotted in Figure 8 as a function of the ordinal presentation of the recurrent item. Analysis of the performance of the four

Figure 7

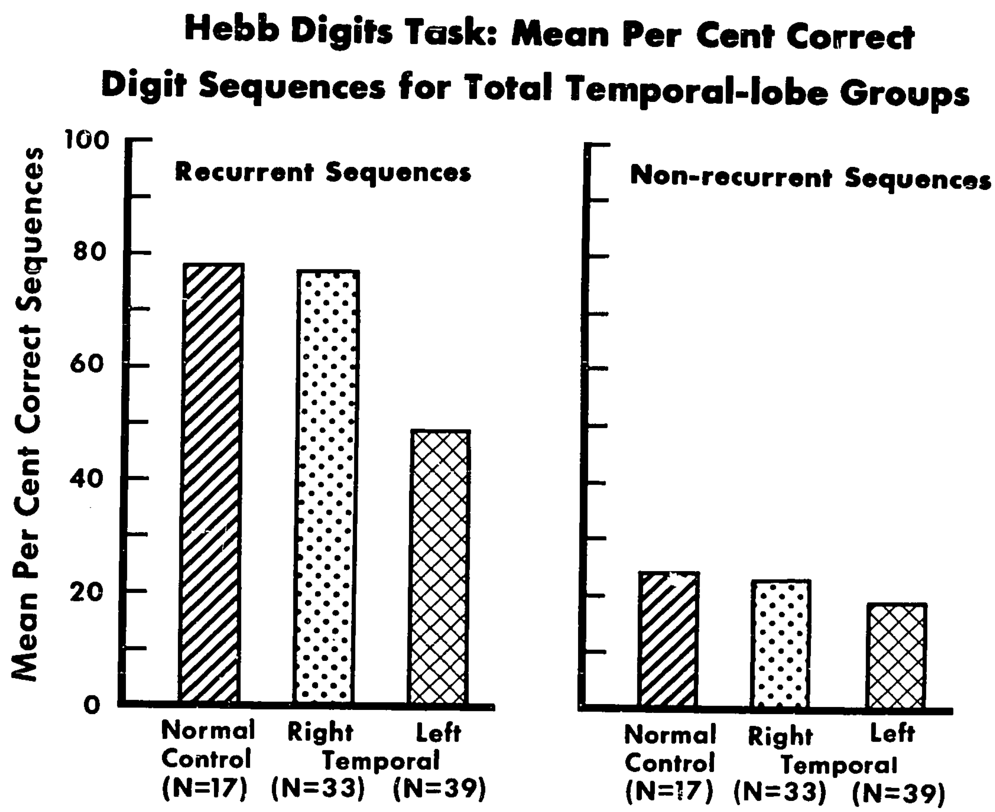
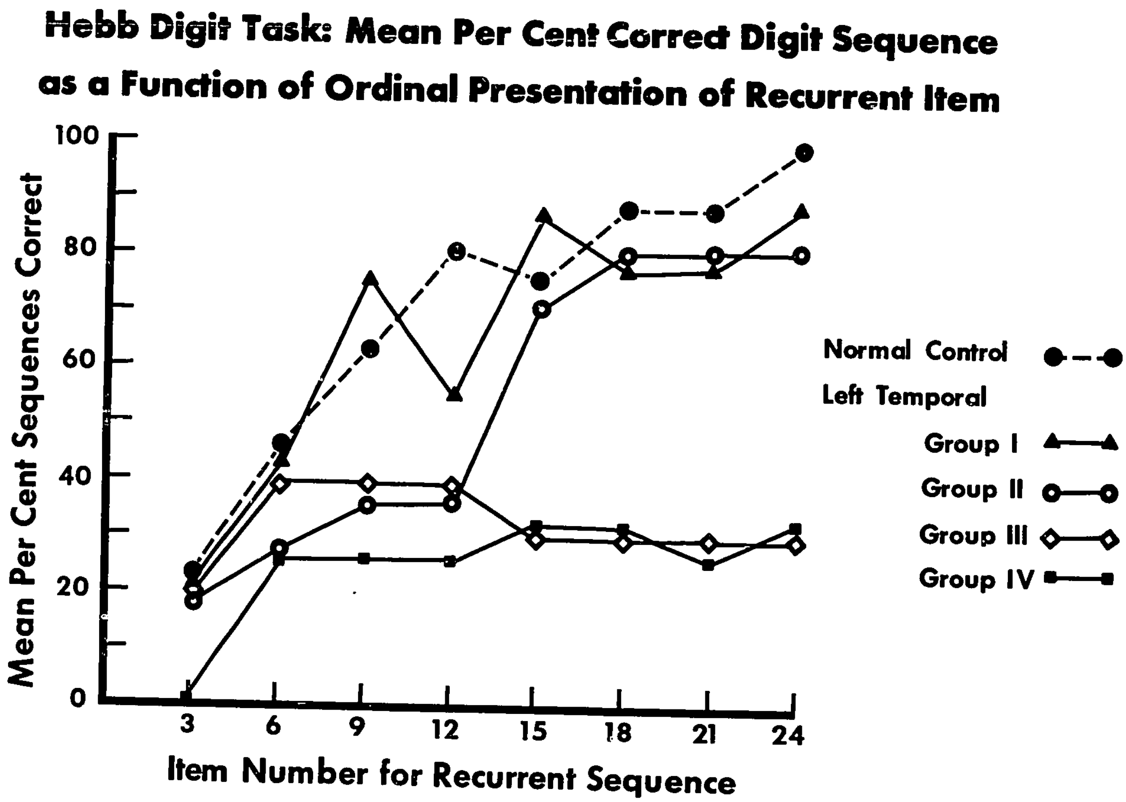

Hebb Digits Task: Mean Per Cent Correct
Digit Sequences for Total Temporal-lobe Groups
Mean Per Cent Correct Sequences
100
80
60
40
20
0
Recurrent Sequences
Non-recurrent Sequences
Normal Control (N=17)
Right Temporal (N=33)
Left Temporal (N=39)
Normal Control (N=17)
Right Temporal (N=33)
Left Temporal (N=39)

Table 3

Hebb Digits Task: Mean Per Cent Correct Digit Sequences for Left Temporal Subgroups

Group	N	Mean Per Cent Correct Sequences	
		Recurrent Sequences	Non-Recurrent Sequences
Right Temporal	33	77.4	23.4
Left Temporal I	9	73.0	22.9
Left Temporal II	11	61.0	19.2
Left Temporal III	10	32.9	20.6
Left Temporal IV	9	28.6	15.8

Figure 8


Hebb Digit Task: Mean Per Cent Correct Digit Sequence
as a Function of Ordinal Presentation of Recurrent Item
Mean Per Cent Sequences Correct
100
80
60
40
20
0
3
6
9
12
15
18
21
24
Item Number for Recurrent Sequence
Normal Control
Left Temporal
Group I
Group II
Group III
Group IV

left temporal sub-groups for the recurring sequence scores revealed significant variation across these groups ($F = 11.90$, $p < .001$). No significant variation was observed for the non-recurrent sequence scores ($F = 1.00$, $p > .25$). Those patients with the hippocampus spared (Group I) correctly recalled the recurring digit sequence more frequently than patients in Group II ($t = 1.81$, $p < .05$) who, in turn, were superior to the patients with more extensive mesial removals in Group III ($t = 3.18$, $p < .005$). Groups III and IV did not differ statistically ($t = 0.41$, $p > .50$).

The performance of left temporal patients in Group I was not statistically different from that of the right temporal patients ($t = 0.75$, $p > .25$) or normal control subjects ($t = 0.82$, $p > .25$). However, patients with the pes hippocampi excised in the left hemisphere (Group II) did show an impairment for recall of the recurrent sequence relative to the right temporal patients ($t = 2.91$, $p < .005$) and normal controls ($t = 2.77$, $p < .005$). No significant variation was found across the four right temporal sub-groups for the recall of either the recurrent sequence ($F = 0.71$, $p > .50$) or the non-recurrent sequences ($F = 0.65$, $p > .50$).

From the analysis of results for the Hebb digits-task it is apparent that the magnitude of verbal learning impairment is proportional to the extent of medial temporal-lobe excision in the dominant hemisphere for speech. For patients with large medial removals of the left temporal-lobe, the consolidation of verbal impressions over time seems particularly susceptible to disruption, although immediate memory as sampled by span tasks remains relatively unaffected. Thus, whether one chooses to study the course of forgetting (as in the Peterson task) or the course of verbal learning in these patients, it is evident that the hippocampal zone in the left hemisphere is specifically involved in the verbal consolidation process.

Studies of Non-Verbal Retention and Learning

In the two experiments described thus far, the severity of verbal memory impairment was found to vary directly with the extent of encroachment upon the hippocampal region in the dominant hemisphere for language. From what is known of hemispheric specialization of function, it is reasonable to look for a corresponding relationship between the recall of non-verbal information and the integrity of the medial portion of the right temporal lobe. For the two previous studies, patients with right temporal-lobe excisions showed normal recall of the verbal information presented to them, regardless of whether or not the hippocampus was spared. However, patients with right temporal-lobe removals do show a memory deficit in the performance of certain non-verbal tasks (Kimura, 1963; Milner, 1968; Shankweiler, 1966). The extent to which this memory impairment can be related to surgical encroachment upon the hippocampal zone in the right hemisphere is the focal problem in the following two studies of learning and retention for non-verbal material.

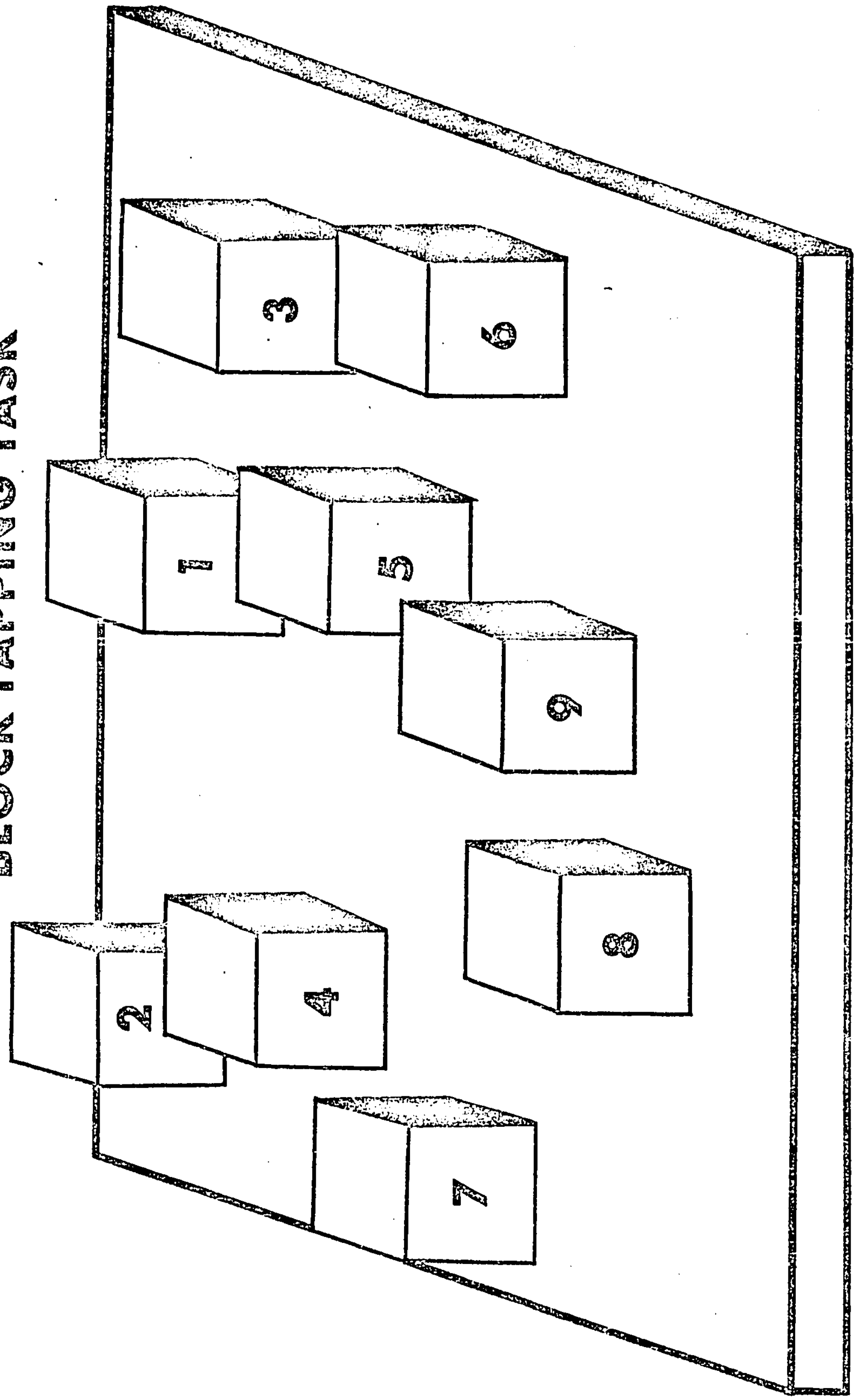
Block-Tapping Task. This task is identical in design to the Hebb digits task, but the items are spatial not numerical.

The test material (see Figure 9) consisted of 9 black blocks (1-1/4" cubes) which were impartially arranged on a black board (9" x 11"). The examiner tapped the blocks with a 6" wooden stick in a particular sequence and, immediately thereafter, the patient was required to tap out exactly the same pattern. The patient's immediate spatial span (i.e. the maximum number of blocks he was able to tap in correct order) was first ascertained and then 24 block sequences which were each one block in excess of the patient's immediate span were presented. Each block was tapped only once in any particular sequence with a 15" interval between sequences. As with the Hebb digits-task, every 3rd block sequence (3rd, 6th, 9th .... 24th) was repeated, whereas the intervening sequences occurred only once. The blocks were numbered on the examiner's side of the board for ease in recording the patient's performance. However, from his position, the patient was unable to see the numbered block faces. Two scores were obtained: the first was the number of recurring block sequences which were tapped in correct order (7 maximum), and the second was the number of non-recurring sequences correctly tapped (17 maximum). In scoring, the first presentation of the repeated sequence was considered as a non-recurring sequence.

Thus far, 24 patients with left temporal-lobe removals, 36 patients with right temporal-lobe removals, and 16 normal control subjects have been tested. The mean immediate span for block tapping for these groups was as follows: normal control 4.9; left temporals 4.9; right temporals 4.8. No

Figure 9

BLOCK TAPPING TASK



Examiner's view

significant variation occurred across the three groups with respect to this variable ($F = 0.12$, $p > .50$). Furthermore, no significant variation was observed for block span across the four right temporal sub-groups ($F = 1.42$, $p > .25$).

Analysis of variance for the combined right temporal, left temporal, and normal groups yielded an F-ratio of 15.93 ($p < .001$) for the recurrent-sequence scores and 9.72 ($p < .001$) for the non-recurrent-sequence scores. As illustrated in Figure 10, the right temporal patients were impaired on this spatial learning task when compared to left temporal patients (recurrent sequence, $t = 4.34$, $p < .001$; non-recurrent sequence, $t = 2.64$, $p < .05$), whose performance did not differ from that of the normal control subjects (recurrent sequence, $t = 0.84$, $p > .50$; non-recurrent sequence, $t = 0.65$, $p > .50$).

Scores expressed as mean per cent correct block-sequences for the right temporal sub-groups are given in Table 4 and are plotted as a function of the ordinal presentation of the recurrent item in Figure 11. Analysis of the performance of the four right temporal sub-groups for the recurring-sequence scores revealed significant variation across these groups ($F = 6.91$, $p < .002$). No significant variation was observed for the non-recurrent-sequence scores ($F = 1.54$, $p > .20$). For recall of the recurrent sequence, those people with the hippocampus spared on the right (Group I) did not differ significantly from the patients in Group II with only the pes hippocampi excised ($t = 0.62$, $p > .50$). In fact, the patients in these two sub-groups were not impaired relative to normal

Figure 10

Block Tapping Task: Mean Per Cent Correct Block Sequences for Total Temporal-lobe Groups

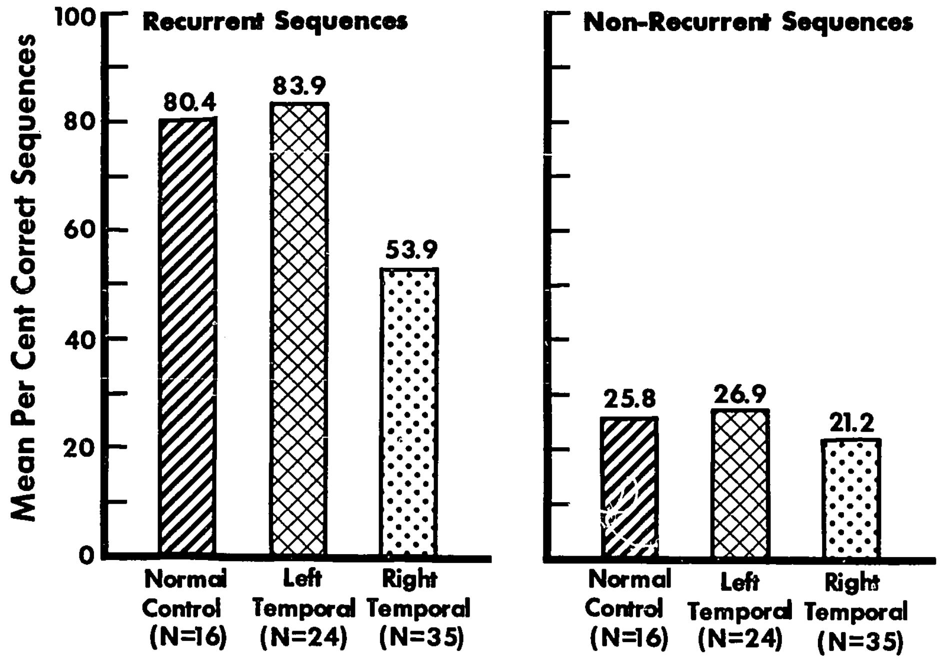


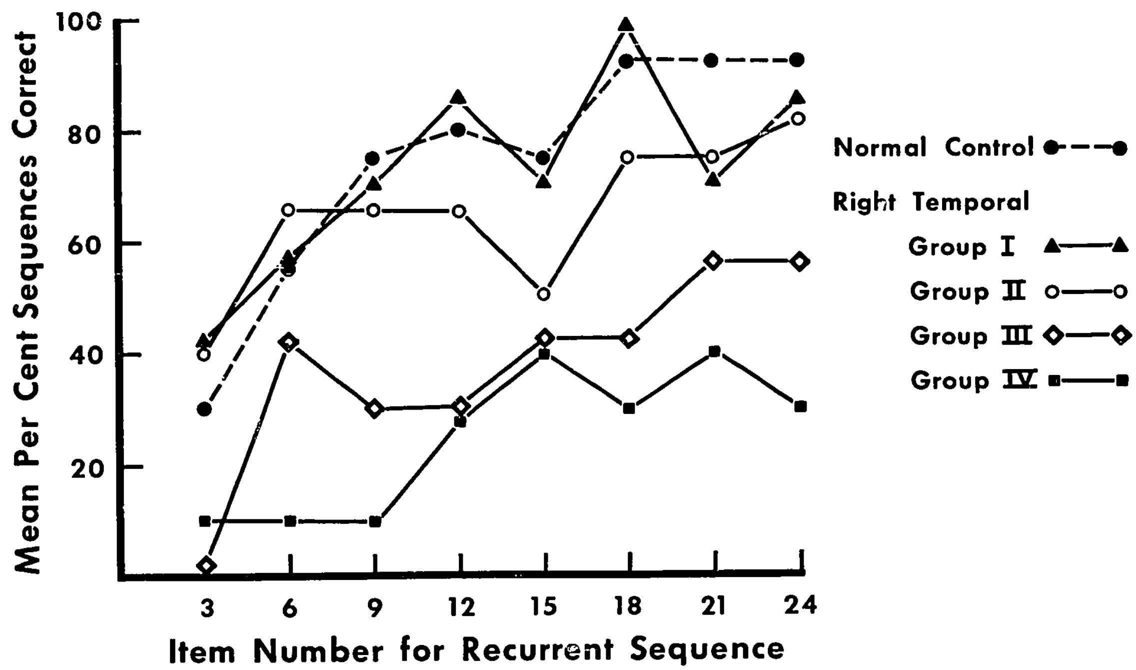
Table 4

Block Tapping Task: Mean Per Cent Correct Block Sequences for Right Temporal Subgroups

Group	N	Mean Per Cent Correct Sequences	
		Recurrent Sequences	Non-Recurrent Sequences
Left Temporal	24	83.9	26.9
Right Temporal I	7	77.6	22.7
Right Temporal II	12	69.0	23.5
Right Temporal III	7	42.9	22.7
Right Temporal IV	10	28.6	15.9

Figure 11

Block-Tapping Task : Mean Percent Correct Block Sequences as a Function of Ordinal Presentation of Recurrent Item



controls for recall of the recurrent sequence (Group I vs Controls, t = 0.31, p >.50; Group II vs Controls, t = 1.37, p >.25). In contrast, the patients with more extensive medial removals in Group III did show an impairment when compared with normal control subjects (t = 4.71, p <.001) and with the patients in Group II (t = 1.99, p <.05). Those people who underwent radical excision of the hippocampal zone in the right hemisphere (Group IV) demonstrated the most severe impairment in recall of the recurrent sequence.

The left temporal-lobe patients were also sub-divided into 4 groups depending on the extent of mesial-temporal removal. However, no significant variation was found across these four sub-groups for either the recurrent sequence (F = 0.46, p >.50) or the non-recurrent sequence (F = 0.83, p >.50).

The results of the block-tapping analysis are analogous to the findings for the Hebb digits task. The right temporal patients show a deficit in non-verbal, spatial learning and this deficit varies directly with the extent of medial temporal removal. Whereas the left temporal patients have difficulty in the consolidation of verbal impressions over time, the right temporal patients show a consolidation impairment for non-verbal material. This impairment is apparent even though immediate, non-verbal, memory span, as measured by the new block-tapping technique, is normal relative to control subjects.

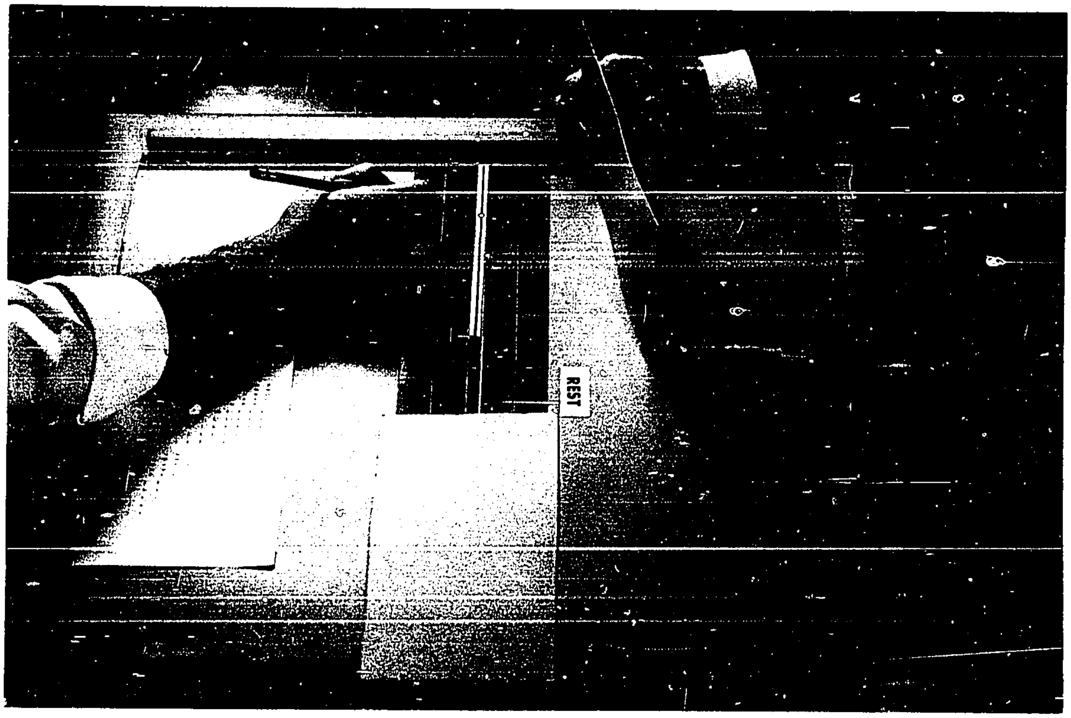
Recall of visual information (Posner task). The final study in this series of experiments was designed to analyse further the non-verbal memory disturbance that results from medial temporal excision in the right hemisphere. The experimental task was a modified form of a simple test which Posner (1966) has utilized in his studies of the short-term retention of visual information. The material to be recalled consisted of a 1/4 inch-diameter circle located at one of 24 positions along an 8-inch line. The 24 positions, in millimetres from the left end of the line are indicated in Figure 12. This figure also serves as a summary of the experimental design. The randomized test material was presented to the subject on a 23 x 23" panel. As illustrated in Figure 13, an inspection line with a small circle on it appeared in the presentation window to the subject's left and was recalled by him on a test line which appeared in the recall window to the right. The information to be remembered (i.e.——0——) was exposed in the presentation window for 5 seconds during which the subject marked the line at the center of the circle with a pencil stroke. The inspection stimulus was then covered and after a short retention interval the recall window was opened, exposing an 8-inch line without the circle referent on it. The subject was instructed to mark this line where he thought the circle should appear (i.e. the same distance from the left end of the line). S was given 15 sec. in which to recall the inspection stimulus and then a new trial began. Retention was tested after three different intervals, 6, 12 or 24 seconds. For half of the trials at each interval (rest trials), the subject was simply instructed to rest quietly with his eyes

Figure 12

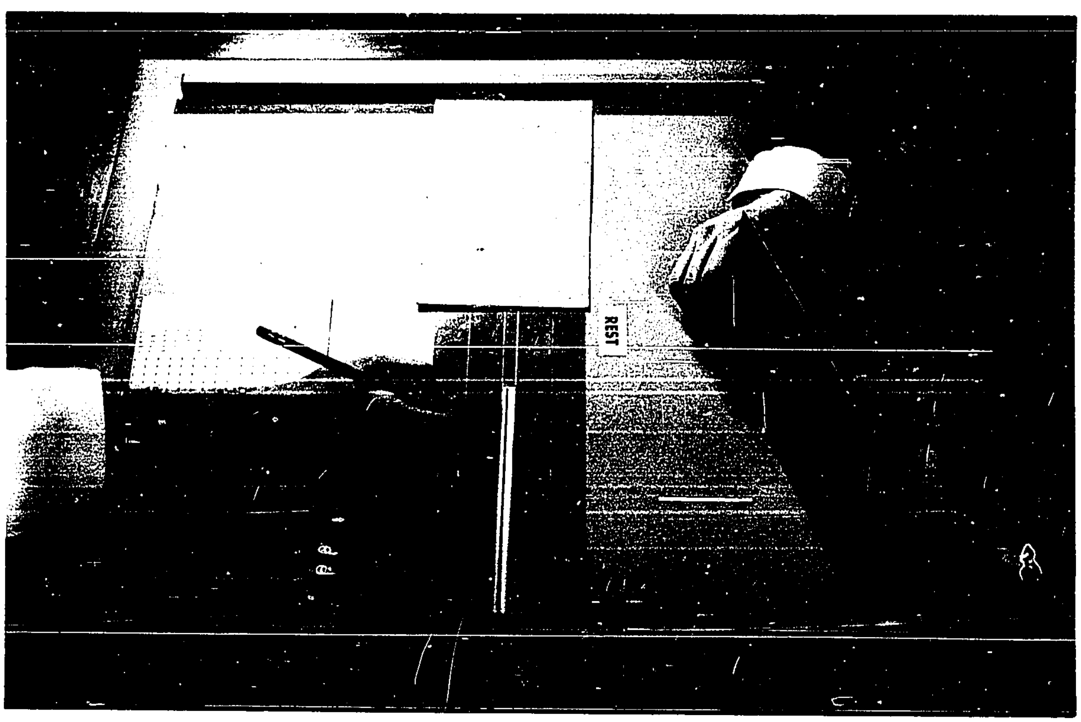
Posner Task: Experimental Design (indicating position (mm) of test stimulus from left end of line)

	Retention Interval (seconds) 6	12	24
Rest	20 60 116 161	22 73 110 165	16 70 123 175
Intepolated Activity Work	38 82 145 180	45 90 140 186	50 95 150 183

Figure 13
Posner Test Apparatus

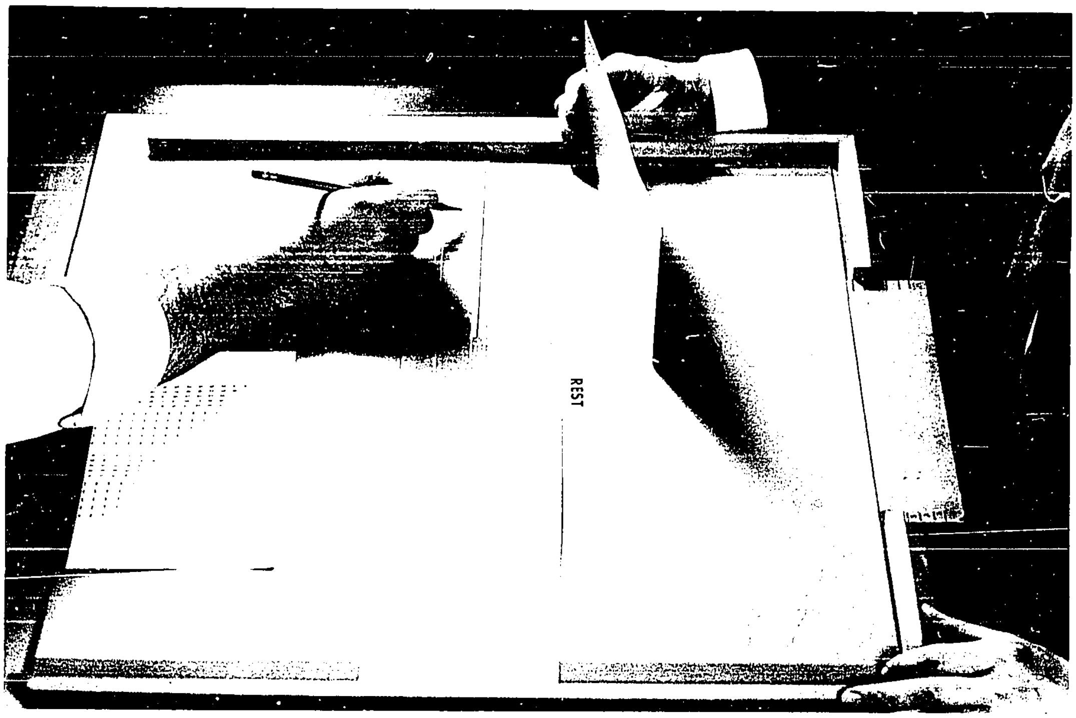


Inspection

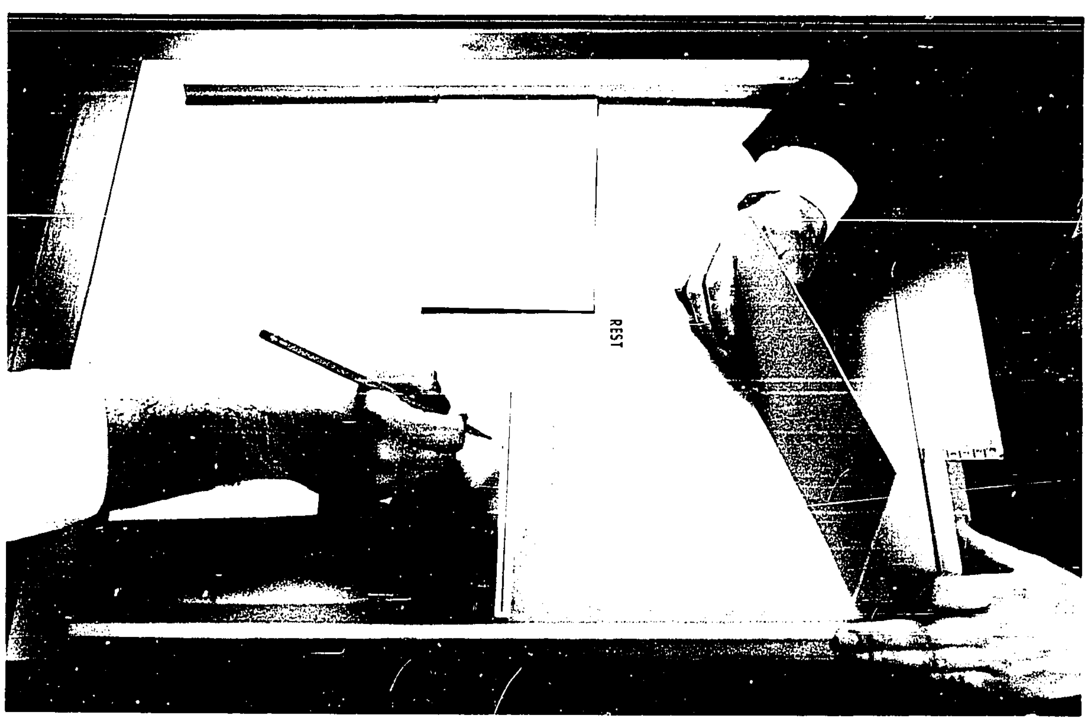


Recall

Figure 13
Posner Test Apparatus



Inspection



Recall

fixated midway between the windows. For the other half (work trials), he was required to arrange strings of 5 random digits in correct ascending order. Two scores expressed in terms of the absolute distance between the correct location of the circle and the recalled position were obtained for each subject. One score was the total error (millimetres) across the three retention intervals for the rest condition and the other was the total error across intervals for the work condition.

To date, 39 patients with right temporal-lobe excisions, 25 patients with left temporal-lobe excisions and 19 normal control subjects have been examined on this task. Mean error scores for the rest and work conditions for these groups are presented in Figure 14. As predicted, the right temporal patients show an impairment on this non-verbal recall task when compared with the left temporal patients (rest condition, $t = 3.73$, $p < .001$; work condition $t = 2.54$, $p < .01$), whose performance was normal relative to the control subjects (rest condition, $t = 0.12$, $p > .50$; work condition $t = 0.60$, $p > .50$).

Mean error scores for the four right-temporal sub-groups are given in Table 5 and their performance as a function of the retention interval is illustrated in Figure 15 for the rest condition and in Figure 16 for the work condition. In the work condition of this task, retention was progressively more impaired as the magnitude of the medial temporal-lobe removal increased. Those people with the hippocampus spared in the right hemisphere (Group I) and patients with only the

Figure 14

Recall of Visual Information (Posner Task): Mean Total Absolute Error (mm) for Work and Rest Conditions

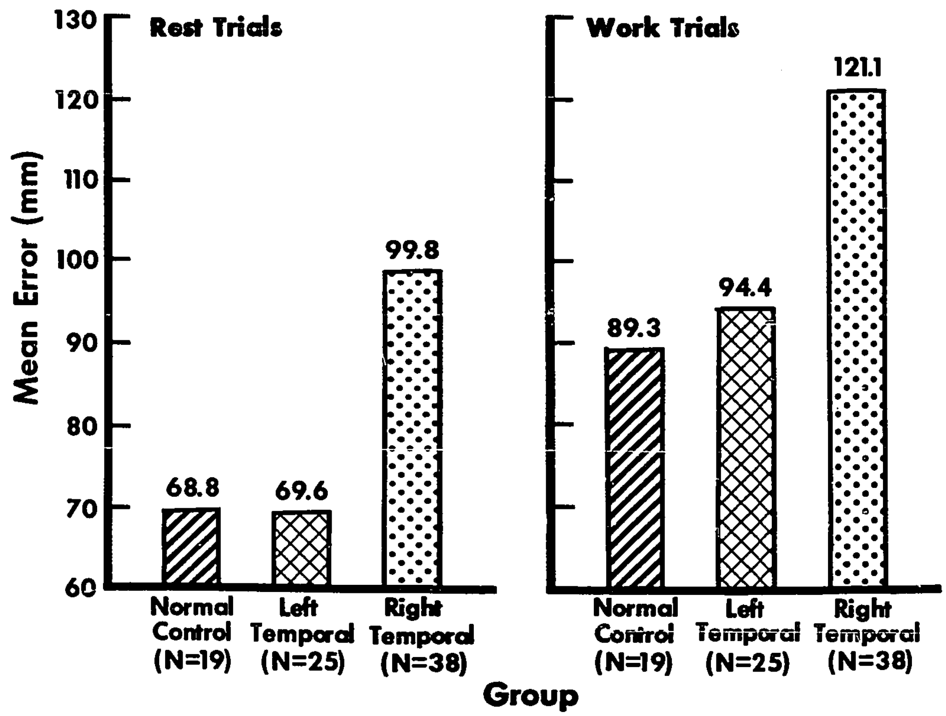


Table 5

Recall of Visual Information (Posner Task): Mean Absolute Error for Right Temporal Subgroups

Group	N	Mean Error in mm	
		Rest Trials	Work Trials
Left Temporal	25	69.6	94.4
Right Temporal I	7	93.7	99.1
Right Temporal II	14	83.6	110.4
Right Temporal III	7	93.6	125.6
Right Temporal IV	11	125.7	145.4

Figure 15

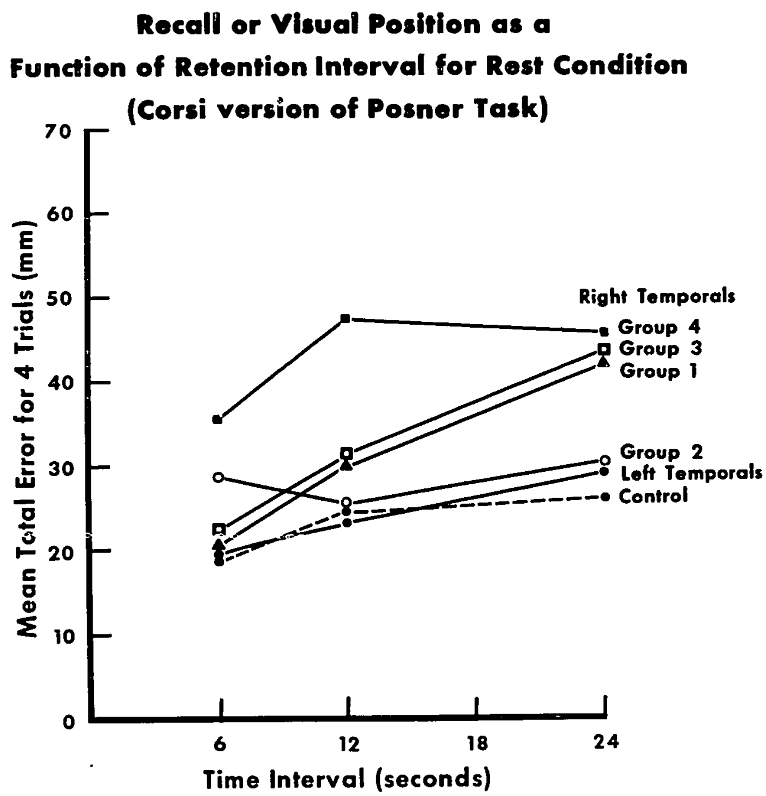
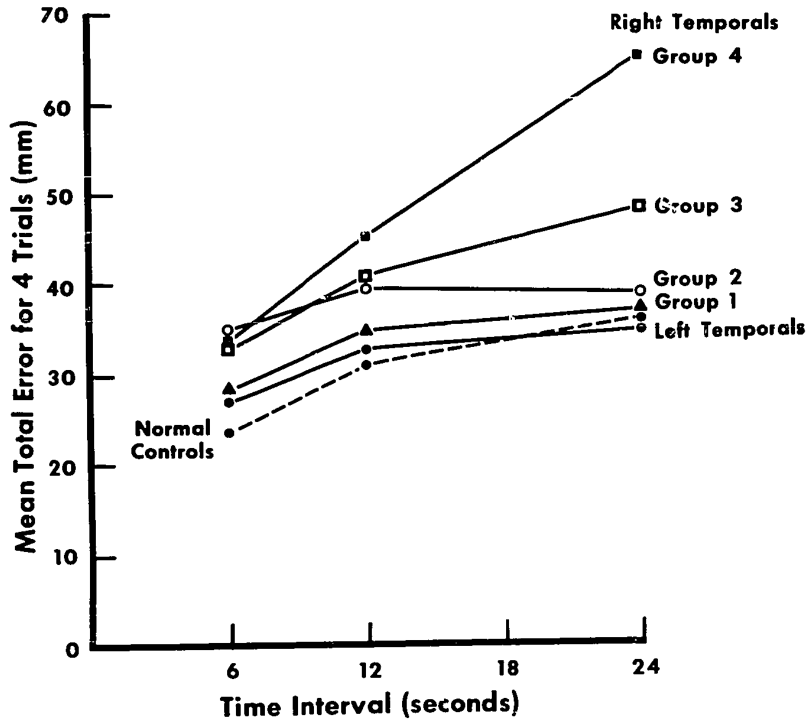

Recall or Visual Position as a
Function of Retention Interval for Rest Condition
(Corsi version of Posner Task)
Mean Total Error for 4 Trials (mm)
70
60
50
40
30
20
10
0
6
12
18
24
Time Interval (seconds)
Right Temporals
Group 4
Group 3
Group 1
Group 2
Left Temporals
Control

Figure 16

Recall of Visual Position as a Function of Retention Interval for Work Condition (Corsi version of Posner Task)



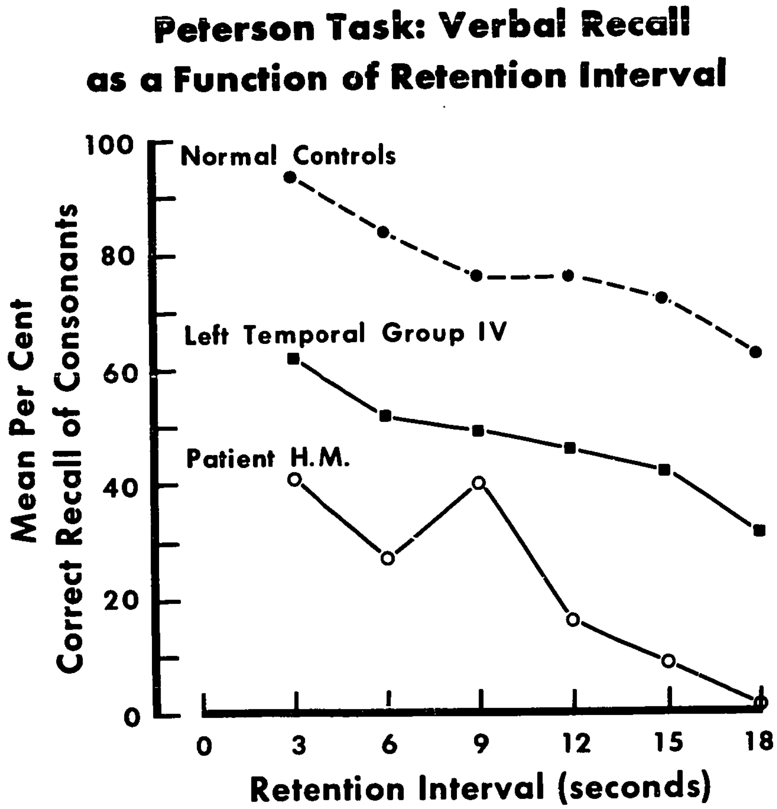
pes hippocampi excised (Group II) did not show a significant deficit when compared to the left temporal patients (Group I vs left temporals, $t = 0.25$, $p > .50$; Group II vs left temporals, $t = 1.44$, $p > .25$). However, the patients in Group III and IV with more radical excisions of the hippocampal region were impaired relative to the left temporal group (Group III vs left temporals, $t = 2.00$, $p < .05$; Group IV vs left temporals, $t = 2.96$, $p < .01$). Although the results for the rest condition are not as orderly across the right temporal sub-groups, it is nevertheless the case that the patients in Group IV with radical removals of the medial temporal region show by far the most severe impairment of recall. The more consistent relationship between performance and the extent of medial removal for the work condition is an indication of the role which intervening activity has in the disruption of non-verbal recall. Those patients with large excisions of the medial temporal-lobe structures appear to be especially susceptible to the interfering effect of distracting activity.

Test Results for Patient H.M.

For the Hebb recurring-digits task, H.M. failed to learn the recurring digit sequence (14 per cent correct) and his ability to recall immediately the supra-span non-recurring sequences was extremely impaired (12 per cent correct). Although his performance was also markedly impaired for the block-tapping task, he did show some marginal learning of the repeated block sequence (29 per cent correct). His immediate recall of the non-recurring block patterns (18 per cent correct) was somewhat better than his recall of the non-recurring digit sequences (12 per cent, as noted above). This severely impaired performance for both verbal and non-verbal learning tasks occurred in spite of his normal immediate span for digits (6) and block patterns (5).

For both formally-similar recall tasks, H.M.'s performance was markedly impaired, and at the longer retention intervals with interpolated activity the test stimuli appeared to exert little control over his responses. Figure 17 shows that his recall of consonant trigrams (Peterson task) was extremely deficient not only relative to normal control subjects but even when compared to the left temporal-lobe patients with the most radical, unilateral-hippocampal excisions. Altogether H.M. recalled 22.2 per cent of the consonants as compared to 47.7 per cent correct recall for the most impaired left temporal group. To assess the immediate registration of information for this patient, four trials were conducted at zero delay. On these trials a trigram followed by a three digit number was presented (e.g. "QZC465") and, immediately thereafter, H.M. was requested to repeat the trigram ("QZC"). For this condition, he correctly recalled 100 per cent of the consonants. It should be noted that the experimental procedure was simplified for H.M. because of his inability to remember the original test instructions. On each trial, the test material was read aloud to him and he was required to count backwards until interrupted by a gentle tap on the shoulder for recall of the consonants. Following six practice trials, H.M. remembered

Figure 17

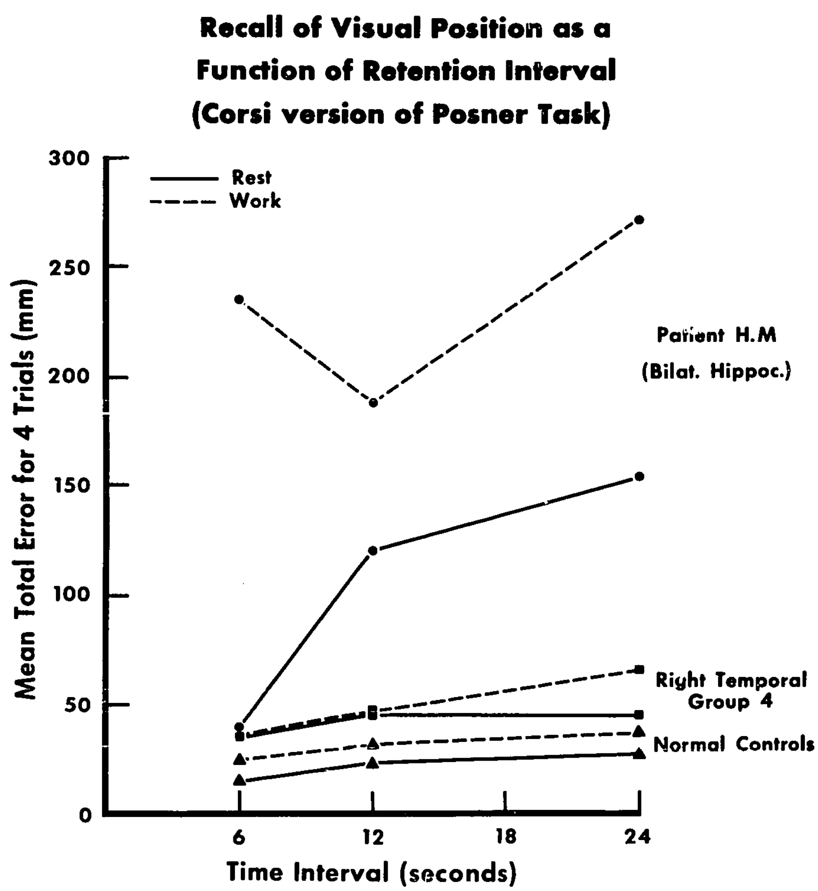

Peterson Task: Verbal Recall
as a Function of Retention Interval
Normal Controls
Left Temporal Group IV
Patient H.M.
Mean Per Cent
Correct Recall of Consonants
100
80
60
40
20
0
0
3
6
9
12
15
18
Retention Interval (seconds)

without prompting on all subsequent test trials to count backwards and then, upon interruption, to attempt the recall of "some letters." Finally, for the Posner task, he demonstrated nearly normal recall after six seconds with no distracting activity during the retention interval, however, as indicated in Figure 18, his non-verbal recall deteriorated very rapidly as the delay period increased. For the work condition with interpolated activity during the retention interval, his performance fell to a "chance" level (i.e. as estimated by the examiner – H.M.'s responses were impartial relative to the position of the test stimulus) across all three delay periods.

Discussion

The results of the experiments reported here provide further evidence of hemispheric specialization of function. The outcome for the two analogous short-term learning tasks, the Hebb recurring-digits test and the block-tapping test, demonstrates a clear double dissociation between the effects of left and right temporal-lobe lesions. The left temporal-lobe patients showed a deficit for the verbal learning task and normal performance for the non-verbal analogue, whereas the converse was evident for the right temporal-lobe patients. This same pattern of results was observed for the two formally similar tests of short-term recall. These findings are consonant with the corpus of evidence gathered from normal and clinical experiments that demonstrate the different functions of the left and right hemispheres in the mediation

Figure 18


Recall of Visual Position as a
Function of Retention Interval
(Corsi version of Posner Task)
300
250
200
150
100
50
0
Rest
Work
Patient H.M
(Bilat. Hippoc.)
Right Temporal
Group 4
Normal Controls
Mean Total Error for 4 Trials (mm)
6
12
18
24
Time Interval (seconds)

of human behavior (see Milner (1971) for the most recent review).

The principal contribution of the present study is the new finding that the severity of the material-specific memory disturbance following unilateral temporal lobectomy is directly related to the medial extent of the removal. The more extensive the surgical encroachment on the hippocampal zone in the left hemisphere, the more severe is the resulting deficit in verbal learning and retention. Similarly, the severity of the non-verbal learning and retention impairment that follows right temporal lobectomy directly depends on the extent of surgical removal in the right medial temporal region. The left temporal-lobe patients show normal performance for the non-verbal tasks, and the right temporal-lobe patients show intact learning and recall of verbal materials, regardless, in each group, of the extent of medial temporal excision. Although the hippocampus was used as the brainmark for delineating the extent of medial temporal removal, it is not suggested that this is the sole structure associated with the memory disturbances that have been reported. Rather, the entire medial aspect of the temporal region, including hippocampus and parahippocampal gyrus, is taken to be associated with the observed impairments.

It should be pointed out that the two verbal tasks employed here were presented in the auditory mode, and the two tests of non-verbal performance were given in the visual mode. An argument could therefore be made that selective impairment is specific, in the case of left temporal-lobe damage, to the auditory modality, and, in the case of right temporal-lobe damage, to the visual modality. At present, there is indeed evidence for a specific defect in acoustico-verbal memory following left posterior temporal or temporo-parietal lesions (Luria, Sokolov & Klimkowski, 1967; Warrington & Shallice, 1969; Warrington, Logue & Pratt, 1971; Luria, 1971). Nevertheless, it seems unlikely that sense modality is a critical variable in the present studies. In cases of left anterior lesions of the temporal lobe, such as those studied here, a selective impairment in verbal memory has been consistently observed regardless of whether the material is heard or read (Blakemore & Falconer, 1967; Milner, 1967). Furthermore, recognition and retention of complex auditory patterns to which a name cannot be easily given is entirely normal for patients with left temporal-lobe lesions, whereas people with right anterior temporal-lobe damage show a deficit on the same acoustic task (Shankweiler, 1966). On the basis of this evidence, it can be assumed that the impairments reported here were material- rather than modality-specific.

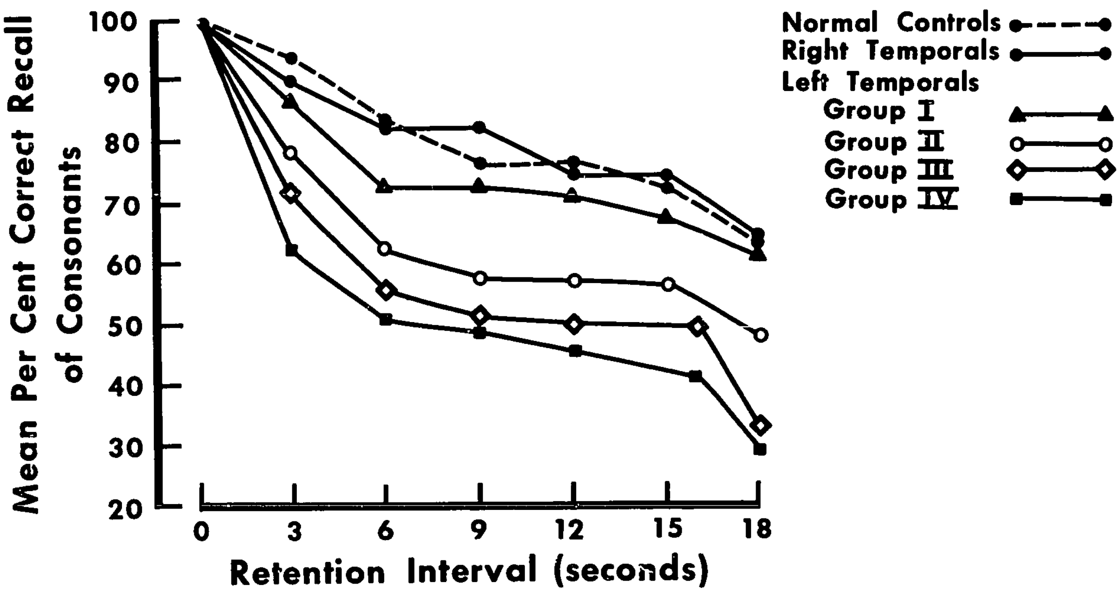
The Pattern of Memory Dysfunction

Before considering any theoretical implications of this work, it is necessary to describe more precisely the pattern of mnemonic dysfunction that emerges after both unilateral and bilateral lesions of the hippocampal region. The experiments have demonstrated that immediate memory span for verbal and non-verbal information was intact in all cases. The registration of new information seemed to occur without impedance. However, the results for the two short-term retention tasks (Peterson and Posner tests) revealed that patients with unilateral removals of the medial temporal-lobe structures were unable to hold inputs for even very short intervals, especially when the opportunities for rehearsal were restricted. Yet, for neither short-term task, was there any sharp discontinuity between the performance of people with extensive medial temporal-lobe excisions and that of normal control subjects.

It is unfortunate that immediate recall at zero delay was not formally investigated for either of the short-term retention tasks. Nevertheless, it was the case that two pretrials at zero delay were presented as practice for the Peterson test and each patient, regardless of lesion site, was able to recall correctly the consonant trigrams under this condition. As pointed out earlier, there was no significant difference in immediate memory span across the patient and control groups, and this finding lends further support to the assumption of intact registration for all subjects. If it is assumed for the Peterson task that at zero delay all subjects were recalling nearly 100 per cent of the test material, then, as indicated in Figure 19, the decay functions between zero and three seconds for the left temporal-lobe patients become progressively steeper as the medial extent of the removal increases. The primary loss for patients with radical left hippocampectomy seems to occur very early in the retention period; in fact, it occurs

Figure 19

Peterson Task: Verbal Recall as a Function of Retention Interval



as soon as attention is distracted. After three seconds the decay curves for the various patient groups run approximately parallel to each other. This phenomenon was not observed for the analogous condition of the non-verbal recall task. In fact, without any assumption about recall at zero delay, it is evident that the right temporal-lobe patients with the most extensive medial excisions (Groups 3 and 4) showed relatively more impoverished performance with increases in the retention interval beyond six seconds. Their decay functions were steeper than those of the other patient groups.

In spite of normal immediate memory, all of the temporal-lobe patients did show a significant disturbance in recalling informational sequences which barely exceeded their immediate memory span (supraspan sequences). In the unilateral cases, this disturbance was material-specific; the left temporal-lobe patients were impaired for the immediate recall of verbal, supraspan sequences (non-recurring Hebb digits) and the right temporal-lobe subjects showed a deficit in the recall of non-verbal supraspan sequences (non-recurring block patterns). For both groups of patients this abnormality was independent of the extent of medial temporal excision. However, it was found that the learning of a repeated supraspan sequence was directly related to the amount of tissue excised from the hippocampal zone.

The test results for patient H.M., who underwent bilateral resection in the medial temporal region, revealed a more severe and generalized disturbance of memory function; yet the pattern of dysfunction was similar to that observed in the cases of radical unilateral hippocampectomy. This man's immediate recall of verbal and non-verbal sequences was normal, his supraspan performance was markedly impaired and he showed little learning of the recurring, supraspan sequences. H.M. did show some marginal improvement in recall of the recurring block pattern. This finding is consistent with his ability to learn a simple maze problem (Milner, Corkin & Teuber, 1968). Moreover, it is possible that additional motor learning, which has been found to be relatively intact for this patient (Corkin, 1968), may have facilitated his performance. Still, his learning in the block-tapping task was impaired and on the analogous verbal form he showed no success whatever in retaining a repeated digit sequence. For the Posner spatial-location task, he was unable to hold non-verbal inputs for more than six seconds even when there was no interpolated activity, and his performance broke down completely when he was required to perform a distracting task during the retention interval. Finally, on the Peterson task, although H.M.'s immediate registration of the consonant trigrams was normal, his delayed recall was extremely impoverished relative even to the most impaired left temporal-lobe group, his retention of the trigrams being at chance level for intervals greater than nine seconds. Sidman, Stoddard & Mohr (1968), using a verbal memory task which involved the matching of trigrams, have demonstrated normal retention for H.M. with delays of 40 seconds. However, in their design H.M. was not distracted during the retention intervals and he succeeded by continuously rehearsing the verbal material (his lips could be seen moving throughout the delay intervals). Taken together, the results for patient H.M. indicate that the memory disturbance that follows bilateral hippocampal damage is not simply the sum of the deficits seen after unilateral left and right hippocampectomy. For three of the four experiments reported here, H.M.'s performance was markedly inferior to that of patients with radical unilateral lesions of the hippocampal zone.

The present findings are in sharp contrast to those of Baddeley and Warrington (1970). Their results are based on observations of four alcoholic, Korsakoff cases, one questionable vascular case, and "a patient with unilateral temporal lobectomy who exhibited symptoms closely analogous to H.M". They compared the performance of amnesic and control subjects on a series of retention tasks, including altered forms of the Peterson and Hebb digits tests. For their version of the Peterson task in which subjects were presented with three letter word triads and tested for recall after delays up to 60 seconds, they found no difference in the decay functions for amnesic and control groups. On their version of the Hebb recurring digits task, the amnesic patients showed at least as much learning as the control group and it was concluded either that amnesic patients are unimpaired on one type of long-term memory or else that long-term memory is not responsible for the Hebb effect.

Differing experimental procedures, in addition to the obvious and important population differences in the etiology, locus and extent of brain damage, may account for the discrepancies between the findings of Baddeley and Warrington and those reported here. First, for the Peterson task the length of the stimulus presentation period differed in the two studies. Baddeley and Warrington required their subjects to read word triads aloud and exposed the verbal material for four seconds after it was read (total exposure, nearly eight seconds). In the present study three consonants of low association value were read to the subject at the rate of one consonant per second (total exposure, three seconds) and he was instructed not to repeat the trigram aloud. Thus, Baddeley and Warrington presented more meaningful material for a longer period with more opportunity for rehearsal and all of these procedures may have inflated retention scores relative to the present study. For the Hebb recurring digits task, these authors presented the recurring digit sequence on every other trial, whereas, on the form reported here, the recurring sequence was presented every third trial. However, even with the more frequent presentation of the recurring sequence, Baddeley and Warrington failed to demonstrate a clear-cut learning effect for either their control subjects or amnesic patients. This lack of effect probably resulted from the presentation of digit sequences (eight digits long) which were far in excess of the immediate memory span of most of their subjects. In the present study, task difficulty was made constant across subjects by selecting sequences which were one digit beyond each subject's immediate span. Although it is true that the amnesic patients tested by Baddeley and Warrington showed "at least as much learning as the control group," this comparison is misleading because neither group demonstrated any significant learning. In spite of these differences in method, it is the case that the patients studied here who underwent unilateral hippocampectomy and who did not demonstrate clinically diagnosed amnesia, nevertheless showed material-specific deficits on the same short-term retention tasks used by Baddeley and Warrington. Unfortunately, these authors do not present separate results for their patient M.T. who supposedly shows symptoms analogous to patient H.M. and therefore no direct comparison is possible.

The results of another recent study (Samuels, Butters, Goodglass & Brody, 1971), while consonant with an earlier report of the present work (Corsi, 1969), are in apparent conflict with the findings of Baddeley and Warrington. Using a series of short-term retention tasks, including a form of the Peterson test, Samuels et al. found a severe impairment in the verbal recall of 13 patients with Korsakoff's disease and they concluded that Korsakoff patients cannot retain inputs beyond a few seconds even when the stimulus material is properly registered. This finding is consistent with Talland's (1965) observation that Korsakoff patients forget as soon as their attention is diverted from the material-to-be-memorized. Finally, Cermak, Butters & Goodglass (1971), who also used the Peterson technique with a design similar to that of Baddeley and Warrington, have demonstrated a retention impairment for Korsakoff patients, regardless of the degree of difficulty or amount of material presented. These authors suggest that Baddeley and Warrington may not have controlled the performance of the distracting task rigorously enough to prevent rehearsal during the retention intervals and that this factor may account for the unimpaired performance of their patients.

Theoretical Implications

At present, the literature of psychology is profuse with theoretical models of human memory (e.g. Atkinson & Shiffrin, 1968; Norman, 1970; Tulving & Madigan, 1970). Some authors view memory as a single, continuous system (Melton, 1963; Bernbach, 1970; Murdock, 1970). Others distinguish two separate aspects of human memory; a labile, "short-term" storage system and a more permanent, "long-term" memory (Waugh & Norman, 1965; Glanzer & Cunitz, 1966; Atkinson & Shiffrin, 1968). Still others regard the dual storage models as too crude and suggest a third, intermediate-term memory system (Wickelgren, 1970). With respect to the problem of forgetting, some theorists hold that items decay with the passage of time (Brown, 1958; Broadbent, 1963) and others claim that interference from the presentation of other material is the cause of forgetting (Underwood & Postman, 1960; Postman, 1961).

To date, the study of patients with brain damage has already had some impact on general notions about the structure and processes of human memory. The present findings are particularly relevant to theoretical issues concerning the organization of memory storage and the role of interference in forgetting. The term "short-term retention" has been used here principally to describe the experimental tasks which involved short recall intervals (Peterson & Posner tasks). In the psychological literature, short-term memory has often been used in a rather different sense to indicate a distinct process which is presumed to underly performance. To avoid possible future confusions, the convention suggested by Waugh & Norman (1965) of the term "primary memory" in place of "short-term memory" and "secondary memory" in place of "long-term memory" as hypothetical constructs is adopted. Whether or not the short-term retention tasks employed here bridge the various storage systems which have been proposed by memory theorists is still an open experimental question.

The test results for patient H.M., with bilateral destruction of the hippocampal zone, suggest a distinction between a temporary storage system (primary memory) and a more permanent store (secondary memory). This man showed normal immediate recall and intact non-verbal recall up to six seconds, and yet he demonstrated an inability to learn supraspan sequences over many repetitions. This finding corresponds with Wickelgren's (1968) observation of normal primary memory for this patient. In this case, it seems that the essential transition process from primary memory to more stable secondary memory was absent, at least for the encoding of verbal information. Milner (1968) has pointed out that H.M.'s anterograde amnesia cannot be accounted for simply in terms of a lack of adequate strategies for memorization. Milner has observed that no amount of previous rehearsal benefits H.M. and other amnesic subjects once their attention is diverted, whereas it may facilitate the acquisition of secondary memory traces for normal subjects (Waugh & Norman, 1965). This same disruption of trace consolidation, although material-specific and less severe, appears to underlie the learning impairment for patients with radical unilateral hippocampectomy.

The evidence from the present experiments suggests that the observed memory defects were not simply the result of increased, spontaneous trace decay but also the consequence of heightened susceptibility to the effects of interfering activity. In particular, for the Peterson task patients with extensive removals in the left medial temporal region were found to be especially sensitive to the interfering effect of interpolated activity which presumably prevented rehearsal and proper organization of the material-to-be-remembered. For patient H.M. the recall of consonants was even more acutely disrupted by interpolated activity, whereas, on a similar verbal task without distraction, H.M.'s retention has been found to be intact (Sidman, Stoddard & Mohr, 1968). The fact that on the Posner task a more consistent relationship between impaired retention and the extent of right medial-temporal removal was found for the work condition than for the rest condition is a further indication of the potent role which intervening activity has in the disruption of recall.

An Interpretation of the Hippocampal Defect

At what phase in the sequence of events presumed to underlie normal memory, namely registration, consolidation, information storage, and retrieval does interference interrupt the performance of amnesic subjects? The explanation favoured here was first formulated by Milner (1968) in terms of a consolidation defect – the failure to achieve any stable memory trace. Müller and Pilzecker (1900), in their original proposal of the consolidation process, suggested that information storage is the result of neural processes which must persist for some time after experience. The longer neural activity continues, the more permanent the memory traces become, and it follows that if the neural activity is interrupted the memory traces are either completely displaced and "forgotten" or attenuated and only partially "remembered." Milner has proposed that in cases of bilateral hippocampal lesions this consolidation process is selectively disturbed and new experiences become acutely vulnerable to interference. Warrington & Weiskrantz (1970) have put forth an interpretation of the amnesic syndrome in terms of interference and disinhibition as an alternative to the consolidation hypothesis. Using the technique of partial information, these authors have demonstrated that for Korsakoff patients retention depends more on the method of retrieval than on the method of acquisition. Like Milner, Warrington & Weiskrantz emphasize the crucial effect of interference, but they attribute the memory disturbance of amnesic patients to defective retrieval rather than impaired storage.

These alternate interpretations may at least partially be the consequence of impressions formed from the study of patients with neurological conditions of different aetiology and cerebral location. To date, reviews of memory loss after brain damage (Whitty & Lishman, 1966; Brierley, 1966; Ojemann, 1966) have served mainly to point out the diversity of amnesic effects and to illustrate the considerable range, both in type and severity, of memory dysfunction that may occur after lesions of different origin and locus. At present, there is specific evidence for a qualitative distinction between memory defects associated with Korsakoff's disease and those seen in patients with bilateral hippocampal lesions. Lhermitte & Signoret (1972) have shown that Korsakoff patients with presumed lesions of the mammillary bodies and medial thalamus were more impaired on a sequential learning task than patients with bilateral hippocampal lesions. On this task, which required the recall of subspan sequences of words, the Korsakoff patients appeared to be especially vulnerable to the interfering effect of previously presented material. On the other hand, the hippocampal patients showed a severe impairment for the retention of supra-span spatial information relative to the Korsakoff patients. On this rather different memory task, which was specifically designed to rule out, as far as possible, any interference from previous responses, the Korsakoff patients showed near normal recall despite denying having seen the test material before. These findings suggest that the retrieval of information may be selectively disturbed for people with Korsakoff's disease, whereas, in the case of bilateral hippocampal damage, the capacity for permanent storage of new information is disrupted.

It has been proposed here that for people with large unilateral lesions of the hippocampal zone (in addition to anterior temporal lobectomy), the material-specific memory loss is also the consequence of a consolidation rather than a retrieval defect. In the case of left medial temporal damage, the consolidation of verbal information is specifically disrupted, and for corresponding excisions of the right hemisphere, the trace formation of non-verbal impressions is affected. Evidence in support of this position comes from an analysis of the results for the two analogous learning tasks. If it is assumed that patients with extensive medial temporal removals were more susceptible to proactive interference during the retrieval stage, then they should demonstrate more impoverished recall of the non-recurring, supraspan sequences than other patients in whom the hippocampal zone was spared. However, this is not the case; for there was no significant variation across the various temporal-lobe groups with respect to recall of either verbal or non-verbal, supraspan sequences. Furthermore, the patients with unilateral hippocampal damage were not any more vulnerable to proactive interference than normal control subjects. For the Hebb digits task, a simple ratio reflecting the effect of proactive interference in the recall of non-recurring sequences was the same (.71) for the control subjects and left temporal-lobe patients with large hippocampal lesions (Group III + Group IV). This proportion was obtained by totalling the number of correct non-recurring sequences across subjects for the last half of the test (the last eight presentations of the non-recurrent items) and dividing this sum by the total number of correct sequences for the first half of the test (the first eight presentations of the non-recurrent items). An analogous comparison for the block tapping task indicated that the right temporal lobe patients (Group III + Group IV) were somewhat less prone to interference from previous material (.61) than control subjects (.49). Nevertheless, these same people with unilateral lesions of the hippocampal zone showed a marked, material-specific deficit in the cumulative learning of a recurring sequence relative to control subjects and patients without hippocampal involvement, and this finding favors the notion of a selective interruption in the consolidation of traces.

At the physiological level, little is known of the role of the hippocampal system in the establishment of secondary memory traces. From a structural point of view, there is general agreement that the hippocampus is not the locus of the changes which correspond to lasting memories (Green, 1964; Ojemann, 1966; Milner, 1970). Present evidence from neuro-behavioral (Grastyan & Karmos, 1962; Douglas & Pribram, 1966; Douglas, 1967) and electrophysiological studies (Adey, Segundo

& Livingstone, 1957) suggests that hippocampal inhibitory activity during acquisition, by blocking the transmission of irrelevant sensory impulses to higher centres, is critical to engram formation at the neocortical level. This notion is at least consistent with the consolidation hypothesis according to which new experience is especially susceptible to interference and some time is required for the permanent storage of information. It has also been proposed (Sweet, Talland & Erwin, 1959; Kahn & Crosby, 1972) that the hippocampal system might operate to prime activity in cortical sites where storage is taking place.

It is possible that in the early stages of learning, the hippocampal system activates cortical areas, and thereby "helps" to establish the neural representation of a salient input; whereas, during later stages of the learning process, it inhibits interference from new sensory impulses. However, the body of present evidence is more supportive of a strictly inhibitory function for this region. A recent neuroanatomical study (Van Hoesen, Pandya & Butters, 1972) has demonstrated that the hippocampus in connection with the entorhinal cortex receives afferent information from the temporal cortex which is a probable multisynaptic link joining the classical sensory areas of the cortex to the limbic system. Upon the reception of afferent impulses from the temporal cortex indicating the "significance" of a new input, the hippocampus might be set to inhibit the further conduction of non-specific inputs through the ascending reticular activating system. In this way, hippocampal inhibitory activity could selectively protect an ongoing excitatory process in the cortex long enough for its consolidation. This speculation is supported by some electrophysiological evidence (Livingstone, 1959) and is consistent with a more elaborate model (Douglas & Pribram, 1966). It still remains more conceptual than physiological, and very rudimentary on both levels. More refined notions await detailed electrophysiological studies of man in the process of learning and remembering.

Practical Considerations

Whatever the contribution of these experiments to the refinement of theoretical ideas, their clinical significance is evident here and now. At present, temporal-lobe surgery is being performed for the relief of focal, cerebral seizures and the control of violent or psychotic behavior. Neurosurgeons are apprised of the critical role which each medial temporal region plays in the memorization process. Their patients who elect brain surgery should have some notion of the psychological impairments which may result. It is not an easy task to inform sick people who are seeking "a cure" for their illness about the negative aspects of surgical intervention. Yet, the evidence of memory loss after unilateral temporal lobectomy is clear and the communication of this information to surgical candidates would seem essential. The brief tests of short-term retention and learning employed here may also be helpful in the differential diagnosis of neurological disturbances. In particular, the Hebb digits task and block tapping analogue provide a nice means of assessing immediate memory span, supraspan recall and cumulative learning for both verbal and non-verbal material.

References

Adey, W. R., Segundo, J. P. & Livingstone, R. B. Corticifugal influences on intrinsic brainstem conduction in cat and monkey. J. Neurophysiol., 1957, 20, 1-16.

Atkinson, R. C. & Shiffrin, R. M. Human memory: A proposed system and its control processes. In Spence, K. W. & Spence, J. T. (Eds.), The psychology of learning and motivation, Vol. 2, New York: Academic Press, 1968, Pp. 89-195.

Baddeley, A. D. & Warrington, E. K. Amnesia and the distinction between long- and short-term memory. J. Verb. Learn. Verb. Behav., 1970, 9, 176-189.

Bernbach, H. A. A multiple-copy model for postperceptual memory. In Norman, D. A. (Ed.), Models of human memory. New York: Academic Press, 1970, Pp. 103-116.

Blakemore, C. B. & Falconer, M. A. Long-term effects of anterior temporal lobectomy on certain cognitive functions. J. Neurol. Neurosurg. Psychiat., 1967, 30, 364-367.

Brierley, J. B. The neuropathology of amnesic states. In Whitty, C. W. M. & Zangwill, O. L. (Eds.), Amnesia. London: Butterworth, 1966, Pp. 150-180.

Broadbent, D. E. Flow of information within the organism. J. Verb. Learn. Verb. Behav., 1963, 2, 34-39.

Brown, J. Some tests of the decay theory of immediate memory. Quart. J. exp. Psychol., 1958, 10, 12-21.

Cermak, L. S., Butters, N. & Goodglass, H. The extent of memory loss in Korsakoff patients. Neuropsychologia, 1971, 9, 307-316.

Cordeau, J. P. & Mahut, H. Some long-term effects of temporal lobe resections on auditory and visual discrimination in monkeys. Brain, 1964, 87, 177-188.

Corkin, Suzanne. Tactually-guided maze-learning in man: Effects of unilateral cortical excisions and bilateral hippocampal lesions. Neuropsychologia, 1965, 3, 339-351.

Corkin, S. Acquisition of motor skill after bilateral medial temporal-lobe excision. Neuropsychologia, 1968, 6, 255-266.

Correll, R. E. & Scoville, W. B. Performance on delayed match following lesions of medial temporal structures. J. comp. physiol. Psychol., 1965, 60, 360-367.

Correll, R. E. & Scoville, W. B. Significance of delay in the performance of monkeys with medial temporal lobe resections. Expl. Brain Res., 1967, 4, 85-96.

Corsi, P. M. Verbal memory impairment after unilateral hippocampal excisions. Paper presented at the 40th Annual Meeting of the Eastern Psychological Association, Philadelphia, April 1969.

Dorff, J. E. The effect of combined subcortical lesions in monkeys on delayed alternation, visual discrimination and extinction of a bar-pressing response. Unpublished Ph.D. Thesis, Catholic University, 1964.

Douglas, R. J. The hippocampus and behavior. Psychol. Bull., 1967, 67, 416-442.

Douglas, R. J. & Pribram, K. H. Learning and limbic lesions. Neuropsychologia, 1966, 4, 197-220.

Drachman, D. A. & Arbit, J. Memory and the hippocampal complex. Arch. Neurol., 1966, 15, 52-61.

Drachman, D. A. & Ommaya, A. K. Memory and the hippocampal complex. Arch. Neurol., 1964, 10, 411-425.

Glanzer, M. & Cunitz, A. R. Two storage mechanisms in free recall. J. Verb. Learn. Verb. Behav., 1966, 5, 351-360.

Grastyan, E. & Karmoz, G. The influence of hippocampal lesions on simple and delayed instrumental conditioned reflexes. In Physiologie de l' Hippocampe. Paris: Centre National de la Recherche Scientifique, 1962, Pp. 225-234.

Green, J. D. The Hippocampus. Physiological Reviews, 1964, 44, 561-608.

Hebb, D. O. Distinctive features of learning in the higher animal. In Delafresnay, J. F. (Ed.), Brain mechanisms and learning. London & New York: Oxford University Press, 1961, Pp. 37-51.

Iversen, S. D. & Weiskrantz, L. An investigation of a possible memory defect produced by inferotemporal lesions in the baboon. Neuropsychologia, 1970, 8, 21-36.

Iwai, E. & Mishkin, M. Further evidence on the locus of the visual area in the temporal lobe of the monkey. Exp. Neurol., 1969, 25, 585-594.

Iwai, E. & Mishkin, M. Two visual foci in the temporal lobe of monkeys. In Yoshii, M. & Buchwald, M. A. (Eds.), Neurophysiological basis of learning and behavior. Osaka: Osaka University Press, 1968.

Kahn, E. A. & Crosby, E. C. Korsakoff's syndrome associated with surgical lesions involving the mammillary bodies. Neurology, 1972, 22, 117-125.

Kimura, Doreen. Right temporal-lobe damage. Arch. Neurol., 1963, 8, 264-271.

Konorski, J. A new method of physiological investigation of recent memory in animals. Bull. Acad. Pol. Sci., 1959, 7, 115-117.

Lhermitte, F. & Signoret, J. L. Analyse neuropsychologique et dissociation des syndromes amnesiques. Unpublished manuscript. Groupe de Recherches Neuropsychologiques, Paris, 1972.

Livingstone, R. B. Hippocampus and higher nervous activity. In Brazier, M. A. B. (Ed.), The central nervous system and behavior (2nd conference). New York: Josiah Macy, Jr. Foundation, 1959, Pp. 153-156.

Luria, A. R. Memory disturbances in local brain lesions. Neuropsychologia, 1971, 9, 367-375.

Luria, A. R., Sokolov, E. N. & Klimkowski, M. Towards a neurodynamic analysis of memory disturbances with lesions of the left temporal lobe. Neuropsychologia, 1967, 5, 1-11.

Mahut, H. Spatial and object reversal learning in monkeys with partial temporal lobe ablations. Neuropsychologia, 1971, 9, 409-424.

Mahut, H. & Cordeau, J. P. Spatial reversal deficit in monkeys with amygdalohippocampal ablations. Expl. Neurol., 1963, 7, 426-434.

Melton, A. W. Implications of short-term memory for a general theory of memory. J. Verb. Learn. Verb. Behav., 1963, 2, 1-21.

Meyer, V. & Yates, A. J. Intellectual changes following temporal lobectomy for psychomotor epilepsy. J. Neurol. Neurosurg. Psychiat., 1955, 18, 44-52.

Milner, Brenda. Psychological defects produced by temporal-lobe excision. Res. Publs. Ass. Res. nerv. ment. Dis., 1958, 36, 244-257.

Milner, Brenda. Les troubles de la mémoire accompagnant des lésions hippocampiques bilatérales. In Physiologie de l'Hippocampe, Paris, Centre National de la Recherche Scientifique, 1962, Pp. 257-272.

Milner, Brenda. Visually-guided maze learning in man: Effects of bilateral hippocampal, bilateral frontal, and unilateral cerebral lesions. Neuropsychologia, 1965, 3, 317-338.

Milner, Brenda. Amnesia following operation on the temporal lobes. In Whitty, C. W. M. & Zangwill (Eds.), Amnesia. London: Butterworths, 1966, Pp. 109-133.

Milner, Brenda. Brain mechanisms suggested by studies of temporal lobes. In Darley, F. L. (Ed.), Brain mechanisms underlying speech and language. New York: Grune & Stratton, 1967, Pp. 122-145.

Milner, Brenda. Disorders of memory after brain lesions in man. Neuropsychologia, 1968, 6, 175-179.

Milner, Brenda. Visual recognition and recall after right temporal-lobe excisions in man. Neuropsychologia, 1968, 6, 191-210.

Milner, Brenda. Memory and the medial temporal regions of the brain. In Pribram, K. H. & Broadbent, D. E. (Eds.), _Biology of memory_. New York: Academic Press, 1970, 29-50.

Milner, Brenda. Interhemispheric difference in the localization of psychological processes in man. _Brit. Med. Bull._, 1971, _27_, 272-277.

Milner, Brenda, Corkin, Suzanne & Teuber, H.-L. Further analysis of the hippocampal amnesic syndrome. _Neuropsychologia_, 1968, _6_, 267-282.

Milner, Brenda & Kimura, Doreen. Dissociable visual learning defects after unilateral temporal lobectomy in man. Paper presented at 35th Annual Meeting of the Eastern Psychological Association, Philadelphia, April, 1964.

Milner, Brenda & Taylor, L. Right-hemisphere superiority in tactile pattern-recognition after cerebral commissurotomy: evidence for nonverbal memory. _Neuropsychologia_, 1972, _10_ (in press).

Milner, Brenda & Teuber, H.-L. Alterations of perception and memory in man: Reflections on methods. In Weiskrantz, L. (Ed.), _Analysis of behavioral change_. New York: Harper & Rowe, 1968, Pp. 268-375.

Mishkin, M. Visual discrimination performance following partial ablations of the temporal lobe II. Ventral surfaces vs hippocampus. _J. comp. physiol. Psychol._, 1954, _47_, 187-193.

Mishkin, M. & Pribram, K. H. Visual discrimination performance following partial ablations of the temporal lobe. Ventral vs lateral. _J. comp. physiol. Psychol._, 1954, _47_, 14-20.

Müller, G. E. & Pilzecker, A. Experimentelle Beiträge zur Lehre vom Gedächtnis. _Z. Psychol._, 1900, _1_, 1-288.

Murdock, B. B. Short-term memory for associations. In Norman, D. A. (Ed.), *Models of human memory*. New York: Academic Press, 1970, Pp. 285-304.

Norman, D. A. (Ed.), *Models of human memory*. New York: Academic Press, 1970.

Ojemann, R. G. Correlations between specific human brain lesions and memory changes. *Neurosciences Res. Prog. Bull.*, 1966, *4*, 1-70.

Orbach, J., Milner, B. & Rasmussen, T. Learning and retention in monkeys after amygdala-hippocampus resection. *A.M.A. Arch. Neurol.*, 1960, *3*, 230-251.

Penfield, W. & Milner, Brenda. Memory deficit produced by bilateral lesions in the hippocampal zone. *A.M.A. Arch. Neurol. Psychiat.*, 1958, *79*, 475-497.

Peterson, L. R. & Peterson, M. S. Short-term retention of individual verbal items. *J. Exp. Psychol.*, 1959, *58*, 193-198.

Posner, M. I. Components of skilled performance. *Science*, 1966, *152*, 1712-1718.

Posner, M. I. & Konick, A. F. Short-term retention of visual and kinesthetic information. *Organizational Behavior and Human Performance*, 1966, *1*, 71-86.

Postman, L. The present status of interference theory. In Cofer, C. N. (Ed.), *Verbal learning and verbal behavior*. New York: McGraw-Hill, 1961, Pp. 152-179.

Prisko, Lilli. *Short-term memory in focal cerebral damage*. Unpublished Ph.D. thesis, McGill University, 1963.

Samuels, Ina, Butters, N., Goodglass, H. & Brody, Betty. A comparison of subcortical and cortical damage on short-term visual and auditory memory. Neuropsychologia, 1971, 9, 293-306.

Scoville, W. B. Amnesia after bilateral mesial temporal-lobe excision: Introduction to case H.M. Neuropsychologia, 1968, 6, 211-213.

Scoville, W. B. & Milner, Brenda. Loss of recent memory after bilateral hippocampal lesions. J. Neurol. Neurosurg. Psychiat., 1957, 20, 11-21.

Shankweiler, D. Defects in recognition and reproduction of familiar tunes after unilateral temporal lobectomy. Paper presented at 37th Annual Meeting of the Eastern Psychological Association, New York, April, 1966.

Sidman, M., Stoddard, L. T. & Mohr, J. P. Some additional quantitative observations of immediate memory in a patient with bilateral hippocampal lesions. Neuropsychologia, 1968, 6, 245-254.

Sweet, W. H., Talland, G. A. & Ervin, F. R. Loss of recent memory following section of the fornix. Trans. Amer. Neurol. Ass., 1959, 84, 76-82.

Talland, G. Deranged memory. New York: Academic Press, 1965.

Tulving, E. & Madigan, S. A. Memory and verbal learning. In Mussen, P. H. & Rosenzweig, M. R. (Eds.), Annual review of psychology, Vol. 21. Palo Alto: Annual Reviews Inc., 1970, Pp. 437-484.

Underwood, B. J. & Postman, L. Extraexperimental sources of interference in forgetting. Psychol. Rev., 1960, 67, 73-95.

Van Hoesen, G. W., Pandya, D. N. & Butters, N. Cortical afferents to the entorhinal cortex of the rhesus monkey. Science, 1972, 175, 1471-1473.

Wada, J. A new method for the determination of the side of cerebral speech dominance: a preliminary report on the intracarotid injection of sodium Amytal in man. Medicine and Biology, 1949, 14, 221-222.

Warrington, Elizabeth & James, M. An experimental investigation of facial recognition in patients with unilateral cerebral lesions. Cortex, 1967, 3, 317-326.

Warrington, E. K., Logue, V. & Pratt, R. T. C. The anatomical localization of selective impairment of auditory short-term memory. Neuropsychologia, 1971, 9, 377-387.

Warrington, E. K. & Shallice, T. The selective impairment of auditory verbal short-term memory. Brain, 1969, 92, 885-896.

Warrington, Elizabeth K. & Weiskrantz, L. New method of testing long-term retention with special reference to amnesic patients. Nature, 1968, 217, 972-974.

Warrington, Elizabeth K. & Weiskrantz, L. Amnesic syndrome: consolidation or retrieval? Nature, 1970, 228, 628-630.

Waugh, N. C. & Norman, D. A. Primary memory. Psychol. Rev., 1965, 72, 89-104.

Waxler, M. & Rosvold, H. E. Delayed alternation in monkeys after removal of the hippocampus. Neuropsychologia, 1970, 8, 137-146.

Wechsler, David. The measurement of adult intelligence. Baltimore: The Williams & Wilkins Company, 1944, p.176.

Whitty, C. W. M. & Lishman, W. A. Amnesia in cerebral disease. In Whitty, C. W. M. & Zangwill, O. L. (Eds.), Amnesia. London: Butterworth, 1966, Pp. 36-76.

Wickelgren, W. A. Sparing of short-term memory in an amnesic patient: implications for strength theory of memory. Neuropsychologia, 1968, 6, 235-244.

Wickelgren, W. A. Multitrace strength theory. In Norman, D. A. (Ed.), Models of human memory. New York: Academic Press, 1970, Pp. 65-102.

Williams, H. L., Beaver, W. S., Spence, M. T. & Rundell, O. H. Digital and kinesthetic memory with interpolated information processing. J. Exp. Psychol., 1969, 80, 530-536.

Witmer, L. R. The association value of three place consonant syllables. J. genet. Psychol., 1935, 47, 337-360.