EFFECTS OF MEDIAL TEMPORAL-LOBE LESIONS
ON INTERMEDIATE-MEMORY IN MAN

by

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READ Ph.D.

Hippocampal contribution to intermediate-memory in man

Ph.D. Psychology

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A word-generation experiment explored the relative contributions of the left temporal (LT) neocortex and the left hippocampal region to verbal recall. Patients with large left hippocampal excisions (LTH) were impaired in immediate recall of synonyms, whereas those with small hippocampal excisions (LTh) were not. Both groups were impaired in immediate recall of rhymes, and in delayed recall of both synonyms and rhymes. A nonverbal associative-learning task, where the stimulus-items came from a visual continuum, also resulted in a deficit for the LTH (but not the LTh) group. Patients with right-temporal lobectomy performed both tasks normally. On an absolute-judgement task involving the accurate numbering of a set of six individually presented rectangles, only the groups of patients with large hippocampal excisions were impaired, regardless of side of lesion. These findings support the view that the temporal neocortex is important for gaining access to information in semantic memory, whereas the hippocampal region is essential for the temporary retention of new information beyond the span of immediate memory.

Ph.D. Psychologie

Donald E. Read

EFFETS DES LÉSIONS DE LA PARTIE MÉDIANE DU LOBE TEMPORAL SUR LA MÉMOIRE INTERMÉDIARE CHEZ L'HOMME

Résumé

A partir d'une expérience impliquant la production de mots, on a étudié l'apport relatif du néocortex temporal et de l'hippocampe gauches au rappel verbal. Des patients ayant subi de larges excisions de l'hippocampe (TGH) se sont révélés déficients dans le rappel immédiat de synonymes, mais tel n'a pas été le cas de ceux qui avaient subi de petites excisions de l'hippocampe (TGh). Les deux groupes ont eu une performance réduite dans le rappel immédiat de rimes et dans le rappel différé de synonymes et de rimes. On a aussi observé une déficience chez le group TGH (et non chez le groupe TGh) lors d'une tâche non verbale d'apprentissage par association, où les stimuli provenaient d'un ensemble d'éléments visuels homogènes. Les patients ayant subi une lobectomie temporale droite ont accompli les deux tâches normalement. Quant à une tâche exigeant un jugement absolu, et impliquant le dénombrement précis d'un ensemble de six rectangles présentés séparément, seuls les groupes de patients ayant subi de larges excisions de l'hippocampe se sont révélés déficients, et ce, indépendemment du côté de la lésion. Ces résultats tendent à démontrer que le néocortex temporal joue un rôle important dans l'obtention d'informations contenues dans la mémoire sémantique, alors que la région de l'hippocampe est essentielle pour l'emmagasinage temporaire de renseignements nouveaux, dépassant la durée de la mémoire immédiate.

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It is by now generally accepted that our ability to understand the world around us depends to a great extent upon what we already know about that world, the general knowledge that is stored in what has been termed "semantic memory" (Tulving, 1972). We recognize new things in terms of their similarity to, or difference from, things already known (Bruner, 1957; Piaget, 1954). Moreover, how well we understand these new things plays a major role in determining how well we are able to remember them later (Bartlett, 1932; Bransford, Barclay & Franks, 1972, Craik & Lockhart, 1972). These working hypotheses, about the interaction between perception and memory, have been formalized in current theories of how people (and by inference, their central nervous systems) process information (e.g., Atkinson & Shiffrin, 1968, 1971; Baddeley, 1976; Baddeley & Hitch, 1974, 1977; Lindsay & Norman, 1972; Norman, 1969; Shiffrin, 1976).

The distinction, made many years ago (James, 1890), between the maintenance of knowledge that is still in conscious awareness (primary, or short-term, memory) and the storage of knowledge that can be recalled after a delay (secondary, or long-term, memory) was revived in early theories of information processing (e.g., Broadbent, 1958). Unfortunately, these terms later came to be used to refer both to experimental situations where recall or recognition was tested, and to hypothetical storage processes. In order to avoid this ambiguity, the expressions short-term memory (STM) and long-term memory (LTM) were adopted for use when referring to experimental situations, with the expressions short-term storage (STS) and long-term storage (LTS) being used when referring to the underlying processes (Waugh & Norman, 1965). A more difficult problem has been the use of the expression 'short-term storage' to refer not only to the maintenance of knowledge in conscious awareness, but also to the storage and retrieval of information that has only recently passed from conscious awareness. For verbal information, Baddeley and Hitch (1974, 1977; Baddeley, 1976) have argued that there is sufficient empirical evidence to support the assumption that short-term storage has two dissociable aspects: a rehearsal buffer, for maintaining information in conscious awareness, and a working-memory system, for the coding and temporary storage of new information beyond the immediate present.

The rehearsal buffer, in Baddeley's model, holds a limited amount of verbal material in a phonemically-coded form (cf. Atkinson & Shiffrin, 1968; Glanzer & Clark, 1963; Morton, 1970). Verbal rehearsal, per se, appears to be an inefficient way of getting new information into long-term storage (e.g., Bower & Winzenz, 1970). Increasing the number of times a particular item is rehearsed does not necessarily increase the probability of its subsequent recall (Craik & Watkins, 1973; Glenberg, Smith & Green, 1977; but see Nelson, 1977), although rehearsal can improve recognition (Bjork, 1975; Craik

& Lockhart, 1972; Woodward, Bjork & Jongeward, 1973). It has also been demonstrated that partial loading of the rehearsal buffer (with digits) does not interfere with the performance of concurrent verbal-reasoning or verbal-comprehension tasks, unless the number of digits to be rehearsed is close to span capacity (Baddeley & Hitch, 1974, 1977). Baddeley and Hitch (1974) had three groups of subjects listen to a list of 15 unrelated words, while concurrently looking at sets of one, three or six digits, which they had to remember and write down. In the subsequent free-recall test for the words, the three groups of subjects did not differ in their recall of the final few items from the list, even though such items are traditionally assumed to be held in primary memory (Waugh & Norman, 1965). Baddeley (1976) uses the evidence presented above to argue that the verbal-rehearsal buffer is separate from other processes of short-term storage. Other studies (e.g. Corsi, 1972; Drachman & Arbit, 1966; Orsini, Schiappi & Grossi, 1981; Wickelgren, 1966, 1969) have pointed to the existence of a similar limited-capacity buffer for certain kinds of non-verbal information.

The working-memory system, together with its own limited-capacity storage ability, is essential for the coding and temporary storage of new information. It is here that information from semantic memory is used for the coding of new sensory information. Once coded, this new information can be stored temporarily for use in reasoning (Hunter, 1964), language comprehension (Baddeley & Patterson, 1971; Rumelhart, 1972) and long-term learning (Atkinson & Shiffrin, 1968; Baddeley & Hitch, 1974; Waugh & Norman, 1965). Such coding is not necessarily material-specific; verbal information can be recoded as visuo-spatial images (e.g., De Soto, London & Handel, 1965; Huttenlocher, 1968; Potts & Scholtz, 1975), and visual information can be recoded in verbal form (e.g., Bower, 1971).

The ability of normal subjects to carry out reasoning tasks (or to recall the final few items from a word-list), at a time when their rehearsal-buffer is loaded with other verbal material, supports the view that there must be a system for storing new information for as long as it is needed in the ongoing performance of a particular task. The evidence in favour of such a storage system for non-verbal or perceptual information is particularly compelling. Helson's work (1948, 1959, 1964) on the effects of context on perceptual judgements, as well as more recent work by Parducci (1959, 1965, 1968; Parducci & Perrett, 1971), supports the view that (for a particular set of stimuli) there must be available some internal representations that influence current perceptual experience. Further evidence in favour of a two-part short-term storage system comes from the work of Wickelgren (1966, 1968, 1969). Based upon his studies of recognition-memory for single tones, he concluded that there were two components in the short-term storage of non-verbal information: a span component, and what he termed an intermediate-memory component.

EFFECTS OF BRAIN-LESIONS ON PERCEPTION AND MEMORY

In the past, behavioural studies of patients with well-localized brain lesions provided some of the best evidence for a distinction between primary (short-term) storage and secondary (long-term) storage (Penfield & Milner, 1958; Scoville & Milner, 1957). In the following selective review of the literature, a case will be made for including both a span component and an intermediate, working-memory system, in order to account for some of the differential deficits in learning and memory that are found in association with particular brain lesions.

Unilateral Temporal-Lobe Lesions

Unilateral anterior temporal-lobe removal is performed for the relief of long-standing epilepsy. The excision includes the anterior temporal neocortex, and most or all of the uncus and amygdala, together with varying amounts of the hippocampus and parahippocampal gyrus (Penfield & Milner, 1958). Residual neurologic deficits may include a partial, or complete, contralateral upper-quadrant visual-field defect, the extent of which depends upon the variable course of the fibres of the optic radiations, as these pass anteriorly around the temporal horn of the lateral ventricle (Marino & Rasmussen, 1968). With rare exceptions, the patients who have undergone such surgery are otherwise neurologically intact. When the excision is from the language-dominant hemisphere, great care is taken to avoid direct or indirect damage to the posterior speech zone, thus guarding against the occurrence of any lasting postoperative dysphasia (Milner, 1958).

The IQ distribution for such patients appears to be the same as the distribution in the normal population (Milner, 1967). The patients have normal immediate-memory spans for both verbal (Milner, 1958) and non-verbal (Corsi, 1972) material. The temporal-lobe ablation does, however, exacerbate pre-existing material-specific perceptual and memory deficits, which vary with the side of the lesion (Milner, 1958).

Perceptual and Cognitive Deficits

Patients with temporal-lobe lesions exhibit mild perceptual and cognitive disorders that suggest a slight difficulty in gaining access to information stored in semantic memory. Thus patients with temporal-lobe excisions from the left, language-dominant, hemisphere are impaired in their ability to identify drawings of familiar objects when these are presented tachistoscopically (Kimura, 1963). They are also impaired in the rapid classification of drawings (or names of objects) as living or man-made (Wilkins & Moscovitch, 1978), although they are unimpaired in their ability to classify similar stimuli as representing objects larger or smaller than a chair. Jaccarino-Hiatt (1978) also found differential effects for left and right temporal-lobe groups in their categorization of words and nonsense designs. Subjects tested after left temporal lobectomy used fewer word- than design-categories, whereas the reverse was true for those tested after right temporal lobectomy. This finding is weakened, however, by the fact that neither group used significantly fewer categories than the normal control group on either of these tasks.

Milner (Note 1) finds that patients with left temporal-lobe lesions perform rather poorly on Newcombe's (1969, 1973) semantic-fluency task, which requires subjects to enumerate objects, then animals, then alternating birds and colours, at 60 seconds for each set. It is particularly interesting that left temporal-lobe patients are worse at this task than are those with left frontal-lobe lesions, given that the latter patient group is markedly impaired on a symbolic-fluency task that requires producing words that begin with a particular letter (Milner, 1967). In contrast, the left temporal-lobe group shows little or no deficit on this latter fluency measure (Milner, 1964, 1967). The difference between the two tasks appears to be that the first requires a search of semantic memory, whereas the second involves a lexical search (Collins & Loftus, 1975; Guilford, 1967; Jones-Gotman & Milner, 1977).

For patients with right temporal-lobe lesions, some of the earliest, and best-replicated, findings have been the mild perceptual difficulties that these patients exhibit when required to interpret complex visual material. Thus they perform poorly on tests that require the comprehension of sketchy or incomplete drawings, such as those of the McGill Picture-Anomaly Series (Meier & French, 1966; Milner, 1954, 1958, 1968) and the Mooney Closure Test (Lansdell, 1968; Milner, 1980). Such disorders can be interpreted as a mild difficulty in gaining access to semantic memory. The patients are also impaired at spotting quickly the "odd man-out" from amongst four sets of fragmented concentric circles (Meier & French, 1966), and at recognizing overlapping nonsense shapes when these are presented tachistoscopically (Kimura, 1963).

Memory Deficits

In comparison with the mild perceptual and cognitive deficits found after unilateral temporal lobectomy, the memory deficits are substantial. Patients with left temporal-lobe lesions are often very much aware of their poor verbal memory, particularly if their jobs require them to remember verbal material. Left temporal lobectomy has been shown to impair verbal learning and verbal memory (Meyer & Yates, 1955; Milner, 1958), regardless of whether the words are spoken or written (Blakemore & Falconer, 1967; Milner, 1967), and regardless of whether recall or recognition is tested (Milner, 1958; Milner & Kimura, Note 2). The verbal-recall ability of such patients is impaired both for drawings of common objects (Jaccarino-Hiatt, 1975; reported by Milner, 1978) and for real objects (Smith, 1980; Smith & Milner, in press). When recall or recognition is tested immediately after presentation of the test materials, any deficits are usually mild. When a delay intervenes, however, the verbal-memory deficits are more marked (Milner, 1967). Memory for such non-verbal material as faces (Milner, 1968), melodies (Shankweiler, 1966) or nonsense patterns (Kimura, 1963) is typically normal.

Patients with excisions from the right temporal lobe are impaired in the learning of, and memory for, auditory and visual information that is difficult to code verbally. This includes both recall and recognition of complex visual patterns (Kimura, 1963; Milner, 1975; Taylor, 1969, 1979) and tunes (Milner, 1962a; Shankweiler, 1966). These patients are also impaired in the delayed recall and recognition of drawings of common objects (Hiatt, 1975; in Milner, 1978) and in the delayed recall of toy objects (Smith, 1980, Smith & Milner, in press). Such findings, of course, have provided good supporting evidence for the existence of separate, material-specific memory systems, which play a complementary role in the storage of new information (Bower, 1970; Haber, 1970; Paivio, 1969, 1971; Shepard, 1967).

<u>Effects of hippocampal excision</u>. The extent of the removal in a unilateral temporal lobectomy is determined at the time of operation by taking into account the observed physical condition of the brain, together with the electrocorticographic findings. The extent of lateral neocortical excision can vary independently of the extent of removal in the more mesial areas, including the hippocampus and parahippocampal gyrus. Because of this variation, it has been possible to compare the performance of subgroups of patients whose excisions differed only with regard to the extent of hippocampal removal. On

certain types of learning and memory tasks there is a clear positive correlation between the extent of hippocampal excision and the level of behavioural impairment.

Milner (1967) first suggested that the degree of verbal memory difficulty observed after left temporal lobectomy might depend, in part, upon the extent of hippocampal removal. The most systematic evidence for the role of the hippocampus comes, however, from work of Philip Corsi (1972; Milner, 1971, 1972, 1974, 1978), the understanding of which is critical to an appreciation of this thesis. Corsi divided his left and right temporal-lobe groups into four subgroups, based upon the surgeon's report at the time of operation (see Milner, 1971, 1972, 1974). Patients in Group I had complete sparing of the hippocampal region, or less than 1/3 of the pes hippocampi removed; Group II subjects had removals that included from 1/3 to all of the pes hippocampi; Group III patients had the pes and up to 1 cm of the body of the hippocampus excised, and Group IV comprised all patients with more radical excisions of the hippocampal region. Using a modified version of Hebb's (1961; Melton, 1963) recurring digit-sequence task, Corsi showed that the only groups that failed to learn the recurring supraspan sequence were the left temporal-lobe patients with large hippocampal excisions (Groups III and IV). Subjects in left temporal-lobe Groups I and II did learn the sequence, although more slowly than normal subjects. On a verbal-memory task requiring the recall of nonsense trigrams after a filled delay-interval (Brown, 1958; Peterson & Peterson, 1959), Corsi found graded deficits for the four left temporal-lobe subgroups, the severity of the deficit depending upon the extent of hippocampal excision. Patients in Group I were only marginally impaired on the task. None of the right temporal-lobe subgroups showed an impairment on either the supraspan sequences or the trigrams task.

Patients with right temporal-lobe lesions perform certain learning and memory tasks poorly, regardless of the extent of hippocampal excision (e.g., Kimura, 1963; Milner, 1962a; Shankweiler, 1966; Taylor, 1969). On other tasks, however, this is not the case. Thus patients with right temporal lobectomy show deficits in stylus-maze learning, both visual (Milner, 1965) and tactual (Corkin, 1965) when, and only when, there has been a radical excision of the right hippocampus and parahippocampal gyrus. Corsi (1972) again provided the clearest evidence for the differential effects of hippocampal excision in these patient groups. On a visuo-spatial analogue of the recurring-digits task, which involved learning a supraspan spatial sequence (tapped out on a randomly-arranged set of blocks), only right temporal-lobe subgroups III and IV failed to learn the recurring sequence. On a visuo-spatial memory task, derived from Posner and Konick (1966), subjects had to recall the exact position of a dot on a line, after a filled time-interval. Once again, only the patients with large right hippocampal excisions were poor at the task, being particularly impaired with the longer (24-second) delay intervals. Rains (1981) has now extended Corsi's findings to the somesthetic domain. In a tactual analogue of the Posner and Konick (1966) task, Rains had subjects reproduce the spatial location of a pin that was positioned inside a cork circle; only the right temporal-lobe subjects with large hippocampal excisions showed a deficit on this task. Smith (1980; Smith & Milner, in press) has also found that only the patients with large right hippocampal excisions were impaired in the immediate recall of the spatial location of 16 common objects. Patients with left temporal-lobe excisions perform all these tasks normally, regardless of the extent of hippocampal removal.

Up to this point there is clear evidence for the importance of the hippocampus in the performance of tasks where the amount of information to be remembered exceeds span capacity, or where a limited amount of information must be remembered after a filled delay-interval. In general, the effects of hippocampal excision can be characterized as deficits in verbal learning and verbal memory for patients with left-hemisphere lesions, and deficits in spatial learning and spatial memory for patients with corresponding lesions of the right hemisphere. Patients with comparable lesions of the temporal neocortex and amygdala, but with the body of the hippocampus spared, show minimal impairment on these same tasks.

Other findings, though, suggest an additional role for the right hippocampal region; namely, in the re-evocation of visuo-spatial information in circumstances where this can provide a supplementary aid to verbal memory (cf. Milner, 1978, 1980). Smith (1980; Smith & Milner, in press) found deficits for both of her temporal-lobe groups in the delayed recall of the names of 16 common objects, which had been seen originally in a spatial array. For her right temporal-lobe subjects, however, the deficit was restricted to the subgroup with large hippocampal excisions. Jones-Gotman (Jones, 1975; Jones-Gotman, 1979) had subjects rate a set of words for their imageability. She then tested incidental learning of these words, and found, for her right temporal-lobe subjects, that only the subgroup with large hippocampal excisions was impaired. She has also shown differential losses that depended upon the extent of right hippocampal excision, on a task where the subjects were required to use imagery as a mnemonic aid in the recall of highly-imageable words (Jones, 1975) or word-pairs (Jones-Gotman & Milner, 1978). In contrast, the same right temporal-lobe patients were not impaired on a more difficult associative-learning task, where they were required to use a verbal mnemonic (sentence-mediation) as an aid to the recall of pairs of abstract words (Jones-Gotman & Milner, 1978). In none of Jones-Gotman's tasks did the temporal-lobe subjects have any difficulty in making appropriate judgements about imageability, or in generating mnemonic images. The deficit, for the right temporal-lobe group, came out when the re-evocation of such images would normally have provided an additional aid to verbal memory. In contrast, although Jones-Gotman found that using an imagery mnemonic improved the performance of her left temporal-lobe subjects, they were still impaired on these highly verbal tasks, with no relationship being found between the extent of hippocampal excision and the degree of memory impairment in this group (Jones, 1974, 1975; Jones-Gotman & Milner, 1978).

All of these findings go to suggest that the radical excision of the right hippocampus interferes with the retrieval of visual information, where this would normally be used as an aid to verbal recall (cf. Bower, 1970; Paivio, 1969, 1971; Paivio & Csapo, 1969; Shepard, 1967). A complementary mechanism might exist involving the left hippocampus. A strong prediction, based on the evidence presented above, is that it should be possible to create a task on which left temporal-lobe patients with large hippocampal excisions would be differentially impaired. Such a task would involve learning of, or memory for, visuo-spatial material, in circumstances where verbal recoding would normally be effective as a mnemonic aid in the recall or recognition of the visual information.

Effects of Bilateral Hippocampal Excision

The most compelling findings in support of at least a two-process theory of memory came originally from the study of subjects with bilateral lesions of the hippocampal region (Milner, 1959, 1962b; Penfield & Milner, 1958; Scoville &

Milner, 1957). In particular, the case of the patient H.M. has frequently been cited as providing strong evidence in favour of the STS-LTS dichotomy (Atkinson & Shiffrin, 1968). An extensive review of the experimental findings for this patient is included here, because he provides one of the purest examples of an amnesic syndrome of limbic origin, uncomplicated by the effects of neocortical damage. H.M. also shows the clearest dissociation between a spared span-component of short-term storage and a profoundly impaired intermediate-memory component. At the age of 27, this patient underwent bilateral removal of the mesial temporal-lobe structures (including the uncus, amygdala and major part of the hippocampus and parahippocampal gyrus, but sparing the lateral neocortex). Since this operation, which was carried out for the relief of long-standing epilepsy, H.M. has exhibited a profound anterograde amnesia, having extreme difficulty in learning or remembering most kinds of new information. His Full-Scale IQ is, however, slightly above average (and higher than it was preoperatively). He has been reported to show normal comprehension of language, even to the extent of understanding jokes whose point hinges on semantic ambiguity (Milner, Corkin & Teuber, 1968). Jaccarino-Hiatt (1978) reported that H.M. showed normal sorting and categorization of nonsense drawings and words, despite being unable to recall or remember any of them subsequently. All of these findings support the belief that H.M. has adequate access to his premorbid semantic memory system. On most tests of perceptual ability he shows average, or above-average performance. One apparent exception to this is his poor performance on the Gottschaldt Figures test (Milner et al., 1968). However, this task may involve a short-term storage component (Milner et al., 1968). Unlike patients with right temporal-neocortical excisions, he shows no impairment on the McGill Picture Anomalies Series, or the Mooney Closure Test (Mooney, 1956). Unlike patients with left temporal neocortical excisions, his recognition of tachistoscopically presented letters is normal (Kimura, 1963; Milner et al., 1968). In common with other amnesic patients (Warrington & Weiskrantz, 1968, 1970), he has been able to learn to recognize incomplete drawings of objects (Gollin, 1960), and he shows savings on this task when retested as much as three months later (Milner, 1970; Milner et al., 1968).

H.M. has an equally well-preserved ability to attend to, and retain (albeit briefly), new information that is within his span of attention. His digit span (6) is in the low-normal range, but is better, by one digit, than it was preoperatively (Scoville & Milner, 1957). His span for a visuo-spatial block-pattern is also within the low-normal range (5 blocks; Corsi, 1972). He is, however, unable to learn a digit sequence or a visuo-spatial block sequence, once the number of items exceeds his span (Corsi, 1972). H.M. can remember subspan verbal information for a period of minutes, as long as he is allowed to rehearse it continuously (Drachman & Arbit, 1966; Milner, 1959; Sidman, Stoddard & Mohr, 1968), but once his attention has shifted to something new he is unable to recall the previous information. It is of particular interest that he was able to employ an elaborate recoding strategy to help him retain successfully a subspan number series over a 15-minute interval (Milner, 1959). Yet, after he had been momentarily distracted, he was unable to remember anything of the number sequence, or of the elaborate mnemonic system that he had used to help him retain that sequence. He showed no evidence of learning on a 28-choice maze, even with extensive overtraining. However, when the total number of individual steps was reduced to fall within his memory span, he was able to learn, albeit very slowly, a simple visual or tactile maze (Milner et al., 1968). On the former task he still showed significant savings when retested two years later (Milner, 1970).

On all tests of recognition of non-verbal stimuli, H.M.'s performance fell to chance level when the delay interval exceeded 30 seconds. Thus, Prisko (1963), using the Konorski (1959, 1967) delayed-paired-comparison procedure, found that H.M. was performing at chance in his recognition of shades of red or flashes of light for any interval beyond 15 seconds. He was slightly better at recognizing clicks and tones, being able to span a 30-second interval at above-chance levels.

H.M. was also markedly impaired on a tactile delayed matching-to-sample task involving recognition of bent-wire shapes (Milner & Taylor, 1972). In the original task, designed to evaluate non-verbal memory in Sperry's commissurotomized subjects (Gazzaniga, Sperry & Bogen 1962, 1963), four shapes were used as the recognition set. All seven of the commissurotomized subjects were able to match the shapes with their left hands at 0-delay, and four of them were successful with their left hands after a 120-second delay. H.M., although able to do the task when there was no delay, required extensive training to bridge even a 30-second delay when four recognition items were used. Even when the number of choices was reduced to three, his performance did not improve. In contrast, patients with a variety of unilateral neocortical lesions showed no impairment on these same tasks, even with delay intervals of longer than 120 seconds.

The findings of Sidman, Stoddard and Mohr (1968) are particularly interesting, in that these authors were able to measure the degree to which a stimulus still exerted control over H.M.'s behavior, after varying delay intervals. They trained him initially to choose a circle from a set of ellipses, in a discrimination-gradient procedure. His performance on this part of the task was considered to be within the normal range. Following this, he was tested on a delayed matching-to-sample task, using a set of eight ellipses as the samples. The delay interval was increased by 1 second after each correct choice, and reduced by 1 second after each error. H.M. was only completely correct in his choices with delays up to 5 seconds. Analysis of his error choices, however, showed that the sample still influenced his responses at delays of up to 16 seconds. Two normal children, used as control subjects, showed no evidence of any deterioration in their performance, even with delays of 40 seconds, the longest interval sampled.

In contrast to his almost total inability to remember <u>what</u> he has seen or heard in the recent past, H.M. has been able to learn and remember, quite well, <u>how</u> to do certain tasks (see Cohen & Squire, 1980; Ryle, 1949; Winograd, 1975; for discussion of this issue). H.M. showed improved performance, over days, in learning a mirror-drawing task (Milner, 1962b), a rotary-pursuit task and a bimanual tracking task (Corkin, 1968), although he did not remember having seen any of the tasks previously. It has been suggested that learning a kinesthetic or motor skill may be mediated by a different brain system from that which mediates learning of verbal or visuo-spatial information (Posner, 1966, 1967; Posner & Konick, 1966). However, H.M. also shows normal learning, and 3-month retention, of mirror-reading skills (Cohen & Squire, 1980). He has also been able to learn the rules and procedures necessary for performing certain complex tasks (Cohen & Corkin, 1981), such as the Tower of Hanoi problem (Lindsay & Norman, 1972).

Milner (1958, 1959, 1962b) notes that, for normal individuals, many experiences are retained automatically in short-term storage without having to be kept constantly in conscious awareness. She goes on to suggest that it is this initial short-term storage that makes long-term storage possible (Milner, 1959, 1962b), and that bilateral hippocampal lesions appear to interfere specifically with such automatic short-term retention. Further support for this view comes from the work of Wickelgren (1966, 1969). On the basis of the performance of normal subjects on a pitch-recognition task, Wickelgren had postulated the existence of an intermediate-term memory system, which was distinct from the short-term or span system. After testing H.M. on this same task, Wickelgren (1968) concluded that H.M's performance showed no evidence of this intermediate-term component.

In summary, unilateral lesions of the anterior temporal neocortex produce material-specific perceptual and memory deficits. Such deficits are considered, here, to be a consequence of a decreased ability to gain access to information already stored in semantic memory. In this sense, the deficits are considered to be in the initial encoding, rather than in the storage of information. Excision of the hippocampal region, in conjunction with the temporal neocortex, can result in additional material-specific learning and memory deficits that appear to be the result of a decreased ability to retain new information in short-term storage. The special contribution of the hippocampal region to memory is seen most clearly in the amnesic patient, H.M., whose bilateral excision was restricted to the mesial-temporal areas. His immediate span is normal, for both verbal and non-verbal information. He appears to have a normal ability to gain access to information stored in semantic memory. In contrast he is profoundly impaired in his ability to retain any new information that exceeds his span, or to recall or recognize subspan information once it has left his conscious awareness.

Unilateral Frontal-Lobe Lesions

Unilateral frontal lobectomy, when carried out for the relief of focal epilepsy, appears to have little or no detrimental effect upon overall level of intelligence (Hebb, 1945; Milner, 1963, 1964). Patients with frontal-lobe lesions have also been shown to perform normally on a wide variety of perceptual and memory tasks, involving both verbal and non-verbal memoranda (Ghent, Mishkin & Teuber, 1962; Milner, 1967, 1968, 1972).

Yet the effects of a frontal-lobe lesion are easy to detect clinically. Patients with severe traumatic lesions, or with large frontal-lobe tumours, are characteristically described as being disinhibited, perseverative and stimulus-bound (Luria, 1966; Luria & Homskaya, 1964). In patients who have undergone a planned cortical resection for the relief of epilepsy, similar effects are discernible, though in an attenuated form (Milner, 1964). Some years ago, Konorski (1967, pp. 490-503) suggested that a major part of normal frontal-lobe function was in the control of ongoing behaviour, such as planning a course of action for the coming day, and then keeping track of what has been completed and of what still remains to be done (cf. Pribram, Ahumada, Hartog & Ross, 1964). It is particularly in these aspects of behaviour that patients with frontal-lobe lesions appear to have most difficulty in their daily life. In what follows, it will be seen that such patients also show a marked impairment in experimental situations that require them to plan a course of action, or to keep track of what they have, and have not, done (Milner, 1971, 1975).

Studies by Milner and her associates (Milner, 1963, 1964, 1972; Prisko, 1963) have demonstrated that patients with unilateral frontal-lobe excisions for epilepsy show no impairment on many tasks on which patients with temporal-lobe lesions do poorly. Thus, on most tests of recall or recognition, patients with unilateral frontal-lobe resections perform normally, as long as a set of non-repeating test items is used (Milner, 1964, 1972; Prisko, 1963). In contrast, when a limited number of test items are presented repeatedly and a decision has to be made about each one, frontal-lobe patients are often markedly impaired (Milner & Teuber, 1968). This finding has been demonstrated for delayed paired-comparison tasks (Milner, 1964; Prisko, 1963), continuous-recognition procedures (Kimura, 1963; Milner, 1964; Milner & Teuber, 1968; Milner, Taylor & Corkin, Note 3), and tests requiring judgements of temporal recency (Milner, 1972). On certain memory tests a lesion of the left frontal lobe results in a more severe impairment than is found after a lesion of the right frontal lobe. This has been shown nicely by Petrides (Petrides & Milner, 1981), using a task in which patients are shown sets of high- or low-imagery words, drawings of common objects, or abstract designs. Initially, the same six items are shown, in different locations, on six different pages. The subject is told to touch any item on the first page, then to turn to the next page and touch a different item, and so on, trying never to touch the same item more than once during the course of that set. Then the test is repeated, with new arrangements of the same six items having to be touched again, in any order. The procedure is then repeated a third time. Following this, eight new items are given, with the same task instructions, and then ten new items, and finally twelve new items. On this task, which requires both planning a few moves ahead, and monitoring of ongoing behaviour, Petrides's left frontal-lobe group was impaired, irrespective of the type of test materials used. His right frontal-lobe group, in contrast, was only impaired on the 12-item list of the drawings and of the abstract designs.

On tasks where there is a major spatial component, as in the learning of visual or tactile mazes (Corkin, 1965; Milner, 1965), patients with right frontal-lobe lesions are generally more impaired than those with left frontal-lobe lesions, thus reflecting the general role of the right hemisphere in the successful performance of spatial tasks. Petrides (Note 4) has adapted conditional-response tasks (which produce a major deficit in non-human primates after bilateral frontal lobe excision; e.g., Goldman & Rosvold, 1970) for use with patients. In such tasks subjects are required to discover by trial and error, and then remember, how two sets of stimuli have been paired off, when there are no natural associations between any of the stimulus and response items. Petrides has demonstrated marked associative-learning deficits on this type of task, for groups of patients with unilateral frontal-lobe lesions. Where the visuo-spatial aspects of the task were of primary importance, his right frontal-lobe group was more severely impaired than his left frontal-lobe group.

In summary, the effects of frontal-lobe lesions on learning and memory are most apparent where the planning and monitoring of ongoing behaviour are important for successful completion of a task. This has led to the suggestion that the control processes of working memory are specifically affected by frontal-lobe lesions (Konorski, 1967; Pribram et al., 1964), whereas it may well be that the short-term storage aspects, per se, are intact.

THE PRESENT INVESTIGATION

The experiments to be reported here were designed to explore further the effects of unilateral temporal lobectomy on learning and memory. More specifically, they were designed to evaluate the relationship between encoding and storage of verbal information in patients with temporal-lobe lesions, and to assess the effects of left temporal lobectomy on the maintainance and storage of new information in working memory. In addition to the groups of control subjects and of patients with unilateral neocortical excisions, the patient H.M., who underwent a bilateral removal of the mesial-temporal region, was also tested on the word-generation and absolute-judgement tasks. His performance provides a reference-point from which to assess the extent of the memory disturbance that can follow unilateral temporal lobectomy.

Subjects

Each of the patients studied had undergone a unilateral brain operation at the Montreal Neurological Hospital, the operation being carried out for the relief of cerebral seizures. In the majority of cases, the cause of the seizures was focal cerebral atrophy dating from birth or early life, although a few cases of indolent tumour and one case of adult head trauma were also included. Patients with diffuse cerebral damage, or with fast-growing tumours, were excluded, as were cases of bilateral independent electrographic abnormality.

Because Wechsler-Bellevue Intelligence and Memory Quotients were known for all patients, it was also possible to eliminate those patients with Full-Scale IQ ratings below 75. This left a total of 105 patients, 14 of whom were subsequently excluded because pre-operative intracarotid Amytal[1] tests had shown them to have atypical representation of speech (Wada & Rasmussen, 1960; Branch, Milner & Rasmussen, 1964).

Main Subject Groups

Of most interest in all of the experiments to be reported here was the performance of the 68 patients who had undergone a unilateral anterior temporal lobectomy. Of this group, 34 had excisions from the left hemisphere, and 34 had excisions from the right.

Left temporal-lobe group. In the patients tested after left temporal lobectomy, the mean extent of removal along the Sylvian fissure was 4.7 cm, ranging from 4.0 cm to 6.0 cm, and the mean extent along the base of the temporal lobe was 5.6 cm, with a range from 4.0 cm to 7.5 cm. The amygdala was said to have been completely removed in 30 cases and partially removed in 4. For 12 patients (subgroup LTH), the removal included the pes hippocampi plus part of the body of the hippocampus. The remaining 22 patients (subgroup LTh) had had smaller hippocampal excisions, including four patients in whom the hippocampus

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[1] Sodium amobarbital. Eli Lilly and Company, Indianapolis, Ind., U.S.A.

had been completely spared. The total group included one case of hamartoma, four of indolent astrocytoma, one of oligodendroglioma, and one case of closed head injury. Ten patients were seen from two to three weeks post-operatively, the remainder being seen in follow-up study, one or more years after surgery.

Right temporal-lobe group. For the patients in this group the mean extent of removal along the Sylvian fissure was 5.0 cm, with a range from 4.0 cm to 6.5 cm, and the mean extent along the base of the brain was 6.1 cm, ranging from 4.5 cm to 8.5 cm. The amygdala was said to have been completely removed in 31 cases and partially removed in the remaining 3 cases. Thirteen patients (subgroup RTH) had had removals that included the pes plus some portion of the body of the hippocampus; the remaining 21 (subgroup RTh) had had smaller hippocampal removals, including one case in which the hippocampus was completely spared. The right temporal-lobe group included one case of hamartoma and three cases of indolent astrocytoma. Fifteen patients were seen from two to three weeks after operation and the remainder one or more years later.

Normal control group. Twenty-four right-handed normal control subjects were chosen to match the temporal-lobe subjects as closely as possible with respect to sex, age and level of education. Their intelligence was not assessed.

Table 1 shows the distribution by sex, age, and education for the normal control subjects and the temporal-lobe patients,

Table 1

Main Subject Groups

	Sex		Age (yrs.)		Education (yrs.)		Wechsler I.Q.	
Group	M	F	Mean	Range	Mean	Range	Mean	Range
Left temporal	17	17	29.6	19-50	12.4	7-20	108.2	92-131
Right temporal	19	15	27.7	16-48	11.9	8-18	113.4	79-134
Normal control	12	12	28.6	17-52	13.3	10-18	Not Assessed	

together with Full-Scale Wechsler IQ ratings (taken from the most recent assessment of each patient) for the temporal lobe groups. The composition of the two temporal-lobe groups varied somewhat from experiment to experiment, because the research was conceived progressively. Tables showing the number of subjects participating in each task are given in the Appendix.

Patient H.M.: Bilateral Medial Temporal-Lobe Removal

In addition to the patients with unilateral temporal-lobe excisions, the patient H.M. (Scoville & Milner, 1957), who had undergone a radical bilateral medial temporal-lobe resection for the relief of medically intractable seizures, was also tested on the word-generation and absolute-judgement tasks. In his case, the surgical excision was said to have extended posteriorly along the medial aspect of the temporal lobes for a distance of 8 cm, destroying bilaterally the anterior two-thirds of the hippocampus and parahippocampal gyrus, together with the uncus and amygdala, but sparing the lateral neocortex. At the time of testing (27 years after the operation) H.M. was 54 years old, with a Wechsler-Bellevue I.Q. of 104 (Verbal 97, Performance, 108) and a Wechsler Memory Quotient of 64.

Additional Subject Groups

The additional subjects comprised 23 patients with unilateral frontal-, parietal- or occipital-lobe lesions. These subjects were included in the experiments that comprise Part II of the thesis. Table 2 shows the sex, age, education and mean Full-Scale Wechsler I.Q. ratings of these patients, grouped

Table 2

Additional Subject Groups

	Sex		Age (yrs.)		Education (yrs.)		Wechsler I.Q.	
Group	M	F	Mean	Range	Mean	Range	Mean	Range
Left frontal	3	2	31.0	17-46	8.8	5-11	100.6	92-110
Left fronto-temporal	0	3	28.0	17-43	15.3	13-17	110.7	101-124
Right frontal	4	5	25.1	12-51	10.6	6-14	100.3	85-114
Left parietal	2	0	31.0	27-35	15.0	14-16	106.5	96-117
Right parietal	2	1	28.7	28-30	15.0	12-20	101.0	80-112
Right occipital	0	1	11.0	n.a.	6.0	n.a.	93.0	n.a.

according to side and site of lesion.

Left frontal-lobe group. Figure 1 shows the cortical excisions for four of the five patients with lesions restricted to the left frontal lobe. No brain map was available for the fifth patient (Su.Gi.), who had had an arterio-venous malformation removed from the left parasagittal region. The removals ranged from small parasagittal excisions (e.g., Al.Qu.), to more radical frontal lobectomies that still always spared Broca's area (Hu.Ma.). The epileptogenic lesions in this group of patients included one hamartoma (Ch.Kn.) and one case of hamartomatous ganglioglial dysplasia (Hu.Ma.).

Left fronto-temporal group. The removals in the three patients who make up this group are shown on the right of Figure 1. In no case did the temporal-lobe excision extend mesially beyond the pes of the hippocampus. Included in this group is one case of indolent astrocytoma (Je.Ga.). One other patient (Su.Kr.) had had a thrombosed angioma, situated where Broca's area would normally have been. Preoperative sodium Amytal tests revealed that most, and probably all, of her speech was represented in the left cerebral hemisphere. The left-sided speech representation was confirmed at operation, dysphasic errors being elicited by electrical stimulation of the cortex anterior and superior to the lesion. The excision itself, although followed by a transient post-operative dysphasia, did not cause any permanent impairment in speech. Since the results from such a small group cannot be analyzed separately,

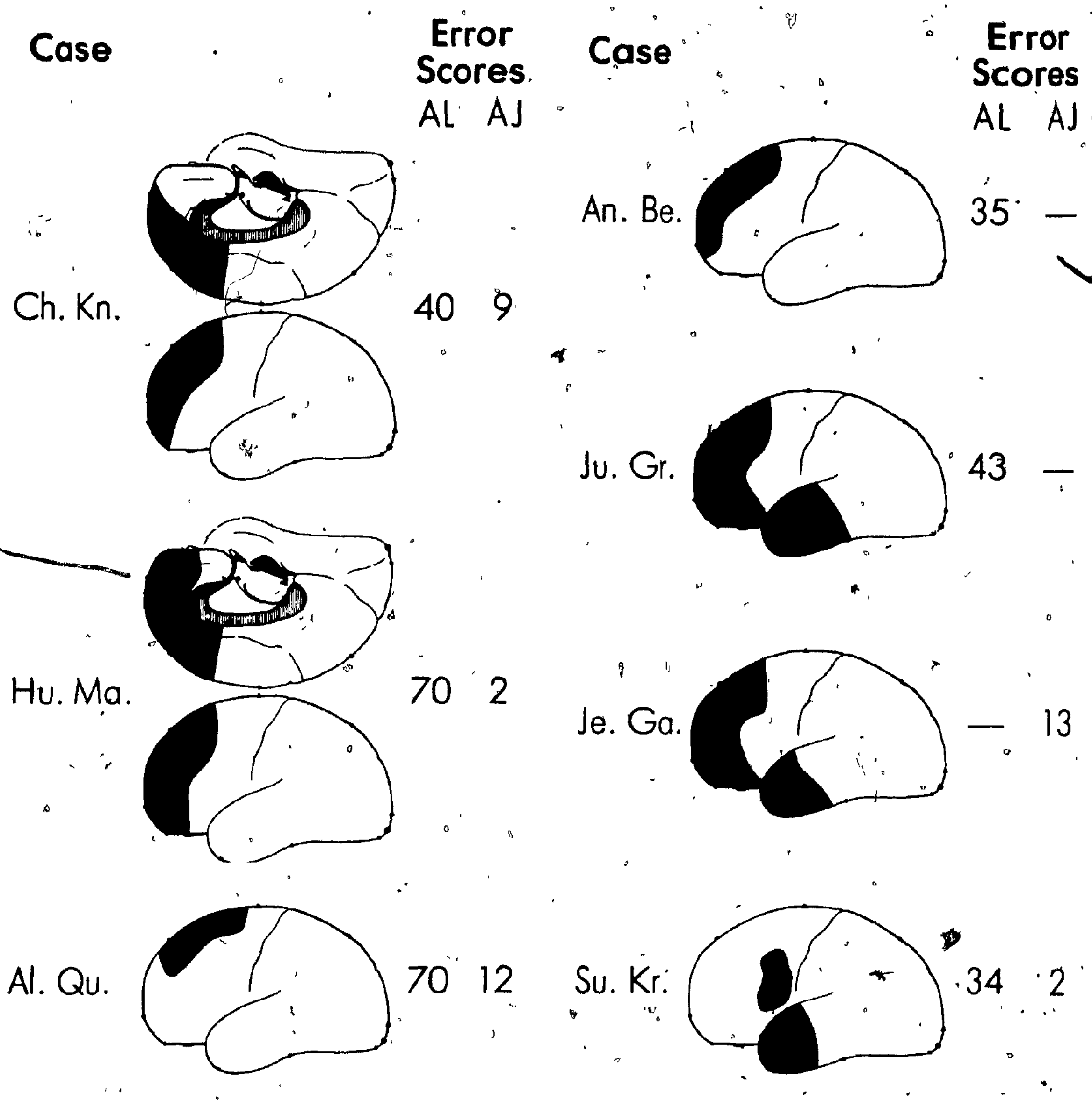

Figure 1. Left frontal-lobe and left fronto-temporal groups: brain maps based on the surgeon's drawings at the time of operation, showing (in black) the estimated lateral extent of cortical excision. The brain maps on the left side, and at the top right, are those for the left frontal lobe group. The remaining three maps on the right side are those for the left fronto-temporal group. All excisions spare Broca's area, as mapped out by electrical stimulation. (For patients Ch.Kn. and Hu.Ma.: mesial aspect above, lateral aspect below.)

these cases are combined with the other left frontal-lobe subjects for the purposes of statistical analysis.

Right frontal-lobe group. Figures 2 and 3 show the cortical excisions in these nine patients. They range from small inferior-dorsolateral (Da.Co.), or parasagittal (Ja.Ro.) removals, to radical lobectomies (Gl.Mc.; Ma.Si.). In one case (Co.Ha.) the anterior 4 cm of the temporal lobe were also removed, but the hippocampal region was essentially spared. Included in this group is one case of porencephalic cyst (Je.Bi.), one case of tuberous sclerosis (Ja.Ro.), and one case of venous hemangioma (Do.Co.).

Left and right posterior-cortex groups. The removals of five of the six patients in these two groups are illustrated in Figure 4. No brain map was available for the remaining patient (Gu.Ch.), who had had a large (5-cm diameter) arteriovenous malformation removed from the left superior parieto-occipital region. One case of low-grade astrocytoma (Yv.Ga.) was included in the right posterior group.

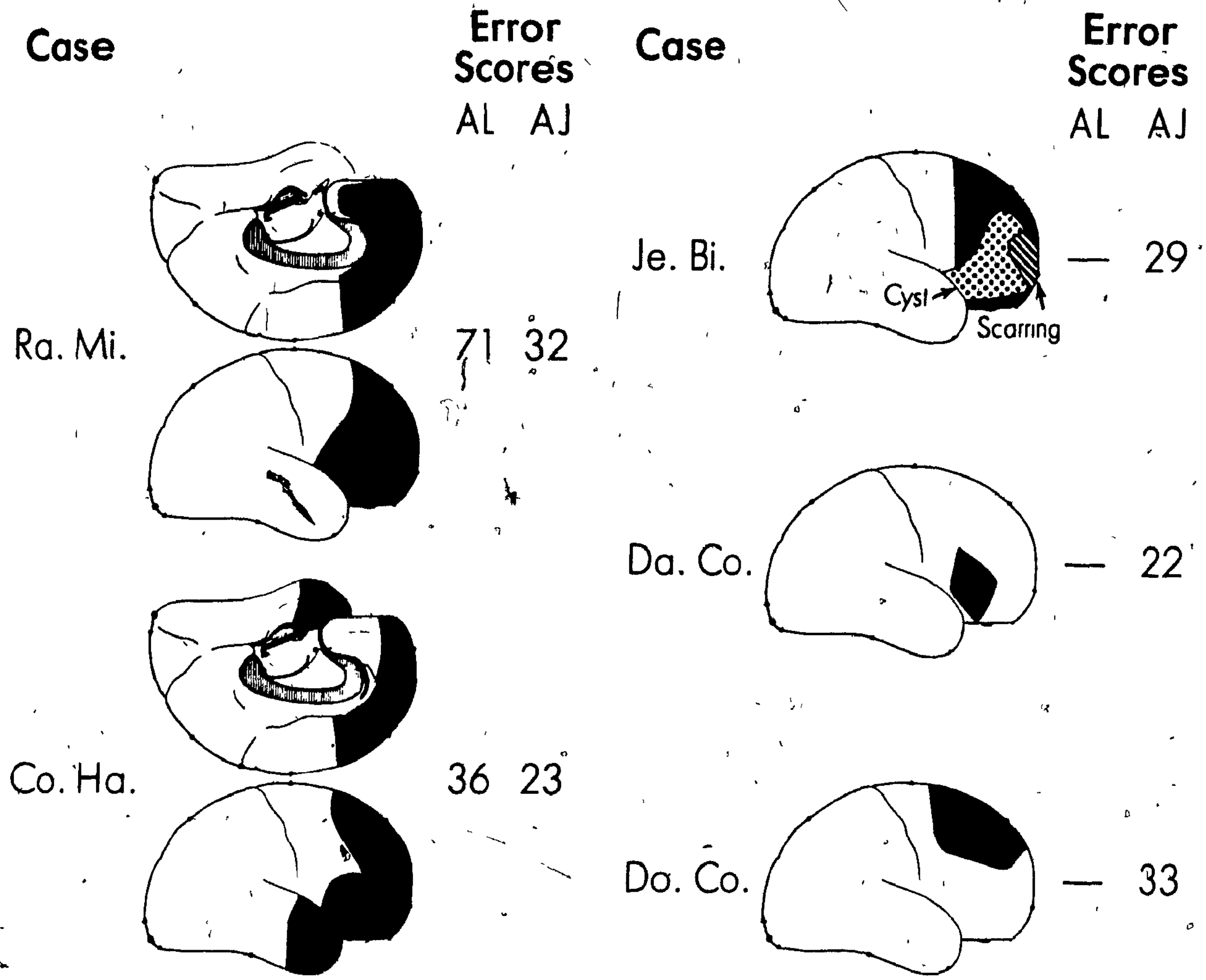

Figure 2. Right frontal-lobe group: estimated extent of removal in five of the patients from the right frontal-lobe group. (For Ra.Mi. and Co.Ha.: mesial aspect above, lateral aspect below.)

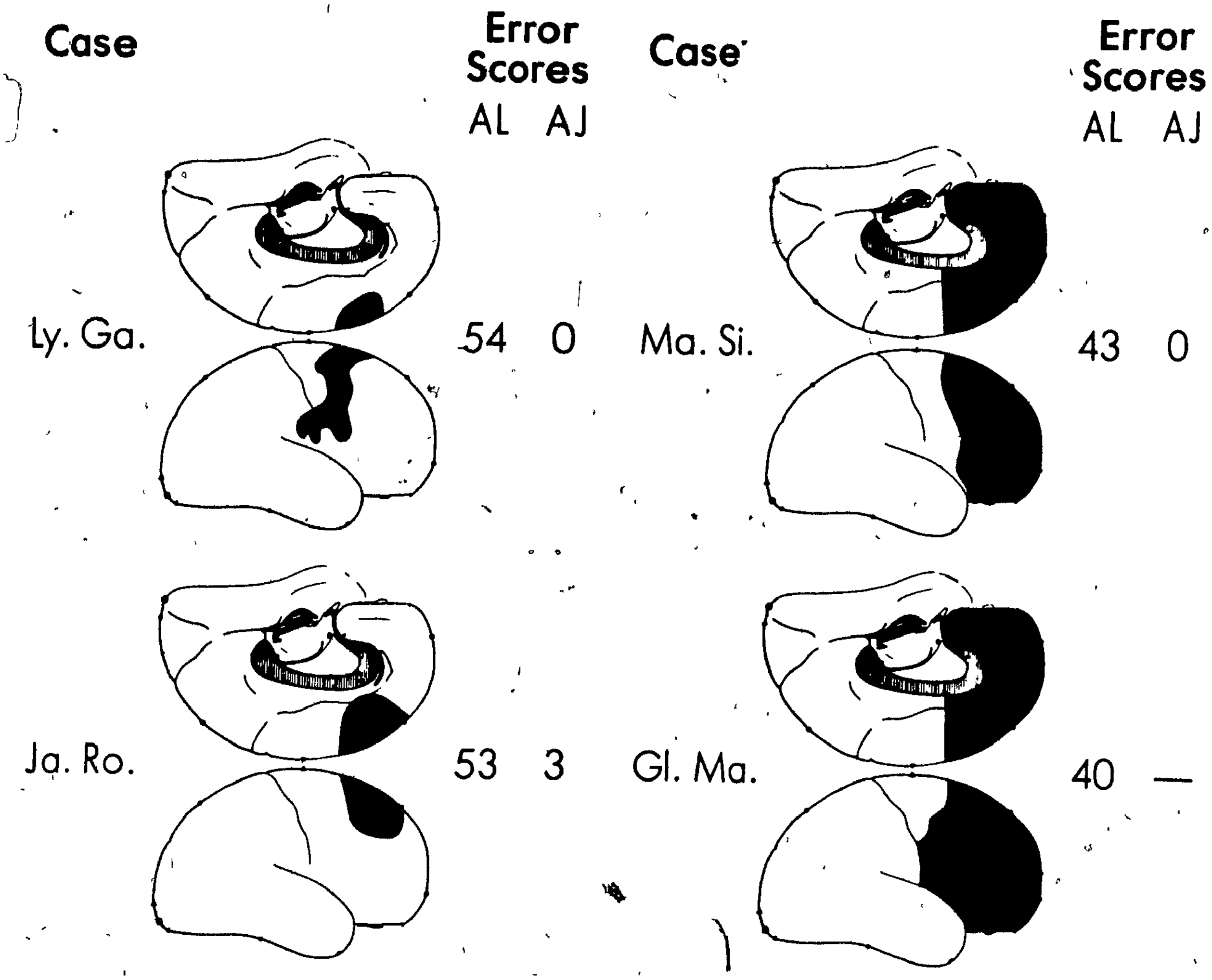

Figure 3. Right frontal-lobe group (continued): brain maps showing estimated lateral and mesial extent of cortical excision in the four remaining patients from the right frontal-lobe group. In Figures 1 to 4, scores to the right of each map show the total number of errors made by that patient on the associative-learning (AL) and absolute-judgement (AJ) tasks discussed later in the thesis.

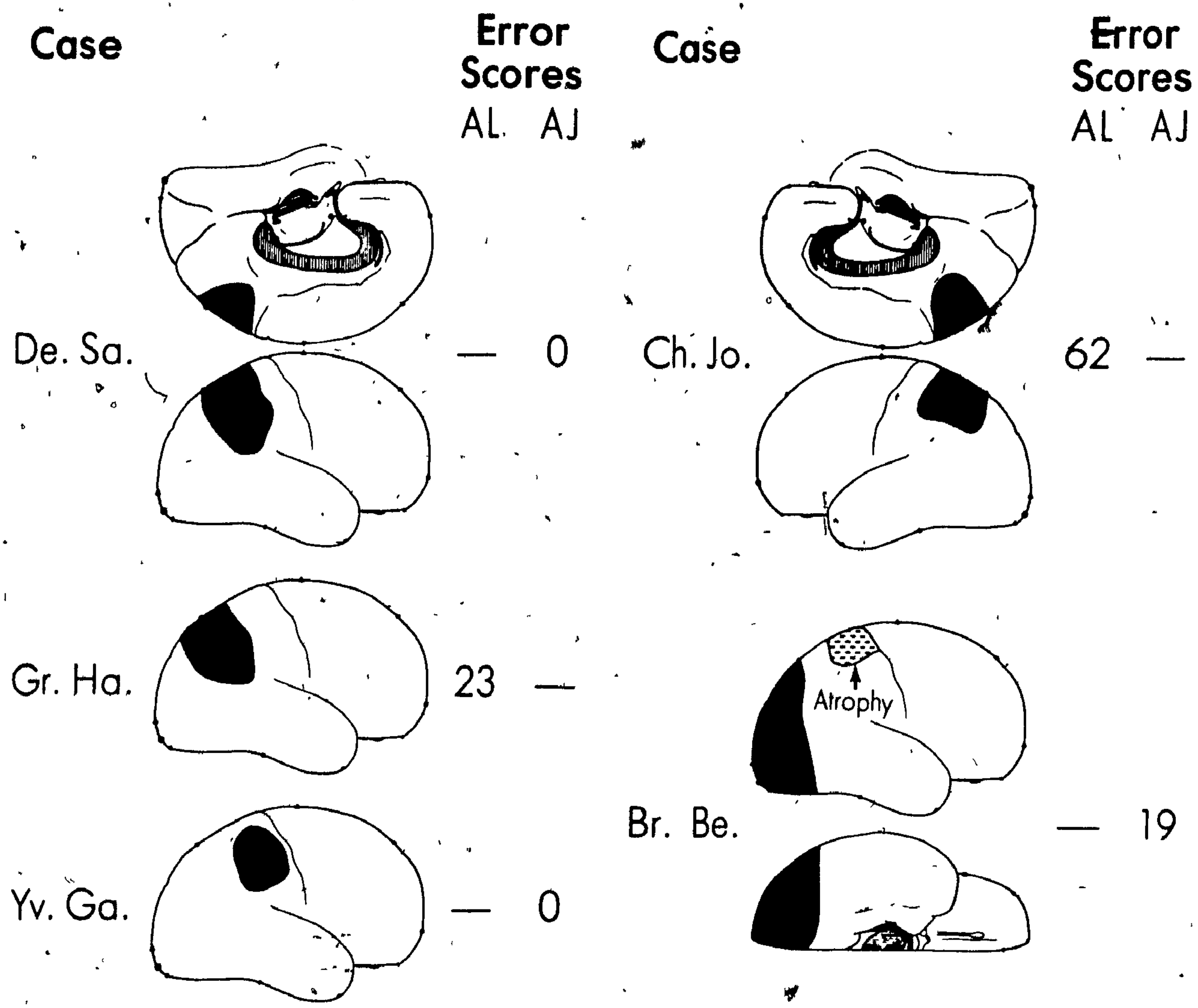

Figure 4. Left and right posterior-cortex groups: brain maps showing estimated lateral extent of cortical excision in the two patients from the left posterior-cortex group and the three patients from the right for whom brain-maps are available. (De.Sa. and Ch.Jo.: mesial aspect above, lateral aspect below; Br.Be.: lateral aspect above, inferior aspect below.)

Experiment 1: Word Generation

The first experiment explores the relationship between the encoding of verbal material and its subsequent recall by subjects who have undergone a unilateral temporal lobectomy. The focus of interest of the study was on the performance of the patients in the left temporal-lobe group.

The ability to understand verbal information is largely dependent upon our ability to evoke rapidly, and accurately, the stored meanings of words contained in our semantic memory system. The hypothesis put forward here is that a left-temporal neocortical lesion impairs the ability to gain access to semantic memory. Such an impairment would be expected to interfere with the accurate semantic encoding of new verbal information, and the verbal memory deficit seen in such patients is considered to be a consequence of that poor encoding. If this hypothesis is correct, then, for left temporal-lobe patients who have had the body of the hippocampus spared (subgroup LTh), a test that ensures precise semantic encoding should offset the verbal memory impairment that would otherwise be expected. A formally similar task that involves phonetic encoding should result in the verbal memory impairment usually found in such patients. In contrast, patients with large left-hippocampal excisions, because of their reduced short-term storage capacity (Corsi, 1972), should be impaired on both the semantic and the phonetic tasks, even in immediate recall. Patients with right temporal lobectomy, given the highly verbal nature of the tests, should show no impairment, regardless of the extent of right hippocampal excision.

A variant of the Slamecka and Graf (1978) word-generation task was developed to test these hypotheses. In this task subjects were required to generate a word list, having been given a cue word and the first letter of a target word. The basis for generating the words could be either semantic (e.g., a synonym; BIG? - L....), or phonetic (e.g., a rhyme; RICE? - N...). Normal subjects, on this type of task, show significantly higher levels of recall for the self-generated items than do subjects who are given the same set of words in a standard depth-of-processing procedure (e.g., Does LARGE mean the same as BIG?: Does NICE rhyme with RICE?; Slamecka & Graf, 1978). The beneficial effects of generating one's own word list is found for both immediate and delayed testing and for both recall and recognition. This holds true regardless of whether incidental or intentional tests of memory are given (Dunlap & Dunlap, 1979; Jacoby, 1978; McFarland, Frey & Rhodes, 1980). This type of task seemed particularly appropriate for use with temporal-lobe patients, because it requires the subject to search for, and produce, a set of specific items from semantic memory.

The rhyme- and synonym-generation tasks were given on separate days, with blocked presentation, in order to heighten the expected differences in the performance of the LTh subgroup on the two tasks. In previous studies with normal subjects the two types of generation tasks have usually been presented with rhymes and synonyms intermixed, in much the same way as in the typical depth-of-processing experiment (e.g., Craik & Tulving, 1975).

For normal subjects the first few items and the last few items presented in a word list are remembered better in immediate recall than are items from the middle portion of the list. It has been assumed that these primacy and recency effects are related, respectively, to the long and short-term storage components of memory (Atkinson & Shiffrin, 1968; Glanzer & Cunitz, 1966; Waugh & Norman, 1965). Because of Jaccarino-Hiatt's finding of a reduced primacy effect for patients with large left-hippocampal excisions (Jaccarino-Hiatt, 1978; reported in Milner, 1978, 1980), and because of the theoretical interest in the role that the hippocampus plays in the transfer of new information to long-term storage, special attention was paid to the immediate recall of the first two words and the last two words generated in each of the two tasks.

Test Materials and Procedure

Two separate sets of words were created for the rhyme- and the synonym-generation tasks. For the phonetic task, 16 pairs of medium or high-frequency words were chosen, such that they rhymed with each other and had at least one other rhyme in common (e.g., RICE-NICE-mice). Ten of the cue words had Thorndike-Lorge (1944) frequency ratings of A or AA, with the remaining six words having an average frequency of 25.0 words per million (ranging from 4 to 45 words per million). Nine of the target words had A or AA ratings, the remaining 7 words having an average frequency of 30.1 words per million (ranging from 27 to 41 words per million).

For the semantic task, 16 pairs of words were used, similar in frequency of occurrence to the rhymes. The two words in each pair were synonymous and had at least one other synonym in common (e.g., BIG-LARGE-huge). Eight of the cue words were rated A or AA, with the other eight having an average rating of 25.8 words per million (ranging from 2 to 48 words per million). All but one of the target words had A or AA ratings, with the remaining word having a rating of 39.0 words per million. None of the target words in the rhyme-generation task was a synonym for any of the words used in the synonym-generation task, and only two of the target words in the synonym-generation task rhymed with any of the words of the rhyme-generation task (see Table A in Appendix for complete set of words). For each task, eight different arrangements of the word-pairs were created.

On each of two separate days subjects were required to generate orally a list of 16 common words, for each of which they were given a cue word and the first letter of the target item. For the rhyme-generation task, subjects were given the following instructions:

> I am going to say a word, and then say the first letter of another word that rhymes with the one I gave you. I want you, as quickly as you can, to tell me the word I am thinking of. I am going to get you to produce a long list of words in this same way. Then, at the end of the list, I will ask you to tell me as many of the words that you gave me as you can remember. I will never ask you to remember any of the words that I gave you.

Subjects were allowed up to 30 seconds to produce each correct target word. The time between presentation of a target letter and the correct response was measured to the nearest tenth of a second, using a hand-held stop-watch. If the subjects gave no response (or an incorrect response) within the first 15 seconds, they were provided with the first syllable of the target word (or the first two or three letters for monosyllabic words) as an additional cue. If, after 30 seconds, they still had not produced the correct target word, the word was given to them by the examiner. A minimum time-interval of 10 seconds was maintained between presentation of successive cue-words, in order to keep presentation-time as constant as possible for all subjects. The minimum presentation-time for each set of 16 words was 155 seconds.

Immediately after giving the last correct target word, subjects were asked to recall aloud as many of the target items as they could remember, in any order. Both the items and the order in which they were produced were recorded. Subjects were allowed up to 5 minutes to recall the items but most subjects completed their recall within three minutes. On the other test day (with order of presentation of tasks counterbalanced within each group), subjects received essentially the same instructions as before, except that this time they were asked to produce words that had the same <u>meaning</u> as the cue words.

Following the immediate free-recall portion of the task subjects were given, on Day 1, the associative-learning task described in Part II; and on Day 2, the absolute-judgement and matching-to-sample tasks, also described in Part II. At the end of these tasks, which took about 45 to 60 minutes, all subjects were asked without warning to try to remember the words that they had produced originally. Five minutes were again allowed for recall, and no prompting of any kind was given.

Table B, in the Appendix, shows the composition of the temporal-lobe groups taking part in the word-generation tasks.

Results

Preliminary t-test comparisons of all the results to be reported showed no significant differences, within any of the groups, attributable to sex of subject or to order of word- or task-presentation. Within each temporal-lobe group there was also no significant difference between the performance of subjects tested in the immediate post-operative period and those who were tested in follow-up study. Within each group, therefore, the data were pooled for all subsequent analyses.

Response Times

In a pilot study, it was noted that there were many subjects in each group who took a long time to respond to one or two items, especially during performance of the synonym-generation task. Patients in the left temporal-lobe group appeared to display more of this word-finding difficulty than other subjects. Because of these long-latency items, it was considered appropriate to use the median response-time for each subject (rather than the mean), as a rough measure of difficulty for each of the two tasks. These times were used in a two-way analysis of variance (Group x Task). In this analysis there were significant differences among the three groups ($F\ (2,54) = 6.41$, $p < .01$), and between the two tasks ($F\ (1,54) = 9.79$, $p < .005$), but no interaction effect ($F = 1.26$). Paired comparisons, using a pooled error-term and a Satterthwaite approximation to the degrees of freedom ($df = 107$), revealed the left temporal-lobe group to be significantly slower than either the normal control group (rhymes; Q = 3.29, $p < .05$: synonyms; Q = 4.56, $p < .01$), or the right temporal-lobe group (rhymes; Q = 3.41, $p < .05$: synonyms, Q = 4.54, $p < .01$). The normal control and right temporal-lobe groups did not differ from one another (rhymes; Q = 0.97: synonyms, Q = 0.87). Within the left temporal-lobe group, the two subgroups did not differ from one another (rhymes; t = 0.67: synonyms; t = 0.89).

Free Recall

Because of the particular interest in the effects of both Task and Time of Recall on the performance of the left temporal-lobe group, planned comparisons involving simple-simple main effects were calculated for Groups at both levels of those two factors. These were followed by paired comparisons between the normal control group and each temporal-lobe group or subgroup, as well as paired comparisons between the two left temporal-lobe subgroups, using a Neuman-Kuels procedure. For all of these comparisons a pooled error-term was calculated, using the mean value of the four error terms from the overall analysis of variance (Winer, 1971). The degrees of freedom for the comparisons were calculated using a Satterthwaite approximation (Winer, 1971).

The mean number of words correctly recalled by the three main groups is shown in Figures 5 (immediate recall) and 6 (delayed recall). A three-way analysis of variance (Group x Task x Time of Recall) was performed on the number of items

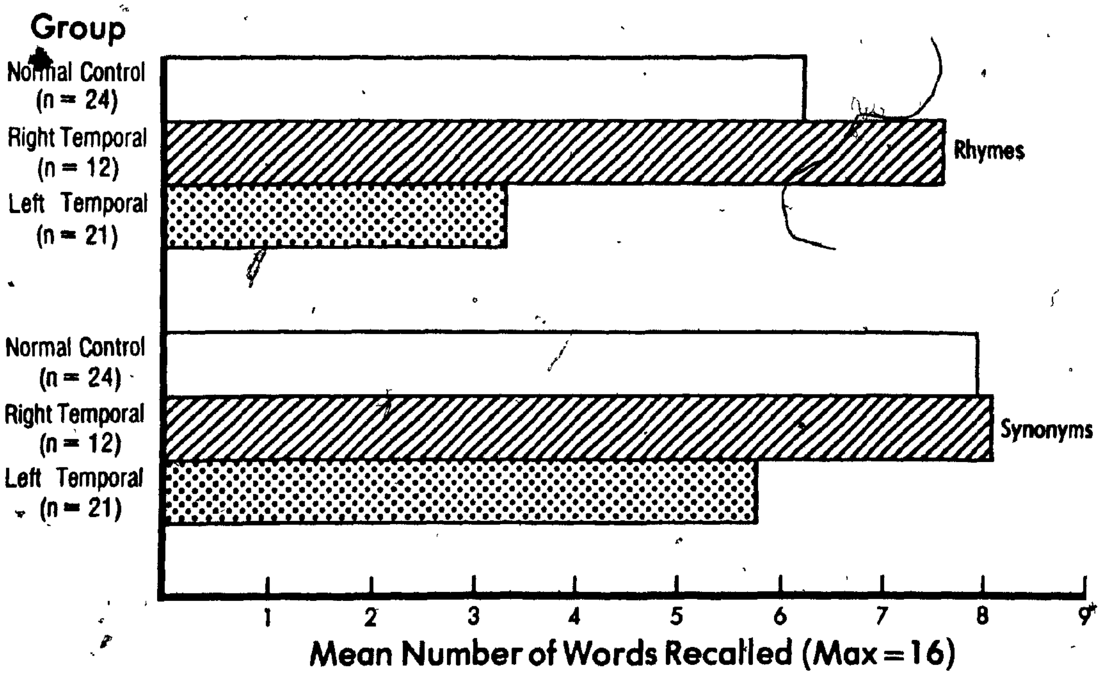

Figure 5. Word generation task: immediate recall. Mean number of words correctly recalled by the normal control and temporal-lobe groups for the rhyme- and synonym-generation tasks, respectively.

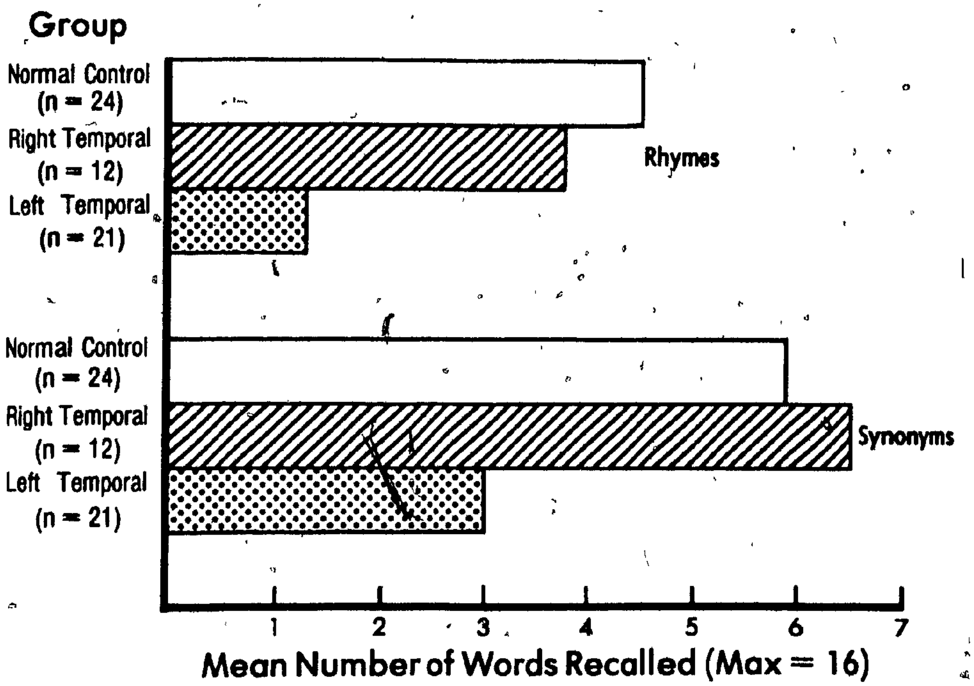

Figure 6. Word generation task: delayed recall. Mean number of words correctly recalled by the three groups for the rhyme- and synonym-generation tasks, respectively.

recalled correctly. This analysis gave significant main effects for Group (F (2,54) = 13.92, p <.001); Task (F (1,54) = 33.85, p <.001); and Time of Recall (F (1,54) = 214.21, p <.001). There was also, however, a significant three-way interaction (F (2,54) =8.63, p <.001). Examination of the simple interactions for Groups X Time of Recall showed a significant effect for both Rhymes (F (2,107) = 8.73, p <.001), and Synonyms (F (2,107) = 3.56, p <.05).

The planned comparisons of the simple-simple main effects (df = 101) gave a significant group effect for the immediate recall of rhymes (F = 14.00, p <.001, see Fig. 5). Paired comparisons showed the left temporal-lobe group to be impaired relative to both the normal control (Q = 5.65, p <.01) and right temporal-lobe (Q = 6.96, p <.01) groups. A similar pattern of results was seen for the immediate recall of synonyms (F = 5.84, p <.005), with the left temporal-lobe group, once again, impaired relative to both the normal control (Q = 3.91, p <.01) and right temporal-lobe (Q = 3.86, p <.05) groups. Significant group effects were also found for delayed recall of both rhymes (F = 10.54, p <.001) and synonyms (F = 11.85, p <.001, see Fig. 6). In each case the left temporal-lobe group was impaired relative to the normal control group (rhymes: Q = 6.32, p <.01; synonyms: Q = 5.73, p <.01) and also relative to the right temporal-lobe group (rhymes: Q = 4.13, p <.05; synonyms: Q = 5.95, p <.01). The right temporal-lobe group did not differ from the normal control group on any of the above comparisons (rhymes - immediate: Q = 2.28; synonyms - immediate: Q = 0.54; rhymes - delayed: Q = 1.11; synonyms - delayed: Q = 1.25).

Left temporal hippocampal effects. In order to explore the relationship between extent of hippocampal excision in left temporal-lobe subjects and performance on the word-generation task, a three-way analysis of variance (Group x Task x Time of Recall) compared the two left temporal-lobe subgroups (LTh and LTH) with the normal control group. The mean recall scores for these groups, broken down by Task and by Time of Recall, are shown for rhymes in Figure 7, and for synonyms in Figure 8. The analysis gave significant main effects for Groups (F (2,42) = 13.29, $p < .001$); Task (F (1,42) = 16.59, $p < .001$), and Time of Recall (F (1,42) = 105.00, $p < .001$). None of the interactions reached significance.

In the planned comparisons (df = 83), the group effect was significant for the immediate recall of rhymes (F (2,83) = 8.61, $p < .001$; see Fig. 7), both left temporal-lobe subgroups being impaired relative to the normal control group (for LTh: Q = 4.90, $p < .01$; for LTH: Q = 4.46, $p < .01$), but not differing from each other (Q = 0.54, n.s.). In marked contrast, although the overall group effect for immediate recall of synonyms was of a similar magnitude (F (2,83) = 8.53, $p < .001$, see Fig 8), on this task the group with large hippocampal excisions was impaired relative to both the normal control group

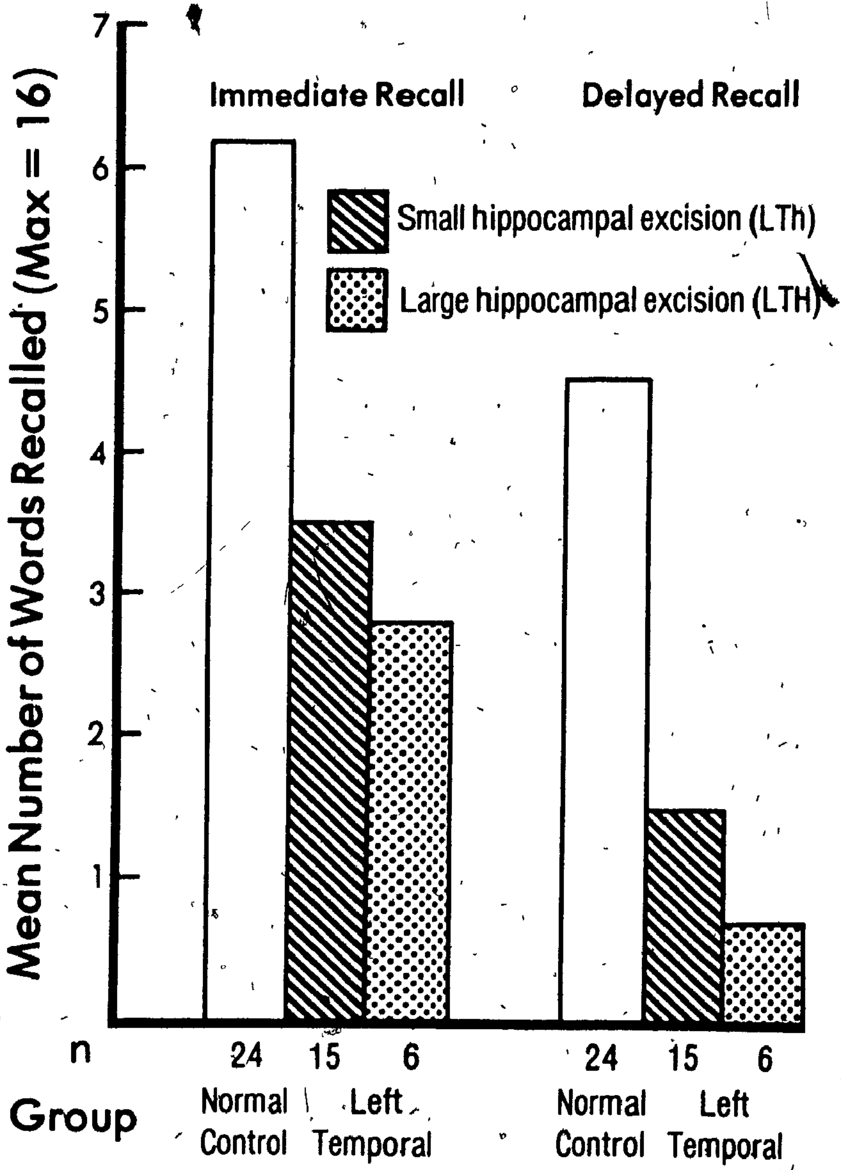

Figure 7. Left-temporal hippocampal effects: rhyme-generation task. Mean number of words correct in immediate and delayed recall. Results for the normal control group and the two left temporal-lobe subgroups, respectively.

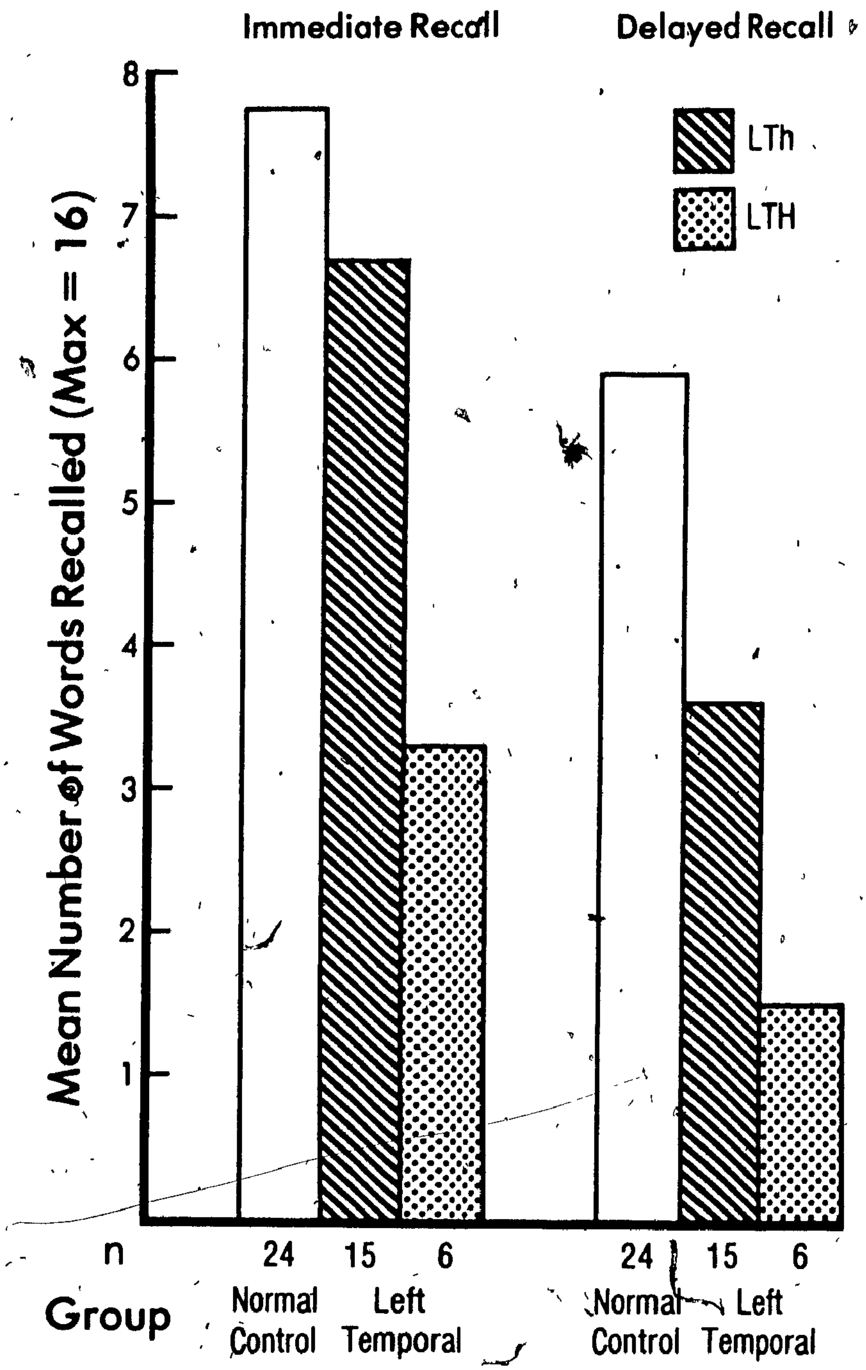

Figure 8. Left-temporal hippocampal effects: synonym-generation task. Mean number of words correct in immediate and delayed recall. Results for the normal control group and the two left temporal-lobe subgroups (LTh and LTH), respectively.

($Q = 5.84$, $p < .01$) and to the group with small hippocampal excisions ($Q = 4.25$, $p < .01$). The difference between the normal control group and the group with small hippocampal excisions did not approach significance ($Q = 1.86$). Significant group effects were found for delayed recall of both rhymes (F (2,83) = 10.82, $p < .001$); and synonyms (F (2,83) = 10.39, $p < .001$). In each case both of the left temporal-lobe subgroups were impaired (rhymes; LTh, $Q = 5.44$, $p < .01$: LTH, $Q = 5.07$, $p < .01$: synonyms; LTh, $Q = 4.25$, $p < .01$: LTH, $Q = 5.84$, $p < .01$) but did not differ significantly from one another (rhymes; $Q = 1.08$: synonyms; $Q = 2.62$).

Serial-Position Effects in Immediate Recall

Figure 9 shows the serial-position curves for the immediate recall of the rhymes by each of the three groups. The immediate free-recall scores, for each task, were tabulated according to the position in the list that each word had occupied when it was first generated.[1] For the analyses, these input positions were grouped into eight sections of two words each. The groups were then compared in two separate two-way analyses of variance (Group x Recall Position), one for each task. Following these analyses, planned comparisons of the groups for the first two (primacy) and last two (recency) items generated were carried out, using the pooled error-term from each of the overall analyses. Following Greenhouse and Geisser's (1959) recommendation, conservative df were used for evaluating the significance of all repeated-measure effects. Where the

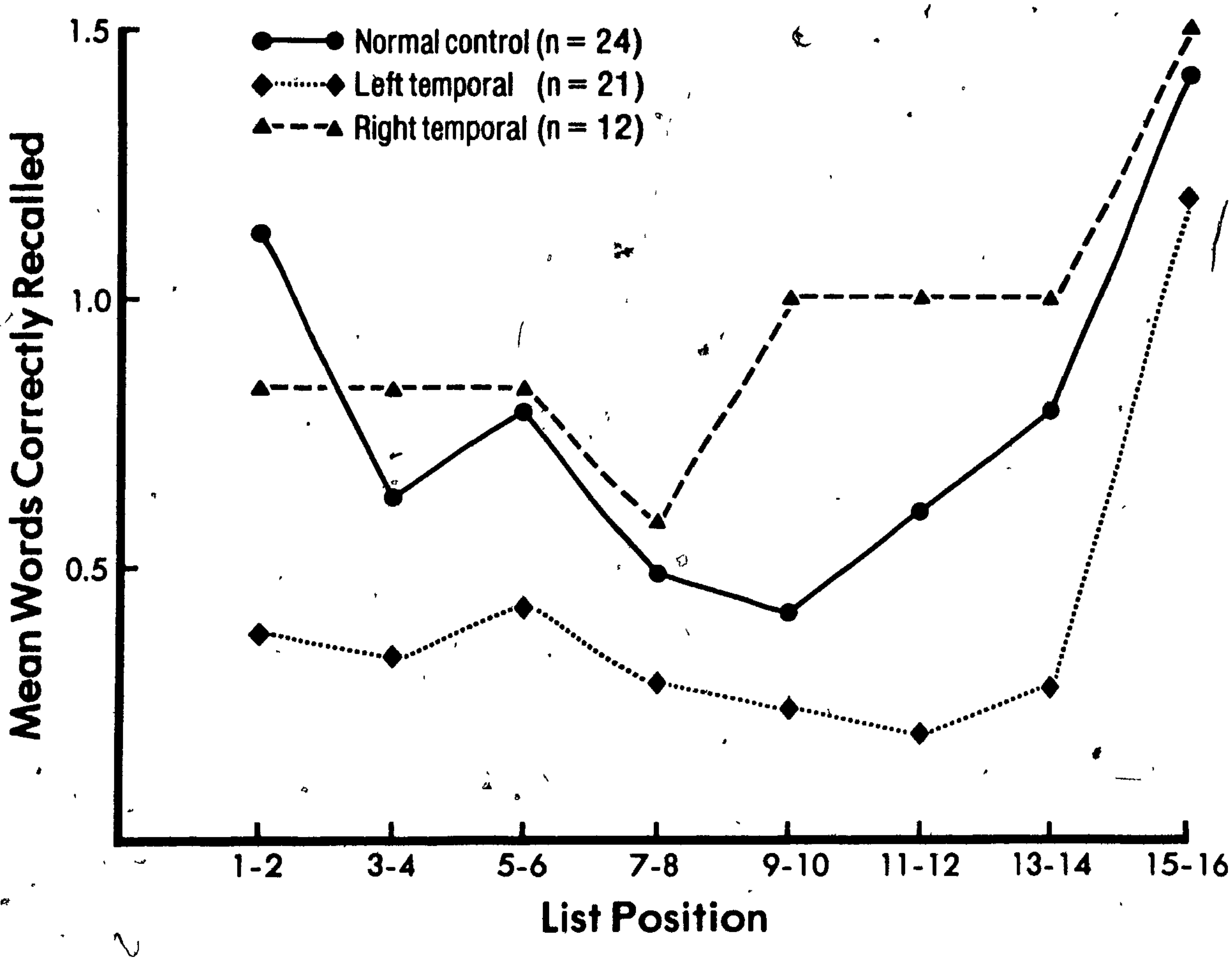

Figure 9. Word-generation task: all groups. Serial-position effects for the immediate recall of rhymes.

group effects were significant, paired comparisons of the groups were carried out using a Neuman-Kuels procedure.

Figure 9 shows the serial-position curves for immediate recall of rhymes. The Group effect was significant (*F* (2,54) = 14.95, $p < .001$), as was the Serial-Position effect (*F* (7,378) = 11.22, $p < .001$). However there was no significant interaction (*F* (14,378) = 1.14). In the planned comparison of the primacy effects (*df* = 407), the group differences were significant (*F* (2,407) = 7.55, $p < .005$), and the paired comparisons revealed the left temporal-lobe group to be significantly impaired relative to both the right temporal-lobe group (*Q* = 2.94, $p < .05$) and the normal control group (*Q* = 4.83, $p < .01$). The latter two groups did not differ significantly from one another (*Q* =1.89). In contrast to this, the group differences for the recency portion of the curve did not approach significance (*F* = 1.10). For the immediate recall of the synonyms, both the overall Group, and Serial-Position, effects were significant. (Group; *F* = 4.36, $p < .05$: Serial-Position; *F* = 5.37, $p < .01$). In this case, however, there were no differences between the groups in either the primacy (*F* (2,397) = 2.81) or the recency (*F* = 0.02) portions of the curve.

Relation between left hippocampal removal and serial-position effects. In the analysis of the serial-position effects, the most interesting results were those for the two left temporal-lobe subgroups (see Figs. 10 and 11). A two way (Group x Serial Position) analysis of variance for the

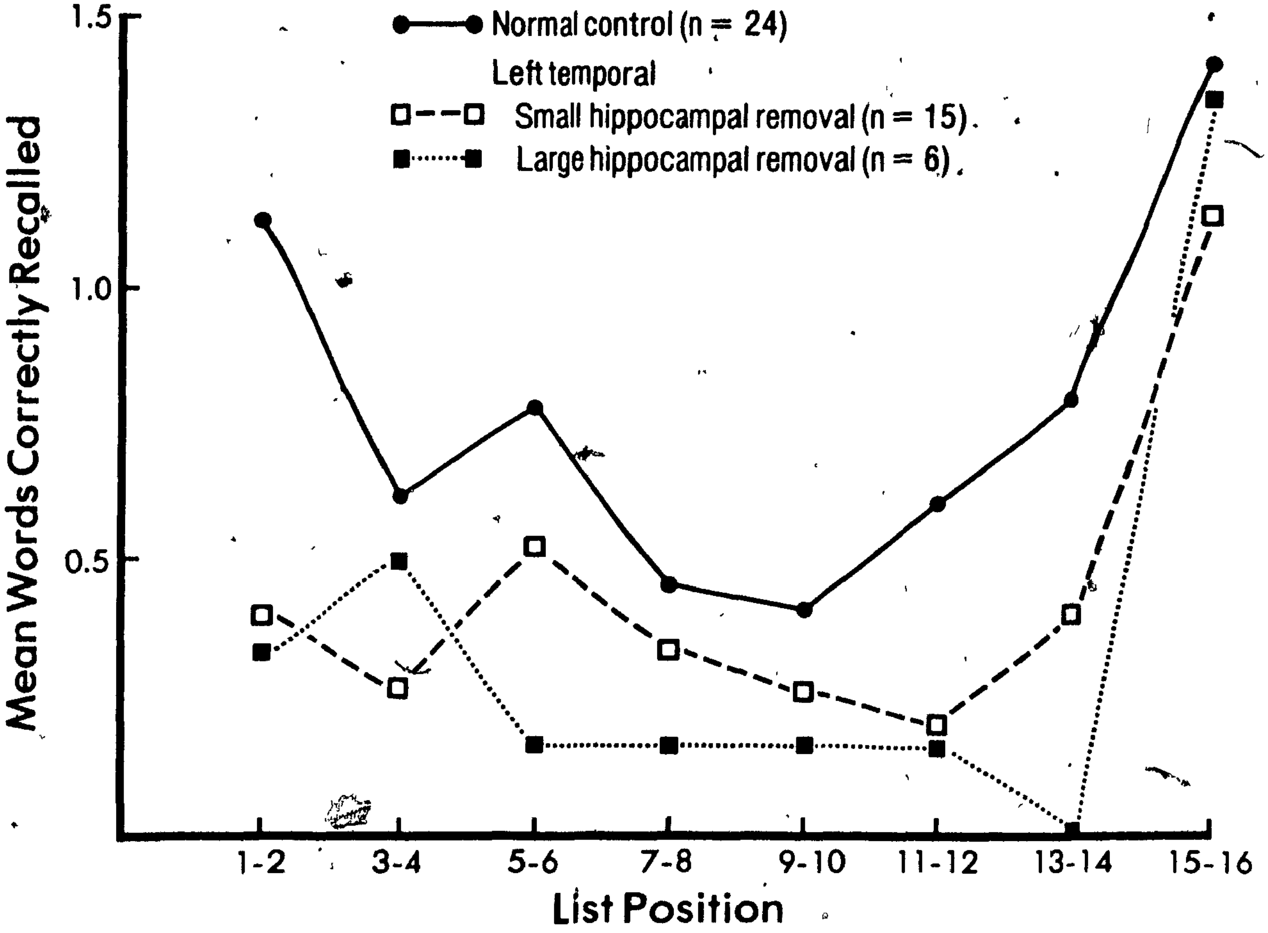

Figure 10. Left-temporal hippocampal effects: serial-position curves for immediate recall of rhymes.

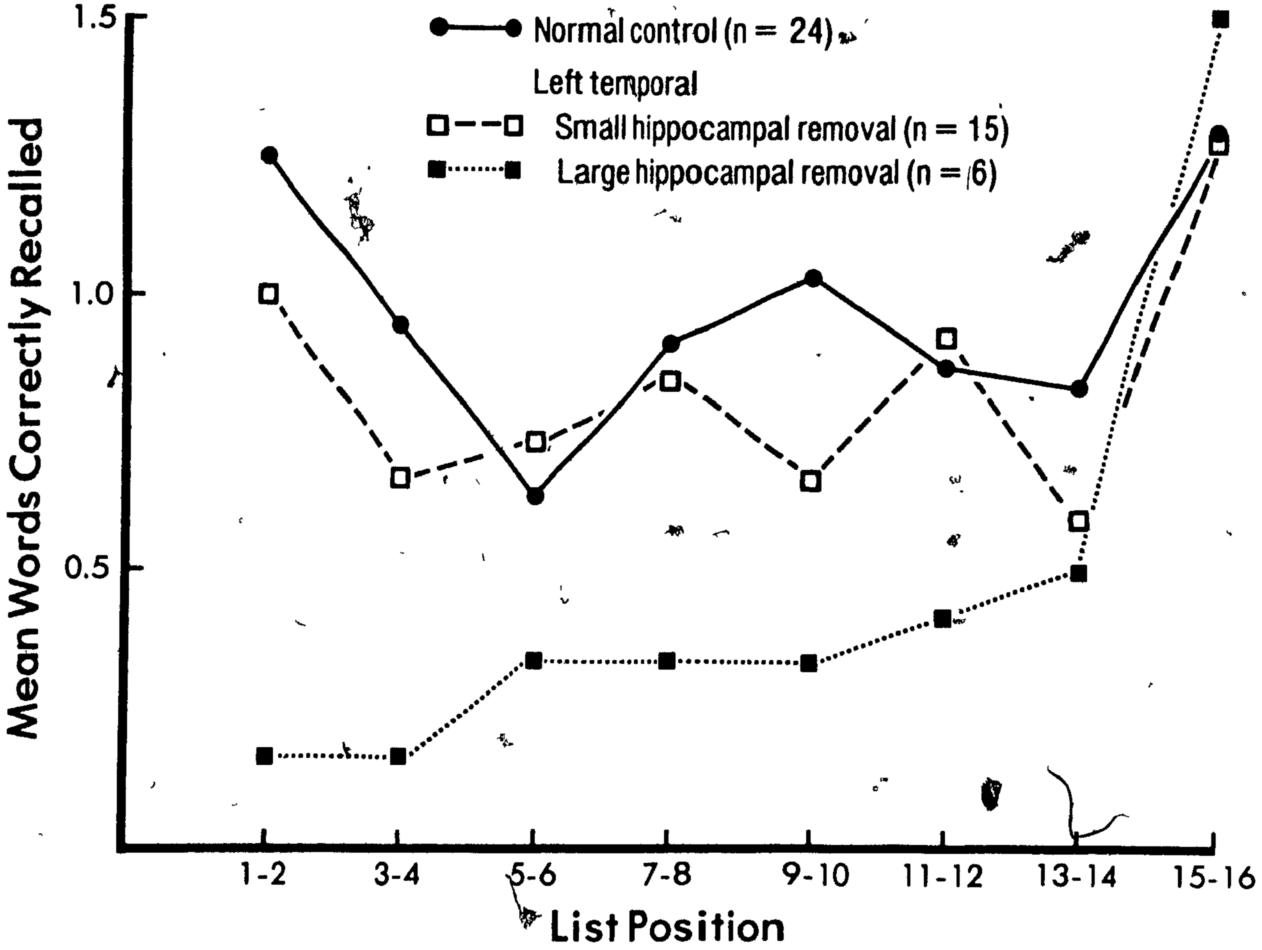

Figure 11. Left-temporal hippocampal effects: serial-position curves for immediate recall of synonyms.

immediate recall of the *rhymes* gave significant main effects for Group (F (2,42) = 9.18, $p < .001$) and Serial Position (F (7,294) = 10.29, $p < .001$), but no interaction (F = 0.93; see Fig 10). The group differences, for the primacy portion of the curve (df = 314), were significant (F = 6.74, $p < .005$), and paired comparisons revealed that both left temporal-lobe subgroups were impaired relative to the normal control group (LTh; Q = 3.52, $p < .05$: LTH; Q = 3.85, $p < .05$) but did not differ from one another (Q = 0.32). There were no differences among the groups for the final (recency) portion of the curve (F = 0.81).

The overall analysis for immediate recall of the *synonyms* was also significant for Groups (F = 7.50, $p < .005$) and Serial Position (F = 5.26, $p < .01$), with a nonsignificant interaction (F = 1.26; see Fig. 11). Once again the groups differed in the primacy portion of the curve (F (2,315) = 7.33, $p < .005$), but this time the paired comparisons showed that only the patients with large hippocampal excisions (LTH) failed to show any primacy effect (NC; Q = 5.77, $p < .01$: LTh; Q = 4.44, $p < .01$). The left temporal-lobe subjects with small hippocampal excisions (LTh) did not differ from the normal control group in their ability to recall the first two synonyms that they had generated (Q = 1.33). There were, again, no differences among the three groups in their ability to recall the final two items (F = 0.33).

Performance of H.M. on the Word-Generation Task

H.M. received the same task-instructions as did the other subjects with regard to producing and remembering the self-generated items. He had no difficulty in producing the appropriate responses in both the rhyme and the synonym conditions. In immediate recall of the rhymes, he was able to produce the last two words correctly. After a three-minute delay, filled with general conversation, he was unable to remember any of the words that he had given earlier. In the synonym-generation task, he produced only the final item from the list in immediate recall, and no items at all after a three-minute filled delay interval.

Discussion

For the normal control and right temporal-lobe groups, the results of the word-generation tasks accord well with the results of similar studies in normal subjects (e.g., Slamecka & Graf, 1978). Thus, for both groups, the synonyms were recalled better than the rhymes, in immediate and in delayed recall. On both tasks the right temporal-lobe and normal-control groups performed at the same level. Although the left temporal-lobe group also recalled the synonyms better than they recalled the rhymes, this group was significantly poorer than either of the other two groups on both tasks. The left temporal-lobe group was also slower than the other two groups at generating both the synonyms and the rhymes. This finding is in keeping with previous observations of slight word-finding difficulties as a sequel to left temporal lobectomy (Milner, 1958).

For the left temporal-lobe subgroups the results for immediate recall fit well with the original hypotheses that motivated the study. Both the subgroup with the hippocampus spared (LTh) and the subgroup with large hippocampal excisions (LTH) were equally poor in their recall of rhymes, suggesting that a lesion of the left temporal neocortex is sufficient to cause a deficit when the initial encoding is on a purely phonemic basis, rather than being directed towards the meaning of the words presented. Good support for this view comes from a recent study by Rains (1981), in which he tested groups of right and left temporal-lobe patients taken from the same population as the subjects in this thesis. Using the depth-of-processing paradigm developed by Craik and Tulving (1975), Rains had his subjects first make one of three types of judgement about each word from a 48-word list. Subjects had to decide whether or not the word described an item from a given semantic category (<u>semantic</u> condition), or rhymed with a given word (<u>phonemic</u> category), or was printed in upper or lower-case letters (<u>physical</u> condition). Immediately after completing the task, subjects were given tests of incidental recall and recognition for the set of words about which they had had to make judgements. Rains found the expected depth-of-processing effects for his normal control and right temporal-lobe groups, with words from the semantic condition being recalled best, those from the phonemic condition being recalled next best, and those from the physical condition being recalled most poorly (cf. Craik & Tulving, 1975). Rains's left temporal-lobe group was impaired on all conditions, although this group was better at recalling words from the semantic condition than from either of the other two conditions. Their recall of words from the phonemic condition, however, was as poor as their recall of words from the physical. As in the word-generation study, Rains found that the two left temporal-lobe subgroups (LTh & LTH) were equally impaired in their recall of words from the phonemic condition. The findings from the two studies help confirm that excision of the left temporal neocortex results in a marked impairment in verbal recall when the orienting task that is used does not require any semantic encoding for its successful completion.

This view also fits well with recent observations by Roldan (Note 5), who has been carrying out directed-forgetting experiments (Bjork, 1970) with temporal-lobe patients. In Roldan's task subjects are required to read aloud, and remember, sets of words presented individually on a video screen. At a given signal subjects must either recall the words from the most recently-presented set, or forget that set of words and begin to memorize a new set. This task, in which dozens of words are presented within a single test session, is very demanding on short-term storage and recoding processes. Left temporal-lobe patients are the only subjects who make phonemic errors in recall on this task, despite having read the words correctly as these were presented (e.g., they might have read the word BIRD, but recalled it as BREAD). Taken together, the results from the above studies suggest some impairment in the phonemic encoding of verbal material by patients with left temporal-lobe lesions.

In the rhyme-generation task, the serial-position curves for immediate recall (see Fig. 9) show clearly that, for the left temporal-lobe group, very litle of the phonemically coded information got into long-term storage. It can be seen from Figure 10 that this was the case for both left temporal-lobe subgroups, neither of which showed any evidence of a primacy effect in the immediate recall of the rhymes. In contrast, the normal recency-effect displayed by both of the left temporal-lobe subgroups suggests that they had no difficulty in retaining the final few items in primary memory. It appears, therefore, that, in the rhyme-generation task, the left temporal-lobe subjects were just retaining the most recently generated items in their rehearsal buffer, without doing any of the recoding necessary to effect a transfer of that information to long-term storage. In a recent paper, Zaidel (1978) has commented on the inability of the isolated right hemisphere to employ phonemic encoding, in contrast to its normal, or near normal, ability to understand the meaning of single words. It may well be that left temporal-lobe damage results in impaired encoding of all auditory-verbal material, but that the intact right hemisphere can provide some assistance in the encoding of meaningful material.

On the synonym-generation task, the immediate recall of the LTh subgroup was as good as that of the normal control group, with many of the temporal-lobe subjects scoring above the mean of the control group. This does not appear to be because the task was an easy one, as no subject was at ceiling, and the mean number of words recalled by the normal control group was only 50 per cent of the total number of words generated originally (see Fig 5). Moreover, the LTH subgroup was markedly impaired in the immediate recall of the same set of words. In this case, Rains's (1981) depth-of-processing study provides a nice counterpoint to the results from the word-generation study. Rains's left temporal-lobe subgroups were equally impaired in the immediate recall of words for which they had previously made a semantic judgement. Thus it appears that having to search for, and produce, a specific item from semantic memory (as in the word-generation task) is sufficient to offset, at least temporarily, the verbal-memory deficits for the group of left temporal-lobe patients with small hippocampal excisions.

The serial-position curve for immediate recall of the synonyms (see Fig. 11) provides evidence for a normal pattern of recall for the LTh subgroup. This group is not different from the normal control group in either the primacy or recency portions of the curve. According to the traditional view of memory (e.g., Waugh & Norman, 1965), this means, for the

LTh subgroup, that items generated at the beginning of the test list have been successfully consolidated in long-term storage. In contrast, the curve for the LTH subgroup shows no evidence of any primacy effect, suggesting an almost complete failure on the part of subjects in this group to consolidate new verbal information. Once again, however, both of the left temporal-lobe subgroups were unimpaired in their recall of the final two items from the list. Jaccarino-Hiatt found a similar dissociation for her left temporal-lobe subgroups in their immediate free recall of items from a word-list, with only her LTh subgroup showing any primacy effect (Jaccarino-Hiatt, 1978; reported by Milner, 1978, 1980).

Although the verbal-memory deficits seen in left temporal-lobe patients are typically more severe in delayed recall than in immediate recall (Milner, 1967), the impairment of the LTh subgroup in their delayed recall of the synonyms was somewhat suprising, given their good level of immediate recall for these items. Normal subjects, after a delay, usually recall few of the items that were originally presented in the final list-positions, even though they had produced them in immediate recall. This finding is generally interpreted as confirming that the recency effect is the result of such items being originally held in phonemic form in the verbal buffer, and never coded for transfer to long-term storage (Baddeley, 1976). In contrast, items that are produced from the earlier parts of a list in immediate recall are considered to have been recalled from long-term storage and, hence, are more likely to be recalled again after a delay. The patients in the LTh subgroup showed an average loss of more than 40% of all the items that they had recalled initially, in contrast to a 25% average loss for the normal control group. This differential loss of verbal information for the LTh subgroup cannot be interpreted as being the result of poor initial encoding, given the requirements of the task and their normal immediate-recall scores. It seems most likely that in immediate recall the information was still being held in intermediate memory, where it would normally be retained prior to its consolidation (cf. Wickelgren, 1970). The loss of much of this information after a delay suggests that little of it was actually consolidated.

The findings from these experiments support the original hypothesis, that a left temporal-neocortical excision is sufficient to impair the encoding of verbal material, which then leads to poor storage of that same material. For patients with the hippocampus spared (subgroup LTh), precise semantic encoding can offset that deficit for a time, resulting in normal storage of verbal information in intermediate memory. In contrast, the patients with large hippocampal excisions (subgroup LTH) were unable to take advantage of precise encoding, being equally impaired in their immediate recall of both rhymes and synonyms. This strongly suggests that the intermediate-memory system of this latter group does not function properly.

PART II

Experiment 1

The associative-learning experiment described in Experiment 1 was designed originally to evaluate the ability of patients with left temporal-lobe lesions to create, and maintain, an internally-ordered continuum in working memory.

In a previous study, Read (1978, 1981) showed that patients who had undergone a left anterior temporal lobectomy were markedly impaired in their ability to solve deductive-reasoning problems of the general form 'A is taller than B: B is taller than C. Which one is shortest?' Patients with comparable excisions from the right temporal lobe performed normally. On this type of task the more difficult items (e.g., A is not as tall as B: C is not as short as B. Which one is tallest?) impose a considerable load on short-term verbal storage processes. By recoding the information given in each premise into a visuo-spatial image, this working-memory load can be reduced considerably. Hence, the performance of normal subjects improves significantly when they are told to form a mental image of the information contained in each premise (Potts & Scholtz, 1975). Despite being encouraged to use such mental images, most of the subjects in Read's left temporal-lobe group reported being unable even to form these images. This finding suggested that the deficit shown by the left temporal-lobe group on the deductive-reasoning task might be the result of a more general impairment, either in the ability to recode verbal information into visuo-spatial form, or in the ability to store this recoded information temporarily as an aid to problem solving. An alternative explanation, that the inability of these patients to form mental images might have been due to a primary impairment in their ability to understand and remember all of the verbal information contained in the premises, could not be ruled out. Most of these patients, however, scored within the normal range on De Renzi and Vignolo's (1962) Token Test of language comprehension, where the verbal commands can be as long as those in the deductive-reasoning problems. Lesser (1976), moreover, has pointed out the large verbal-memory component inherent in the Token Test. It was assumed, therefore, that the impairment seen on the deductive-reasoning task after left temporal lobectomy reflected an impaired ability to recode, or store temporarily, the verbal information given in the premises of the problem.

In order to find out whether this impairment was limited to the verbal domain, it was decided to assess the ability of patients with left temporal-lobe lesions to form, or maintain, internal representations on a learning task in which there were no verbal stimuli. Such a test would require, for its successful completion, the creation and maintenance of an internal representation of perceptual stimuli. A modified version of an associative-learning task, in which the stimulus items were taken from a physical continuum, was created especially for this purpose.

In previous studies of this type, the stimulus items have been taken from a perceptual continuum (e.g. different line lengths; or different shades of grey), but have been paired (randomly) with a set of verbal response-items. Stimulus items were never presented in the order in which they occurred along their continuum. Either a fixed number of trials was given, or testing was continued until some criterion level of performance was reached. When the total number of errors made for each pair of items was plotted against the stimulus items ordered along their continuum, an inverted U-shaped function was obtained, which has been described as a serial-position curve (Bower, 1971). Subjects made fewest errors on the stimulus items at the ends of the range, and most errors on those pairs where the stimulus items came from the middle of the range (Bower, 1971; Ebenholtz, 1963, 1966; Jensen, 1962; McCrary & Hunter, 1953; Murdoch, 1960). Bower suggests that the reason for this effect is the gradual formation, beginning with the end items, of an internal representation of the relationships between the stimulus items ordered along their continuum. Such a representation is held to be almost essential for the correct pairing of the complete set of stimulus and response items (c.f. Potts, Banks, Kosslyn, Moyer, Riley & Smith, 1978).

In the associative-learning task used in Experiment 1, a set of non-verbal response items was used, which remained in full view of the subject at all times. In this way it was hoped to prevent the left temporal-lobe group from being handicapped by possible verbal-comprehension or verbal-memory difficulties. It was assumed that if the left temporal-lobe subjects were indeed impaired in their ability to form, or to maintain, an internal representation of the stimulus items, then the pattern of error responses made by that group should reflect this difficulty. If the impairment was great, the serial-position curve for the number of errors made to each stimulus-item should be essentially flat, with no savings in the number of errors made in response to items from the ends of the continuum.

Experiment 2

The comments of a number of subjects suggested that one of the most difficult parts of the associative-learning task was in knowing which stimulus item they were being shown on a particular trial. In order to explore this aspect of the task more directly, an absolute-judgement task was created (using stimuli similar to those used in the associative-learning task), in which subjects were required to number each stimulus item in the order in which it occurred along its continuum (i.e., the smallest item was number 1, the next smallest, number 2, and so on).

Experiment 3

The matching-to-sample tasks were included as control tasks, to guard against the possibility that patients who had difficulty with the absolute-judgements task might have been impaired because of a visual-discrimination deficit.

The same stimulus materials used in the absolute-judgements task were employed for the matching-to-sample tasks.

Experiment 1: Associative Learning

The Paired-Associate method is a time-honoured way of studying the course of verbal learning (Gibson, 1940; Kling & Riggs, 1971; Woodworth & Schlosberg, 1954). In its most basic form, the reinforce-test procedure, a list of N pairs of nonsense syllables or words is presented to a subject, one pair at a time. Then the stimulus items from these pairs are re-presented in a new order, and the subject tries to recall the corresponding response items. The pairs are presented in different orders on successive trials. A correction procedure is used, in which the subject is told the correct response if he fails to give it within a few seconds. The measure used is normally the total number of correct responses in a fixed number of trials. The method was originally developed to study such variables as meaningfulness of nonsense syllables or familiarity of words.

In the method of anticipation, each stimulus item is given separately, and a response made to it, following which both the stimulus and response items are presented simultaneously. Then the next stimulus item is presented, and so on, until all the items have been presented. Order of presentation of the complete set of stimulus-response pairs is randomized for each separate block of trials. The task usually continues until all pairs have been learned to some criterion.

Effects of Unilateral Brain Lesions on Associative Learning

Previous studies have shown that patients with left temporal-lobe lesions are impaired in their ability to learn verbal paired-associates (Meyer & Yates, 1955; Milner, 1962a), regardless of whether these are presented in spoken or in written form (Blakemore & Falconer, 1967; Milner, 1967). For the associative-learning of pairs of non-verbal stimuli, the little evidence that is available would seem to suggest that neither left nor right temporal-lobe subjects are impaired (Meyer, 1959). It is possible, however, that Meyer's nonverbal tasks were simply too easy for all of his subjects.

De Renzi (1968) has suggested, on the basis of his findings in patients with unilateral vascular lesions of the brain, that all associative-learning tasks, whether the stimuli themselves are verbal or non-verbal, have a large verbal component, because subjects tend to name all the stimuli in an effort after meaning (Bartlett, 1932). De Renzi, however, used the reinforce-test method for his non-verbal tasks, subjects being shown five pairs of non-verbal stimuli before being tested for recognition of each appropriate response item. Under such conditions, it would indeed be helpful to use some verbal mnemonic. De Renzi's findings, therefore, may have been due more to the method of presentation than to any necessary use of a verbal code in associative-learning tasks.

Recent studies by Petrides (Note 4) have shown clearly that associative-learning tasks can be created that appear to have a minimal verbal component. Petrides has adapted the conditional-response paradigm, previously used to test non-human primates (Goldman & Rosvold, 1970), for use as an associative-learning task with human subjects. He has six stimulus items and six response items, which remain in front of the subject throughout the test. The experimenter indicates one of the stimulus items, and the subject discovers, by trial and error, the correct response item, and then must remember it. The test continues, with randomized presentation of the stimulus items, until the subject has reached a stringent criterion, or until a certain number of trials have been given. Using simple stimuli (a set of identical blue lights grouped together in a spatial pattern, one of which lights up as the stimulus on any given trial) and simple response items (six blank file cards laid out in a row in front of the subject), Petrides has been able to demonstrate a major associative-learning deficit for patients with unilateral lesions of the right frontal cortex, and a more variable deficit for patients with left frontal-lobe lesions. On this same task, the only patients with temporal-lobe lesions who were impaired were those with extensive encroachment upon the right hippocampal region (RTH), consistent with their known deficits on other tasks that involve memory for spatial location (e.g., Smith, 1980; Smith & Milner, in press). These findings demonstrate that, given appropriate stimuli and test conditions, patients with left temporal-lobe lesions, even those with radical excisions of the hippocampal region, may be unimpaired on an associative-learning task.

The associative-learning task used in the present investigation involved associating each of a set of six colour photographs, laid out in a spatial array, with one item from a set of easily-discriminable rectangles, which were only shown one at a time. The method of testing was the same as that used by Petrides, in that subjects were required to discover, by trial and error, and then remember, which photograph was paired with each stimulus item. The spatial position of the photos was changed on every trial, in order to eliminate the possibility of a subject's using spatial location as an aid to memory. It was hypothesized that any impairment found for left temporal-lobe subjects on this task, could be interpreted as being due to their inability to retain an accurate representation of the stimulus items in memory, rather than to an associative-learning difficulty. Particular importance was attached, therefore, to the shape of the serial-position curve, which would show the number of errors made in relation to each stimulus item (ordered along the continuum).

Test Materials and Procedure

The stimulus items comprised seven identical sets of six different rectangles of black paper, each 8 cm high, ranging from 1 cm to 7 cm in width (see Table 3 for exact measurements). Each rectangle was mounted vertically in the centre of a white

Table 3

Stimuli Used in the Associative-Learning Task

	Number					
Test materials	1	2	3	4	5	6
Rectangles[a] (width shown in cm)	1.0	2.0	3.2	4.4	5.7	7.0

[a] Each rectangle is 8 cm high

file card, 15 cm wide x 10 cm high. The 42 stimulus cards were presented in pseudorandom order, within blocks of six, so that no two consecutive rectangles were identical and not more than two sucessive rectangles were consecutive items within a series. The response items were the set of six colour photographs shown in Figure 12 (photomicrographs showing double histofluorescent staining of the rat brainstem; B. E. Jones, 1981). Seven sets of these same six photos were mounted, each set on a different 43 cm x 30 cm white card, so that each photo occurred at least once in each of the six possible locations.

Subjects were first shown the sets of photos, and were told:

> There are six different photographs mounted on each of these white cards. You'll be seeing the same six photos many times; however, as you can see, the photos are in different positions on each card.

Subjects were next shown the set of black rectangles, and told:

> There are six different rectangles of black paper mounted on these cards. Each different rectangle has been paired with one of the color photos on the large white cards. What you have to do is to discover, by guessing, which photo goes with each different rectangle. I will tell you if you guess wrongly, and I want you to keep

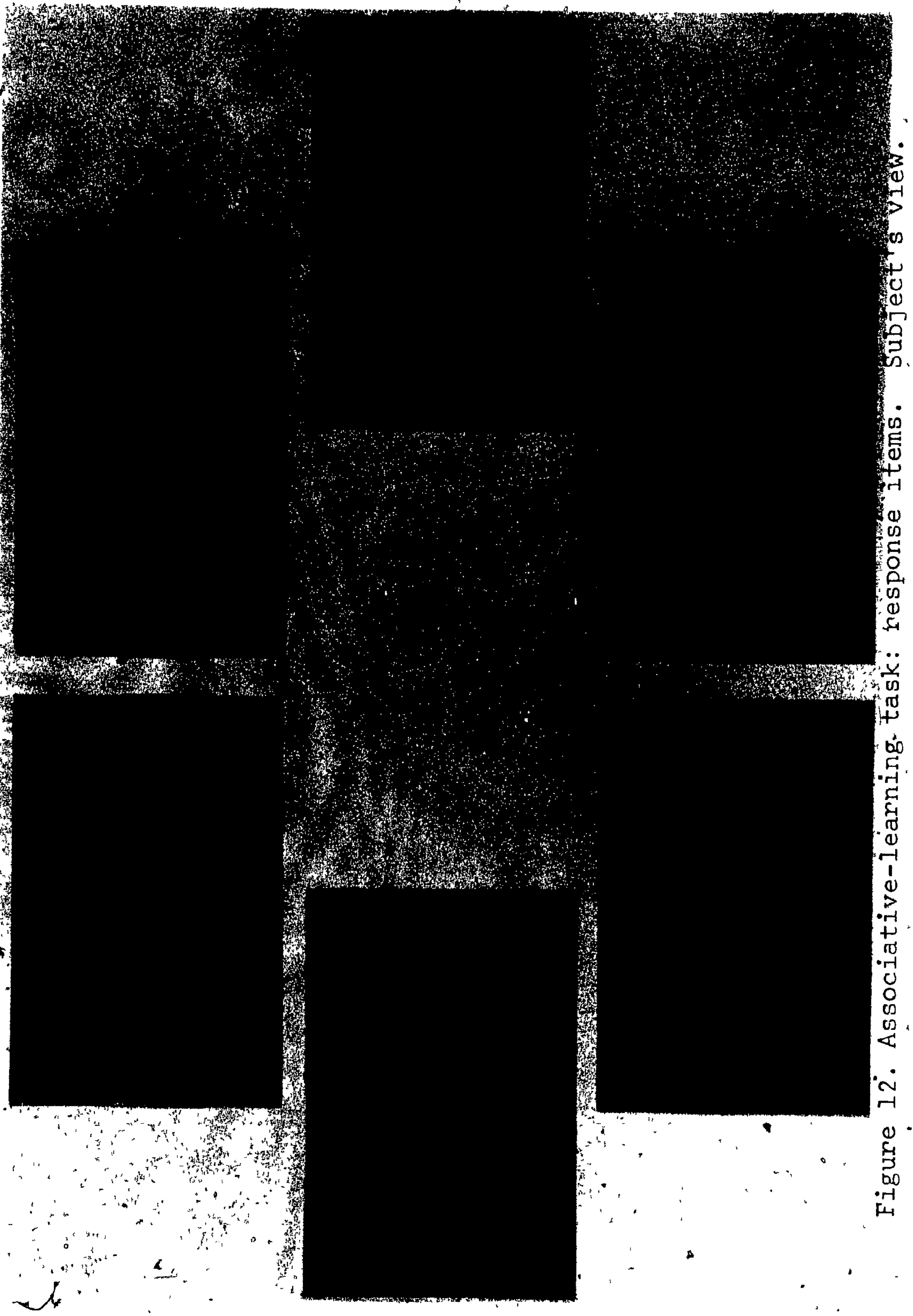

Figure 12. Associative-learning task: response items. Subject's view.

> on guessing until you choose the correct photo. Once you have guessed correctly, that same photo will always be paired with the same rectangle, no matter where the photo is on the card. There is nothing about the colour or the size of the photo that will let you know how the photos and rectangles are paired (see Fig. 13 for experimental set-up).

These instructions were repeated, or clarified, as necessary until the subject understood what was required of him.

A minimum of 42 trials (seven sets of the six pairs of stimuli) was given to each subject. Criterion performance was taken to be three consecutive sets of six correctly-paired rectangles. If a subject did not reach this criterion within 126 trials (21 sets of six), testing was stopped. Subjects were not informed that the rectangles were to be presented in blocks of six; nor were they told what constituted criterion performance.

Each photo was assigned a different letter as a code to enable the experimenter to record each error as it was made. No matter how many incorrect choices were made to a particular stimulus item on a given trial, for scoring purposes these were counted as a single error. The first three sets of six trials were used for practice, and errors made during these trials were not counted in the final error-scores. The experimental subject-groups taking part in this experiment are shown in Table C of the Appendix.

Figure 13. Associative-learning task: experimental set-up. The experimenter is shown presenting one of the stimulus items, while the subject chooses one of the response items.

Results

Because testing did not continue beyond 21 sets of six trials, and given the wide range of error scores within each group, it was considered appropriate to use a non-parametric method of analysis (Siegel, 1956). All subjects were ranked according to the total number of errors that they had made on the task. Paired comparisons of the two temporal-lobe groups, using a Wilcoxon rank-sum test (Ferguson, 1971), revealed that the left and right temporal-lobe groups did not differ from one another ($z = 1.63$, n.s.). A non-parametric Kruskal-Wallis one-way analysis of variance was then run on the rank scores. The significance of the calculated value of H was assessed by comparison with X^2 tables, for $k-1$ degrees of freedom. This test, comparing the performance of the four temporal-lobe subgroups with that of the normal control group, revealed significant group differences ($H = 13.88$, $p < .01$).

Hippocampal Effects

The effects of radical excision of the hippocampal region on performance in this associative-learning task were assessed by means of Wilcoxon Rank-Sum tests (Ferguson, 1971). Separate comparisons were made between the normal control group and each of the temporal-lobe subgroups. Paired comparisons were also made between the small and large hippocampal-excision subgroups, within each temporal-lobe group. These comparisons revealed that the group of patients with small left-hippocampal excisions (LTh) was not impaired relative to the normal control group ($2\bar{R}-R$ = 328, n.s.). In contrast, the group with large left-hippocampal excisions (LTH) was impaired relative to both the normal control ($2\bar{R}-R$ = 77, $p < .002$) and LTh ($2\bar{R}-R$ = 94.5, $p < .02$) groups. Neither of the two right temporal-lobe subgroups was impaired (RTh; $2\bar{R}-R$ = 305.5: RTH; $2\bar{R}-R$ = 99). Thus on this ostensibly non-verbal associative-learning task, the only temporal-lobe group to show any significant impairment was the LTH group.

Pass-Fail Comparisons

Within the limits of testing, just over half of the temporal-lobe patients failed to reach criterion on the associative-learning task. Thus it was possible to explore, within groups, the relationship between the extent of hippocampal excision and the ability to reach criterion.

Separate X^2 analyses (using Yates's correction for small samples) were performed for each temporal-lobe group, comparing the ability of the two hippocampal subgroups to reach criterion on this learning task. As can be seen from Table 4, these results complement those for the ranked error-score comparisons given above. Significantly more left temporal-lobe patients with large hippocampal removals failed to reach criterion, than those with small hippocampal excisions. In contrast, the two right temporal-lobe subgroups did not differ on this measure.

Serial-position effects. The associative-learning task was originally designed to discover whether patients with

Table 4

Chi-Square Comparisons Within Each Temporal-Lobe Group for the Associative-Learning Task

Left Temporal-Lobe Group				Right Temporal-Lobe Group			
	Pass	Fail	Total		Pass	Fail	Total
LTh	11	7	18	RTh	9	8	17
LTH	1	9	10	RTH	3	5	8
Total	12	16	28		12	13	25
	$\underline{X}^2 = 4.93^*$				$\underline{X}^2 = 0.09$		

* = $\underline{p} < .05$

left temporal-lobe lesions could form, and maintain in working memory, an internal representation of an ordered set of stimulus items. The results reported above show clearly that only the subgroup of patients with extensive removal of the left hippocampal region was impaired on the task. An analysis based upon comparison of the total number of errors, or of the ability to reach criterion within a fixed number of trials, does not, however, reveal the reason for the poor performance of the LTH subgroup. Some subjects, from all groups tested, were unable to reach criterion on the task, and many of these commented on the difficulty of knowing which stimulus item they were being shown on any particular trial. It is, of course, possible that the left temporal-lobe patients who failed to reach criterion might have done so for reasons other than a difficulty in forming and maintaining an internal representation of the stimulus items. If this were the case, then the number of errors made in response to each stimulus item might be no greater for these left temporal-lobe subjects than for other subjects who also failed.

In order to assess whether this was the case, serial-position curves were plotted for the normal-control and temporal-lobe groups (see Fig. 14). Those subjects who reached criterion on the task were assigned to a "pass" subgroup, and those who failed to reach criterion were assigned to a "fail" subgroup. Within each subgroup, a mean error score was calculated for

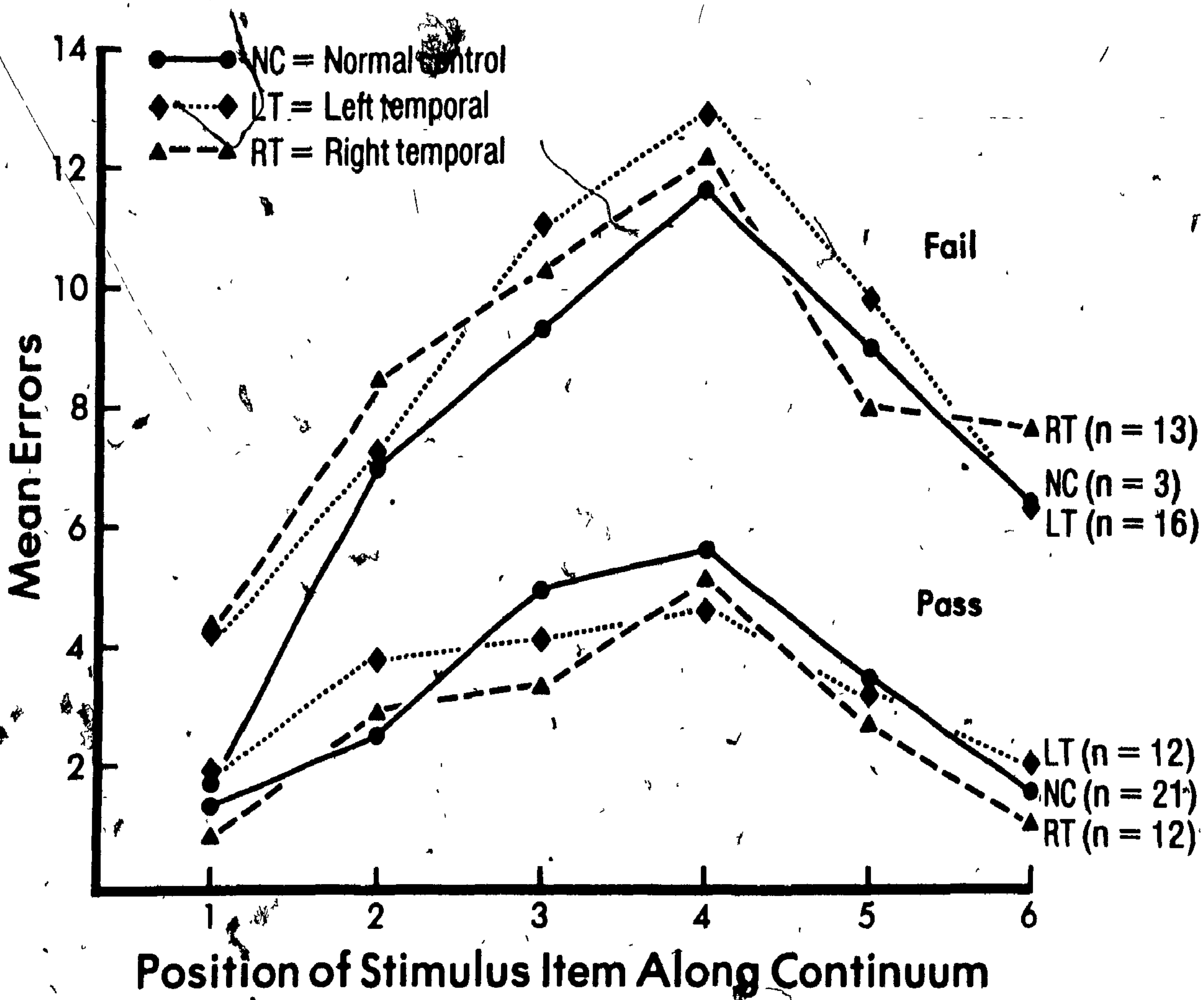

Figure 14. Associative-learning task: serial-position curves. Mean number of errors made in response to each stimulus item, plotted as a function of the position of each item within its continuum. Normal-control and temporal-lobe subjects are divided into groups, based upon whether or not they reached criterion.

each of the six stimulus positions. For evaluation of all repeated-measure effects conservative df were used (Greenhouse & Geisser, 1959). A three-way (Group x Pass/Fail x Serial-Position) analysis of variance gave significant main effects for Pass/Fail (F (1,71) = 73.22, $p < .001$), and for Serial-Position (F (7,355) = 29.10, $p < .001$), as well as a significant two-way Pass/Fail x Serial Position interaction (F (7,355) = 4.29, $p < .05$). Most interestingly though, the group comparisons did not approach significance (F (2,71) = 0.48), and neither did any of the interactions that involved the groups. These findings suggest, therefore, that the left temporal-lobe subjects who failed to reach criterion on this task did not differ, with regard to their ability to create and maintain internal representations of the stimulus items, from the right temporal-lobe or the normal control group subjects who also failed.

Other Groups

Of the 12 patients with excisions that involved the frontal neocortex, not one was able to reach criterion on the associative-learning task. In the comparison of the ranked error-scores of the two frontal-lobe groups and the normal control group, the overall Kruskal-Wallis analysis was significant (H = 15.42, $p < .001$), as were the subsequent paired comparisons of left and right frontal-lobe groups with the normal control group (left; $2\overline{R}-R$ = 29.5, $p < .002$: right; $2\overline{R}-R$ = 25, $p < .002$). The two frontal-lobe groups did not differ significantly from one another ($2\overline{R}-R$ = 35).

The two patients with excisions from the left parietal lobe also failed to reach criterion on this difficult associative-learning task, whereas the patient with a right parietal-lobe excision had no difficulty in doing so.

Experiment 2: Absolute Judgements

The results of the Associative-Learning task suggested that a major reason for subjects failing to reach criterion was an inability to maintain a sufficiently accurate memory trace of the stimulus items from the middle of the continuum. In order to test this hypothesis more directly, an Absolute-Judgement task was created, in which subjects were required to number each of six rectangles as these were presented in random order, "one" being the narrowest, and "six" being the widest. Such tasks make little or no demand on associative-learning ability, appear to have a minimal verbal-memory load, and are easily understood by all subjects.

Previous studies with normal subjects (see Alluisi, 1957; Garner, 1962; Miller, 1956; for reviews) have shown that the maximum number of items that can be correctly identified, using stimuli varying along a single dimension, is rather small (an average of 6.5 items, Miller, 1956). Moreover, increasing the stimulus range, so that individual items are further apart along the physical continuum, makes little difference to the number of items that can be accurately identified (Alluisi, 1957; Eriksen & Hake, 1955a, 1955b; Garner, 1953; Garner &

Hake, 1951; Pollack, 1952, 1953). This, of course, is different from the situation in a discrimination task, or in a delayed matching-to-sample task, where a single stimulus item has to be recognized from among a group of similar stimuli after a short delay interval. In both of these latter cases the physical spacing of items along their continuum is a major factor in the difficulty of the task.

On absolute-judgement tasks, normal subjects usually reach their asymptotic performance level within a few trials, and can rapidly accommodate to a shift in the range of the stimuli, or even to a transposition where the items at one end become the middle items of a new set of stimuli (Bower, 1971; Helson, 1964). To account for such findings it has been suggested (Bower, 1971; Potts et al., 1978) that part of the memory trace of the set of stimuli is an amodal representation of the ordinal relationships between stimulus items, together with an analogue representation of the items themselves (see Potts et al., 1978, for discussion). In contrast, memory for individual stimuli (as in a delayed matching-to-sample task) may involve an accurate internal replica of the actual stimuli, as has been suggested by Paivio (1975; cf. King, 1963, 1965, for some experimental support).

The hypothesis put forward here is that the ability to perform absolute-judgement tasks successfully depends upon being able to encode and store both ordinal and analogue relations in an intermediate-memory system. For the purposes of this thesis, the specific nature of the coding used by the patients is of less interest than the functional status of this intermediate-memory system.

Test Materials and Procedure

Originally, this task was given using the same set of rectangles as had been used in the associative-learning task. This proved, however, to be too easy a test, even for subjects who had failed the associative-learning task. As a consequence, pilot studies were run with normal subjects to find an appropriate level of difficulty for a six-rectangle absolute-judgement task, such that the great majority of the normal subjects tested were able to reach criterion. The difficult set of rectangles used is shown, in order of size, in Figure 15. In order to explore further the limits of the expected deficit in the patient groups an easy set of rectangles was also created, on which all normal control subjects tested were able to reach criterion. Specifications for the two sets of stimuli are given in Table 5. Each stimulus-item was mounted on a 20 cm x 12.5 cm white file card. For each set seven copies of each item were prepared. Within each block of six, the 42 stimuli were arranged in pseudorandom order, such that two identical stimuli never appeared consecutively, and not more than two adjacent items from within a series occurred consecutively. Each set of 42 cards was mounted on two 8 cm rings, so that

Figure 15. Absolute-judgement and delayed matching-to-sample tasks: stimuli. The six rectangles shown are those that formed the difficult set in the absolute-judgement tasks. (*Note*. Stimuli reduced to 43% of original size.)

Table 5

Sets of Stimuli Used in the Absolute Judgement Tasks.

	Number					
Test materials	1	2	3	4	5	6
Rectangles[a] (width shown in cm)						
Difficult set	3.00	4.00	5.00	6.00	7.00	8.00
Easy set	2.50	3.75	5.00	6.25	7.50	8.75

[a] Each rectangle is 10 cm high.

only one stimulus item could be seen by the subject at any one time during the test. A different order of item presentation was used for each set of stimuli.

For the patients, the order of task presentation was always the same; after completing the matching-to-sample and delayed matching-to-sample tasks (to be described in Part II: Expt. 3), each patient was given a short practice session with a set of squares, followed by testing on the difficult set of rectangles. Then another short session with the squares was given, as a filler task, before the final test session with the easy set of rectangles. The instructions to each patient were as follows:

> I'm going to be showing you a series of six-rectangles. All I want you to do is to number each item as you see it. Call the smallest one "number 1", call the next smallest "number 2", and so on up to the largest one, which I want you to call "number 6". I will tell you, for each item, whether you are right or wrong. When you are right we go on to the next item, when you are wrong I want you to try again until you get it right.

A minimum of 42 stimuli were shown to each subject for each set of rectangles, with criterion performance being 18 consecutive correct trials (i.e., three sets of six items). No time limit was set for each judgement, and subjects were permitted to correct their initial choice before being told whether it was right or wrong. The test continued until the subject either reached criterion or completed 126 trials (21 sets of six items). Subjects were not told that test items were given in blocks of six; nor were they told how many items they had to get right in order to reach criterion. As in the associative-learning task, no matter how many incorrect choices were made to a particular stimulus-item on a given trial, for scoring purposes these were counted as a single error. Once again, any errors made during the first 18 trials were not counted in the final error-score. The patients taking part in this experiment, grouped according to side and site of lesion, are shown in Table D of the Appendix.

Special instructions for H.M. Because of H.M.'s extreme memory difficulties, the test instructions were modified for him in the following way. Two hand-written file-cards, one with the words "smallest = 1", the other with the words "largest = 6", were placed in front of him, so that he could refer to them for the duration of the test. He was then given the same instructions as were given to other subjects, with the following addition:

> To help you to remember how I want you to number the widths, I'm going to leave these two cards on the desk in front of you. You may look at them any time you want to during the test.

H.M. was only tested on the easy set of rectangles, his performance being so poor on these that it seemed pointless to try the more difficult set.

Results

As in the associative-learning task, the results for both of the absolute-judgement tasks were evaluated by ranking all subjects in terms of the total number of errors they had made. In this study, the ability of the patients with large hippocampal excisions to create, and maintain, a precise internal representation of a set of rectangles, was of particular interest. Because of this, the performance of the temporal-lobe subjects will be reported before the results for the other patient groups. Each temporal-lobe group is again subdivided on the basis of the extent of hippocampal excision.

Analysis of Ranked Error-Scores

a) Difficult set. A Kruskal-Wallis one-way analysis of variance, performed on the rank scores for the five groups, revealed significant overall differences among these groups ($\underline{H} = 35.99$, $\underline{p} < .001$).

b) Easy set. Once again, the overall analysis revealed significant differences among the five groups ($\underline{H} = 21.66$, $\underline{p} < .001$).

The complete left and right temporal-lobe groups did not differ significantly from one another in their performance on either set of rectangles (Difficult Set; $\underline{R}_{24,24} = 546$: Easy Set; $\underline{R} = 536$).

Hippocampal effects. Subsequent paired comparisons between the normal control group and each of the temporal-lobe subgroups, as well as comparisons within each temporal-lobe group, were performed for each set of rectangles. These results are presented in Table 6. Relative to the normal control group the left and right temporal-lobe subgroups with small hippocampal excisions (LTh & RTh) were not impaired; in contrast, the subgroups with large hippocampal excisions (LTH & RTH) were impaired. The within-group comparisons were also significant: in each case the subgroup with large hippocampal excisions was inferior to the subgroup with small hippocampal excisions.

Pass versus Fail

As in the associative-learning task, there were a number of patients from both right and left temporal-lobe groups who failed to reach criterion on the difficult set of rectangles within the limits of testing. Thus it was possible to compare, within each group, the incidence of patients passing and failing the test, as a function of the extent of hippocampal excision. Separate 2 x 2 tables, showing Pass vs. Fail against Large vs. Small Hippocampal-Excision, were created for each of the two temporal-lobe groups (see Table 7). Probabilities of such distributions occurring by chance were evaluated by a Chi-square test (applying Yates's correction for small samples). For both left and right temporal-lobe groups, patients with

Table 6

Results of Wilcoxon Rank-sum Tests for the Absolute-Judgement of Rectangles

	Set	
Comparison	Difficult	Easy
Normal control vs LTh	280.0	138.0
Normal control vs. LTH	59.5****	44.5*
LTh vs. LTH	65.0*	28.5**
Normal control vs. RTh	255.5	76.0
Normal control vs. RTH	87.0****	37.0****
RTh vs. RTH	76.5***	24.0***

*$p < .05$
**$p < .02$
***$p < .01$
****$p < .002$

Table 7

Chi-Square Comparisons Within Each Temporal-Lobe Group for the Absolute-Judgement Tasks

Left Temporal-Lobe Group				Right Temporal-Lobe Group			
	Pass	Fail	Total		Pass	Fail	Total
LTh	13	3	16	RTh	13	1	14
LTH	2	6	8	RTH	2	8	10
Total	15	9	24		15	9	24
	$X^2 = 5.00^{*}$				$X^2 = 10.29^{**}$		

* = $p < .05$

** = $p < .01$

large hippocampal excisions were significantly more likely to fail to reach criterion on the difficult set of rectangles than were patients with small hippocampal excisions (left temporal-lobe group; $\underline{X}^2 = 5.00$, $\underline{p} < .05$, right temporal-lobe group; $\underline{X}^2 = 10.29$, $\underline{p} < .01$). Of all the patients with unilateral excisions, only one (M.B., a right temporal-lobe subject with a large hippocampal excision) was unable to reach criterion on the easy set of rectangles, making a total of 23 errors in 108 trials.

<u>Serial-position effects</u>. For the difficult set of rectangles, subjects from within the main, right and left temporal-lobe groups were once again divided into subgroups, based upon their ability to reach criterion on the task. Mean error scores for each "pass" and each "fail" group were then plotted against the stimulus items ordered along their continuum (see Fig. 16). Because there was no normal control group in the "fail" condition[2] an initial two-way analysis of variance (Group x Serial Position) was run with the five subgroups. This analysis was followed by planned single-*df* contrasts (using the Group error-term) between the "pass" and "fail" subgroups. Following this, planned contrasts were performed

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[2] The data for the one control subject who failed to reach criterion were excluded from the calculation of the mean error scores for that group.

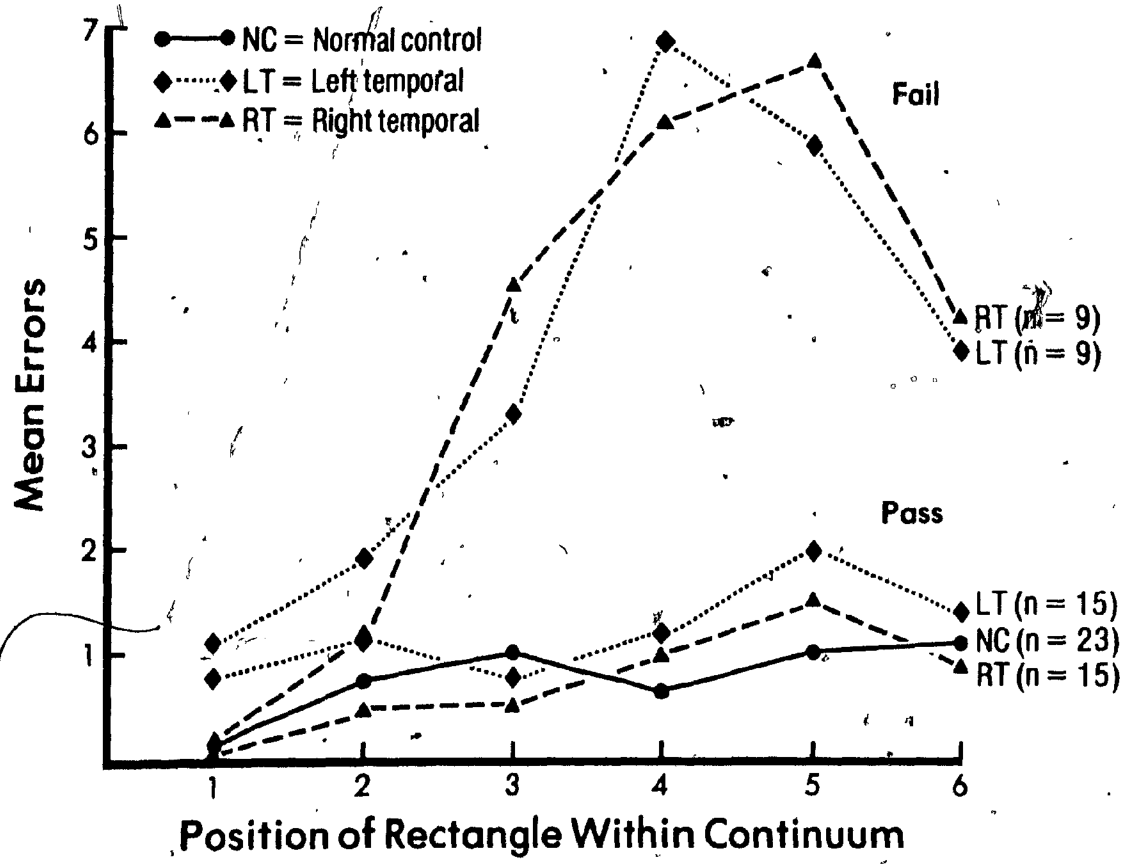

Figure 16. Absolute-judgement task: serial-position curves. The mean number of errors made in response to each stimulus item for the difficult set of rectangles. Temporal-lobe ~~subjects are~~ grouped according to side of lesion and to whether or not they reached criterion.

to assess whether there were any differences between the serial-position curves of the two "fail" groups, or between the curves of the three "pass" groups. Once again, conservative degrees of freedom were used in assessing any repeated-measure analyses. For the overall analysis, as expected, the Group and Serial-Position effects were significant (Group; F (4,67) = 27.27, $p < .001$: Serial-Position; F (5,335) = 48.74, $p < .001$), as was the Group x Serial Position interaction (F (20,335) = 9.26, $p < .001$). The planned comparison between the pass and fail subgroups was also significant (F (1,67) = 60.55, $p < .001$). There were, however, no differences between the three subgroups who passed, or between the two subgroups who failed ($F < 1$, in both cases).

Patient H.M.

The performance of H.M. on the easy set of rectangles provides a good baseline from which to assess the effects of unilateral hippocampal excision. H.M. was able to identify the narrowest width correctly each time that it was shown to him, suggesting that he had no difficulty in understanding the requirements of the task. Out of the remaining 90 trials, however, his first choice was incorrect 49 times. More to the point, he was sometimes out by as many as three places in his first choice (e.g., saying "two" when shown rectangle number five). On this easy set of rectangles, no other subject was ever off by more than one place in their first choice.

Other Patient Groups

The error scores of the patients with frontal-lobe lesions (shown in Figs. 1-3, under the heading AJ to the right of each brain map) and of the normal-control subjects were ranked for a separate Kruskal-Wallis analysis. The frontal-lobe subjects showed no overall impairment on either set of rectangles (Difficult Set; H = 2.31: Easy Set; H = 2.15), even though five of the eight right frontal-lobe subjects failed to reach criterion on the difficult set (fails shown in Fig 2; passes shown in Fig. 3).

The two left parietal-lobe patients who had failed the associative-learning task were not available for testing on the absolute-judgement task. As can be seen from the results tabulated beside the brain-maps (Fig. 4), the two right parietal-lobe subjects who were tested on the absolute-judgement task made no errors on the difficult set of rectangles. The patient (Br.Be.), who had undergone a complete right occipital lobectomy two weeks prior to being tested, was an 11 year-old girl; despite making more than the average number of errors, she was able to reach criterion on the difficult set of rectangles.

Experiment 3: Matching-to-Sample

The matching-to-sample and delayed matching-to-sample tests were introduced as control tasks for the temporal-lobe patients. They were designed to demonstrate that discrimination of, and memory for, single visual stimuli were not impaired in any of the temporal-lobe subgroups. The same set of difficult rectangles was used as in the absolute-judgement task (see Fig. 15). Of particular interest, in this regard, was the performance of the patients with large hippocampal excisions, because they had been so markedly impaired in their ability to retain an accurate internal representation of the complete set of six stimuli.

Materials and Procedure

The stimulus board for these tasks consisted of a wooden frame, 66 cm wide x 46 cm high, into which large white cards could be slid (63 cm x 45 cm; see Fig. 17). On each of these cards were mounted six different rectangles of black paper, identical to the rectangles that formed the difficult set in the absolute-judgement tasks. A 20 cm wide x 12.5 cm high recess, cut into the centre of the board, was used to display a single sample rectangle, which was mounted centrally on a 20 cm x 12.5 cm white file card. In order to avoid the appearance of afterimages the back of the recess was covered with black paper.

Before beginning the matching-to-sample task, subjects were asked to point to each of the six rectangles displayed on the large card, beginning with the smallest one and going

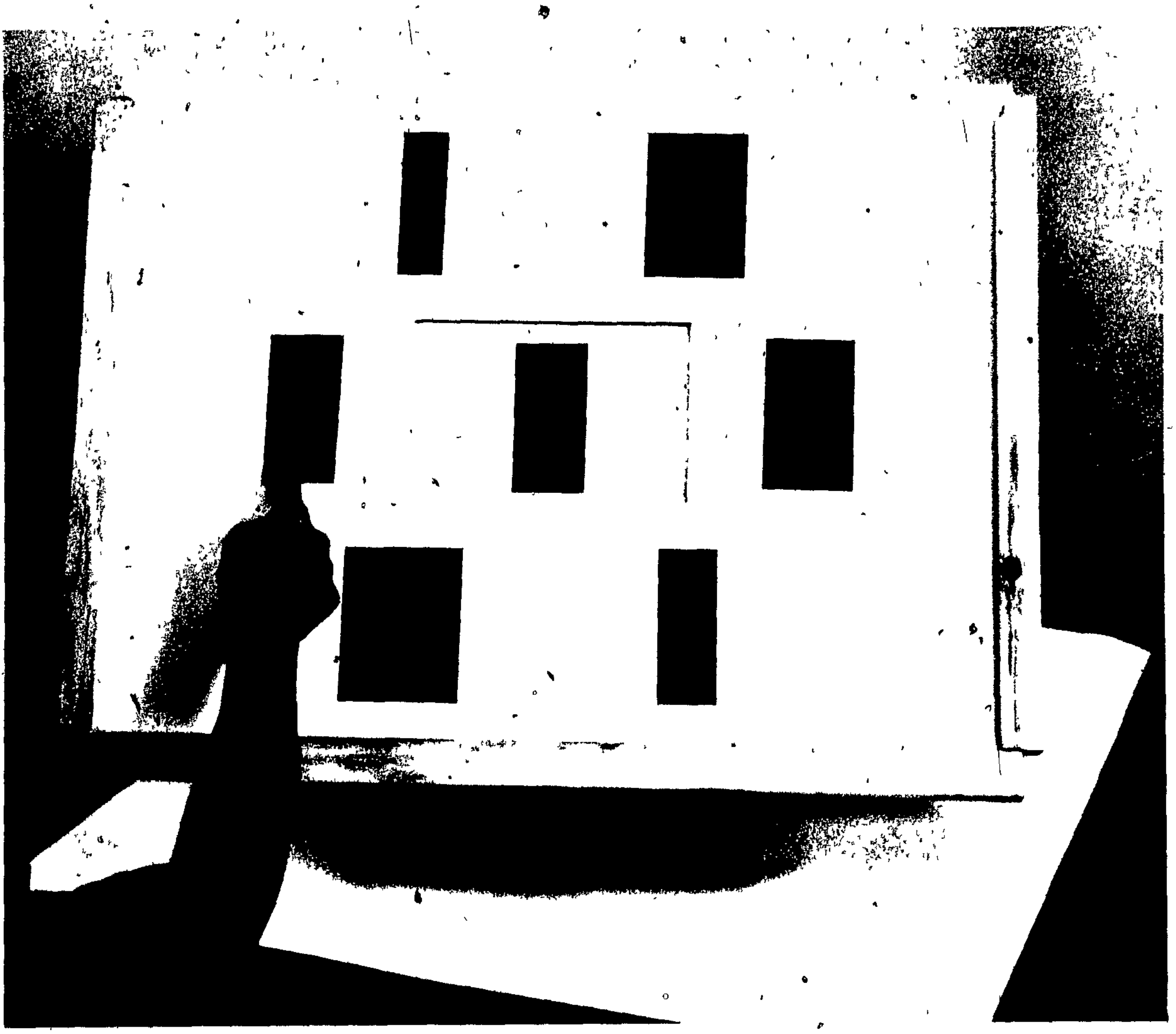

Figure 17. Matching-to-sample task: the experimental set-up. The photo shows a subject pointing to the item that matches the stimlus-item shown in the centre of the board.

in sequence up to the largest one. All subjects were able to do this correctly.

For the matching-to-sample task subjects were told that they would be shown a sample rectangle in the centre of the board, and that they were to point to whichever one of the rectangles around the edge of the board looked the same as the one in the middle.

For the delayed-matching-to-sample task, six different sets of the six rectangles were prepared, each set arranged on one of the large white cards so that the same rectangle never appeared in the same spatial location more than once. Subjects were warned before the start of the test that they would be seeing a different arrangement of the rectangles after each delay interval. A plain 63 cm x 45 cm white card was used to cover up the response cards while the sample item was being shown in the centre of the board. Instructions to the subject were as follows:

> I'm going to show you a sample rectangle in the centre of this board for 5 seconds. Then I'll take the sample away, and for five more seconds all you will see is the large board with the black centre. After that I will uncover one of the sets of rectangles, and you are to point to the rectangle that matches the one you saw a few seconds ago.

There was no limit set on the time taken to respond, and subjects were permitted to correct their choice when they felt it was incorrect. No feedback was given about performance on this task. Each subject was given a total of 18 trials (three complete sets of the six different rectangles).

Results

On the matching-to-sample task there were no subjects, from any group tested, who made even a single uncorrected error. This finding confirms that the individual rectangles that made up the set of difficult items for the Absolute-Judgement task were easily discriminable from one another when they could be inspected simultaneously.

For the delayed matching-to-sample task, subjects in the normal control group, together with those in each of the four temporal-lobe subgroups, were ranked according to the total number of errors made on the 18 trials. The ranked scores were then submitted to a Kruskal-Wallis one-way analysis of variance. This analysis did not come close to significance ($H = 1.89$). A similar analysis, comparing the two frontal-lobe groups with the normal control group, also did not come close to significance ($H = 2.84$). The results of the matching- and delayed matching-to-sample tasks confirm that, in the discrimination and short-term storage of these particular visual stimuli, the performance of the patients with temporal-lobe or frontal-lobe lesions was well within normal limits.

Discussion

The experiments that formed the second part of this thesis were designed to explore the role of the left temporal neocortex in the creation and maintenance of internal representations as aids to memory. The results of the experiments, however, pointed clearly to the importance of the hippocampal region for the temporary storage of such representations.

For the temporal-lobe patients, the results of the associative-learning task were not quite as had been predicted. On this ostensibly non-verbal task, only the left temporal-lobe subgroup with large hippocampal excisions (LTH) was impaired. This finding complements that of Petrides (Note 4) mentioned earlier. In Petrides's study, within each stimulus set (six identical blue lights) and response set (six identical file cards), individual items were discriminable from one another mainly on the basis of their spatial location. Thus a major component of the task was remembering the appropriate spatial locations for each stimulus-response pair. On this task the only temporal-lobe subgroup impaired was the one with large right-hippocampal excisions (RTH). Petrides's finding adds to the weight of evidence demonstrating the importance of the right hippocampal region in the recall of spatial location (e.g., Rains, 1981; Smith, 1980; Smith & Milner, in press). In contrast, spatial location was irrelevant in the present study, because the stimulus items were always presented in the same position, and the position of each response item was changed on every trial. Under these conditions neither of the right temporal-lobe subgroups was impaired.

Two possible explanations suggested themselves as reasons for the deficit of the LTH subgroup in the present study. The first was that the left temporal-lobe subjects were differentially impaired in their ability to retain an accurate representation of the six stimulus items in memory. If this had been so, one might have expected that the number of errors made in response to each stimulus item (shown in the serial-position curve, Fig. 14) would have been different for the left temporal-lobe subjects who failed to reach criterion than for the right temporal-lobe or normal control subjects who also failed to reach criterion. This did not turn out to be the case, however, suggesting that although such a difficulty might contribute to poor performance on the task, there must be another factor involved to explain the consistent impairment of the LTH subgroup.

This additional factor appeared to be that subjects assigned verbal labels to each of the response items as an aid to memory (cf. De Renzi, 1968; Ellis, 1973; Glanzer & Clark, 1963). These verbal labels would also have to be retained in memory for successful completion of the task. The reduced short-term verbal storage capacity of the LTH patients (Milner, 1967) would thus be sufficient to cause their overall difficulty with the task. This explanation for the deficit of the LTH subgroup on the associative-learning task, despite its post-hoc nature, is supported by other evidence. In pilot studies the same set of stimulus widths as had been used in the associative-learning task were tried as stimuli in an absolute-judgement task. In that test all subjects were able to reach criterion, irrespective of how much difficulty they had had in knowing which width was which in the associative-learning task. The poor performance, on the associative-learning task, of the two patients with left parietal-lobe lesions, compared with the good performance of the one patient with a right parietal-lobe lesion, also argues for a verbal component to this task. Indirect evidence for a verbal component comes from the performance of the patients with right temporal-lobe lesions, who would be expected to benefit from using a verbal mnemonic (cf. Jones-Gotman & Milner, 1978) in recoding the complex visual stimuli that were used as the response items. In most other tasks where complex visual stimuli have been used (e.g., Kimura, 1963; Milner, 1975; Taylor, 1969, 1979), patients with right temporal-lobe lesions have been markedly impaired. The fact that the right temporal-lobe group was not impaired on this visual-learning task is a good indication that such verbal recoding was going on.

The fact that in the left temporal-lobe group only the patients with large hippocampal excisions were impaired fits well with the findings for the word-generation task. In that task the left temporal-lobe patients with the hippocampus intact (LTh) were successful initially in remembering a set of words that had been generated on the basis of their meaning, whereas the LTH subgroup was markedly impaired at doing so. It was suggested in the Discussion of those tasks (p. 63) that the reason for the differing abilities of the two left temporal-lobe subgroups lay in the fact that the intermediate-memory system of the LTh subgroup was still functioning relatively normally, whereas that of the LTH subgroup was markedly abnormal. This explanation of the deficit found for the LTH subgroup on the associative-learning task accords well with the strong prediction made in the Introduction, that left temporal-lobe subjects with large hippocampal excisions would be differentially impaired (compared to a group with small hippocampal excisions) on a non-verbal task in which verbal recoding could provide an important aid to memory. This interpretation complements Jones-Gotman's (1975, 1979; Jones-Gotman & Milner, 1978) findings of a more severe impairment for RTH subgroups than for RTh subgroups on tasks where visual imagery provided an additional aid to recall of verbal material.

For the frontal-lobe subjects, the results of the present associative-learning study help to support Petrides's belief (Note 4) that frontal-lobe lesions drastically impair the ability to make associations between stimuli bearing only an arbitrary relationship to one another. In the present study both frontal-lobe groups were markedly impaired. Pribram and his associates have shown (Brody & Pribram, 1978; Grueninger

& Pribram, 1969) that non-human primates with bilateral frontal-lobe lesions do particularly poorly on tasks where the spatial location of the stimuli is changed on each trial. It could be that human subjects with frontal-lobe lesions are also affected by such manipulations, and, if so, this factor may have exacerbated any associative-learning deficits of the frontal-lobe patients in the present study. As in other tasks that result in an impairment for patients with right or left frontal-lobe lesions, so here the method of testing is as important in disrupting performance as the verbal or non-verbal nature of the test materials.

The results for the absolute-judgement tasks were much clearer than those of the associative-learning task. On these tasks only the patients with large hippocampal excisions were impaired, and that regardless of the side of the lesion. The absolute-judgement tasks were also much easier, for all subject groups, than the associative-learning task. Even the patients who failed to reach criterion on the difficult set of rectangles were seldom off by more than one place in their first estimate, and for the easy set of rectangles only one patient with a unilateral lesion failed to reach criterion on the task. The retention of such perceptual information requires the temporary storage of ordinal relationships (e.g., larger than, smaller than) together with some analogue representation of the actual physical size relationships (see Potts et al., 1978, for extensive discussion of these differences). When simple stimuli that vary along a single dimension are used (as in the present study), there appears to be a rapid loss of information from trial to trial (Siegel, 1972), and verbal recoding does not appear to be effective as an aid to retention of the stimulus information (Ellis, 1973). The findings in this thesis suggest that the failure of the temporal-lobe subjects with large hippocampal excisions was due to a reduction in the quality of their internal representation of the stimulus set, rather than to any absolute loss of the ability to form or maintain such representations.

The performance of the amnesic patient, H.M., provides the clearest evidence for the importance of the hippocampal region in the temporary storage of new information. For the easy set of rectangles, the worst performance by any temporal-lobe patient with a unilateral lesion was a total of 23 errors in 106 trials. The combined group of temporal-lobe patients with large hippocampal excisions made a mean of 7.5 errors on the same task. In contrast, H.M. made 49 errors on the easy set of rectangles. He was able to number the narrowest rectangle correctly each time it was shown to him, and was correct on over 55% of trials with widths 2, 3 and 6, suggesting that his internal representation for these items was relatively accurate. Yet he was only correct on 10 out of 36 trials for the other two rectangles (nos. 4 & 5), being off by as many as three positions (e.g., saying "2" when shown rectangle number 5). Like all other subjects H.M. had been required to keep guessing, on every trial, until he gave the correct response.

In absolute-judgement tasks a decision about the correct value to assign to any one stimulus item is determined by the particular set of stimuli being used (Helson, 1964; Parducci, 1965, 1968). Thus individual judgements are made in the context of the complete set of stimuli. This, of course, implies that some internal representation of the stimulus set must be maintained so that accurate judgements can be made. For normal subjects, the five stimuli preceding the one being presented all have a significant effect upon the current judgement (Staddon, King & Lockhead, 1980). It would appear that for the patients with large hippocampal excisions, there must be an abnormally rapid deterioration in the quality of the internal representation, which is equated here with an impairment of intermediate memory.

For the frontal-lobe patients, the results of the absolute-judgement tasks are difficult to interpret. It had been assumed originally that the basis for the predicted frontal-lobe impairment on the associative-learning task would be in the associative aspects of the task, rather than in any difficulty with creating and maintaining an accurate internal representation of the stimulus items. This assumption appears to have been correct for the patients with left frontal-lobe excisions, all of whom were very good at the absolute-judgement task. For the right frontal-lobe group, however, there was a bimodal distribution in test performance. Five patients were very poor at the task (see Fig. 2), whereas the remaining three patients were very good (see Fig. 3). There appears to be no relationship between the number of errors that right frontal-lobe subjects made on the task and either the site or the size of the cortical excision, or the time since operation.

It is important to note that none of the patients, from any group tested, had any difficulty with the delayed matching-to-sample task (although H.M. has still to do this task). The good matching performance of the unilateral temporal-and frontal-lobe groups shows that their discrimination of, and memory for, single examples of the more difficult set of rectangles was normal (cf. Prisko, 1963). Hence, the deficits found for the temporal-lobe patients with large hippocampal excisions were specific to the absolute-judgement task, in which temporary retention of contextual information about the complete set of stimuli was essential for good performance.

GENERAL DISCUSSION

The results of the word-generation tasks have provided new and interesting information about the role of the left temporal neocortex in the comprehension and recall of verbal material. In the immediate recall of phonetically-encoded information (rhymes) both left temporal-lobe subgroups were markedly impaired, whereas precise semantic encoding (required by the synonym-generation task) resulted in normal levels of immediate recall for the LTh subgroup. These findings suggest that the left temporal neocortex normally plays an important role both in the retention of verbal information in verbatim form, and in the recoding of such information on the basis of its meaning.

The concept of a working-memory system for the control and temporary storage of new information is central to current theories of how human beings process information (e.g., Baddeley, 1976; Bower, 1975; Shiffrin, 1976). The results of the experiments in this thesis provide good support for the belief that the hippocampal region of the brain is essential for the temporary storage aspect of the working-memory system. In normal subjects this ability appears to serve a dual function. First, it enters into the temporary retention of newly-encoded item information in material-specific form, prior to consolidation of the information in long-term storage. The findings from the word-generation and associative-learning studies demonstrated that the temporary retention of semantically-encoded verbal information was critically dependent upon the integrity of the hippocampal region in the language-dominant hemisphere. This discovery extends the work of Corsi (1972) into the domain of meaningful verbal material, and complements the findings of Jones-Gotman on the role of the right hippocampal region in image-mediated verbal learning (1975, 1979; Jones-Gotman & Milner, 1978).

Second, the hippocampal region appears to be important for the temporary storage of new information as required during certain kinds of perceptual processing. The results of the absolute-judgement experiments suggest that both hippocampal regions play a critical role in the establishment and maintenance of contextual information on which absolute judgements of simple stimuli are based.

The physiological concept of an intermediate-term memory system, as a prerequisite to long-term storage, has existed for many years. Thus Müller and Pilzecker (1900), in the original discussion of the consolidation theory of memory, suggested that there must be neural processes that persist for some time after the actual perceptual experience, in order to give sufficient time for consolidation of the new information to take place (Glickman, 1961). This idea was revived as a possible reason for the retrograde amnesia seen in cases of closed-head injury (reviewed by Whitty & Zangwill, 1966).

However, it was predominantly the work of Hebb (1949, 1961) and of his students (e.g., P. Milner, 1957) that helped to develop the concept of a brain-system that was necessary for the temporary storage of new information prior to its long-term storage. Hebb's concept of the cell-assembly, as a reverberatory neural circuit that prefigured permanent morphological changes, was seminal to subsequent work on the hippocampal system. A major impetus for much of the later work on the role of the hippocampus and parahippocampal gyrus in memory, was a series of papers by Brenda Milner (1959, 1962b; Penfield & Milner, 1958; Scoville & Milner, 1957). It was in these papers that bilateral damage to the hippocampal region was directly implicated as a causal factor in amnesia. Milner (1959, 1962b) suggested that the role of the hippocampal region was in the temporary retention of new information after it had left conscious awareness, and prior to its more permanent storage. She noted that the amnesic patients appeared not to retain any information once it had passed from their conscious awareness, whereas normal subjects showed automatic retention of new experiences in short-term storage. She went on to suggest that it was this automatic retention of new information that was essential to long-term storage.

Subsequently, other theoretical explanations of amnesia have been proposed. In particular, Atkinson and Shiffrin's (1968) popular model of how human beings process information, which focussed almost exclusively on the retention of verbal information, resulted in the following biased interpretation of the hippocampal amnesic syndrome. Short-term or primary memory was equated with verbal span (H.M.'s digit span was normal; therefore his short-term memory was normal). Long-term or secondary memory was equated with recall of verbal information after a delay (H.M. was unable to recall any verbal information once it had passed from his conscious awareness; therefore his long-term memory was impaired). In the Atkinson and Shiffrin model, verbal rehearsal was held to be the key to transfer of information from short-term to long-term storage. Because H.M. could rehearse verbal material and retain it in short-term storage, the locus of his impairment had to be in the transfer process. Other evidence, showing that H.M. was incapable of retaining limited amounts of nonverbal information for more than 30 seconds (e.g., Corsi, 1972; Prisko, 1963; Sidman, Stoddard & Mohr, 1968; Wickelgren, 1968), was at first attributed to a failure to initiate verbal rehearsal (Sidman et al., 1968), but the subsequent demonstration that the isolated, mute, right hemisphere could retain non-verbal information for much longer than H.M. (Milner & Taylor, 1972) has now ruled out this interpretation of his deficit. Instead, it is argued here, those tasks on which H.M. fails are precisely those that make demands on an intermediate-memory system.

The clearest evidence for such an intermediate-memory system, and the major finding in this thesis, came from the unexpected results of the absolute-judgement tasks. These findings have provided a framework within which to interpret the effects of hippocampal lesions in human beings. What has still to be explored is the relative contribution of the hippocampus and the parahippocampal gyrus, since excision of the parahippocampal gyrus alone appears to be sufficient to cause the same deficits as are found with a hippocampal excision (Milner, Note 1). One must also not forget that in all of the patients in whom the body of the hippocampus was partially excised, the amygdala was also removed, and so it is not possible to say what effects would be seen if the amygdala were spared and the hippocampus removed. Recent work by Mishkin (1978), however, suggests that a combined bilateral removal of both the amygdala and the hippocampal region is necessary to cause a major memory impairment in the monkey.

By now there is a converging body of evidence from studies of lower mammals indicating that the hippocampal region is the physical substrate for an intermediate-memory system (e.g., Vinogradova, 1975). In recent years the work of O'Keefe and Nadel (1978) has demonstrated that lesions of the hippocampal region in rats disrupt the ability to remember information about spatial location, suggesting a parallel with the effects of unilateral right hippocampal excisions in man. The work of Olton and his associates (Olton, Becker & Handelmann, 1979; Olton & Papas, 1979), also with rats, has shown a dissociation after hippocampal lesions between the impaired ability of the animal to remember what it has just done and its preserved ability to remember information about the context of the experiment. Olton et al. (1979) use the term "working memory" to refer to memory for recently past events, and the term "reference memory" to refer to memory for contextual information. On the basis of his own experiments, Olton proposes that the hippocampus is selectively involved in behaviour that depends on working memory, irrespective of the spatial or non-spatial nature of the memoranda. Despite some formal similarity between Olton's working-memory system and the intermediate-memory system proposed in this thesis, one must be cautious about equating the effects found by Olton after hippocampal damage in the rat with the intermediate-memory deficits observed after medial temporal-lobe lesions in man. In particular, one notes that the quality of the deficit in the rat resembles more the effects of human frontal-lobe lesions than it does the effects of hippocampal ones.

In this thesis a distinction has been made between two components of a working-memory system, one for planning and organizing ongoing behaviour, and the other, an intermediate-memory system for the temporary storage of new information. Strong support for such a distinction was found in the partial dissociation observed between the effect of left-frontal and left-hippocampal lesions on the performance of the associative-learning and absolute-judgement tasks. The left frontal-lobe group and the left temporal-lobe (LTH) subgroup were equally impaired on the associative learning task, where planning and monitoring were important, whereas only the left temporal-lobe subgroup was impaired on the absolute-judgement tasks, where the major demands were on the temporary retention of new information.

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APPENDIX

Table A

Test Items Used in Word-Generation Tasks

Materials			
Rhymes		Synonyms	
Cue	Target	Cue	Target
Dish	Wish	Melody	Song
Card	Hard	Speak	Talk
Seal	Real	Revolver	Gun
Save	Cave	Earth	Ground
Rice	Nice	Jump	Leap
Waste	Paste	Timber	Wood
Beat	Seat	Rapid	Fast
Kite	Bite	Repair	Fix
Pail	Nail	Easy	Simple
Malt	Halt	Big	Large
Lamp	Damp	Infant	Child
Mind	Find	Disappear	Vanish
Round	Sound	Attractive	Pretty
Boast	Roast	Yacht	Boat
Face	Race	Road	Street
Hold	Bold	Begin	Start

Table B

Temporal-Lobe Subjects in the Word-Generation Task

	Sex		Age (yrs.)		Wechsler I.Q.	
Group	M	F	Mean	Range	Mean	Range
Left temporal	13	8	29.6	18-50	108.9	93-131
Right temporal	8	7	25.8	16-46	110.5	79-134

Table C

Subjects' Taking Part in the Associative-Learning Task

	Sex		Age (yrs.)		Wechsler I.Q.	
Group	M	F	Mean	Range	Mean	Range
Left temporal	15	13	28.3	18-50	108.4	92-131
Right temporal	15	10	27.3	16-48	115.0	81-134
Left frontal	3	1	30.0	17-46	102.0	92-110
Left fronto-temporal	0	2	20.5	17-24	104.0	101-107
Right frontal	2	4	26.8	12-51	101.0	90-110
Left parietal	2	0	31.0	27-35	106.5	96-117
Right parietal	1	0	28.0	n.a.	111.0	n.a.

Table D

Subjects Taking Part in the Absolute-Judgement Tasks

	Sex		Age (yrs.)		Wechsler I.Q.	
Group	M	F	Mean	Range	Mean	Range
Left temporal	14	10	29.3	18-50	107.2	92-131
Right temporal	12	12	28.8	16-48	114.4	79-134
Left frontal	2	1	34.7	23-46	99.0	92-110
Left frontotemporal	0	2	33.5	24-43	112.5	101-124
Right frontal	4	4	26.0	12-51	101.5	85-114
Right parietal	1	1	29.0	28-30	96.0	80-112
Right occipital	0	1	11.0	n.a.	93.0	n.a.

Table E

Temporal-Lobe Subjects in the Matching-to-Sample Tasks

	Sex		Age (Yrs.)		Wechsler I.Q.	
Group	M	F	Mean	Range	Mean	Range
Left temporal	10	7	26.9	19-43	108.0	92-125
Right temporal	7	8	27.0	16-48	108.8	94-129
Left frontal	2	1	34.7	23-46	99.0	92-110
Left frontotemporal	0	2	33.5	24-43	112.5	101-124
Right frontal	4	4	26.0	12-51	101.5	85-114