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Physiology of short-term verbal memory

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Summary. These studies document a series of brain events accompanying short-term memory functions. For auditory verbal material the sequence involves at least two different sites within auditory cortex subserving sensory and cognitive processes of memorization. During the scanning of the short-term store structures within the medial temporal lobes, presumably the hippocampus, are active. There is an inconsistency between these results and the clinical observations of the need for an intact dominant parietal lobe for auditory short-term memory to function normally. Magnetic recordings showed no focal dipolar source of activity in the parietal lobe during any aspect of auditory short-term memory. The discrepancy could be accounted for by considering the parietal lobe lesion as “disconnecting” the lateral temporal cortex from the deep medial hippocampal structures thereby impeding auditory short-term functions (Geschwind, 1965).

These studies show that the physiological analysis of brain events in the msec range can provide information about relatively complex cognitive processes underlying short-term memory. The magnetic and electrical recording methods provide a noninvasive way to study human brain functions involved in cognition that can then be correlated with behavioral measures of specific cognitive activities.

Short-term verbal memory is essential for our daily activities. For instance, remembering a new phone number, new names, or a list of groceries all engage short-term memory processes that we all wished functioned better. There is a wealth of experimental data about short-term verbal memory that has clarified the workings of this type of cognitive activity. The short-term store has a limited capacity of approximately 7 items with the auditory store being larger than the visual store. Exposure to interfering stimuli can impair short-term verbal memory (Peterson and Peterson, 1959). Reaction time measures show that the length of time needed to scan the short-term store increases linearly as the number of items memorized increases (Sternberg, 1969). Brain lesions in man localized to specific sites can disassociate short-

* Perished in the Pan Am tragedy at Lockerby, 1988

term and long-term memory processes. Lesions of the left angular gyrus of the parietal lobe are associated with disordered auditory short-term verbal memory (Warrington and Shallice, 1969) but are without effect on long-term memories. In contrast, lesions of the hippocampus bilaterally are associated with disordered long-term but not short-term verbal memory functions (Starr and Philips, 1970). Over the past five years I have worked with colleagues at Irvine, London, and Vienna using electrophysiological and magnetic recording methods in normals and in patients with brain lesions to help elucidate brain activity during short-term memory. The results show a sequence of events in different brain regions during memorizing and scanning of the short-term store. These events obey rules that differ from those defined by reaction time measures. This paper summarizes the results of our studies.

Methods

Brain potentials were recorded from at least three midline electrodes (Fz, Cz, and Pz) referenced to linked ears. Eye movements were also monitored so that trials in which they occurred could be excluded from the averaging process. In separate experiments, magnetic fields were measured from up to 63 sites over the skull. The details of the recording parameters and methods of analysis can be found in two of our publications (Pratt et al., 1989; Starr et al., 1990). The short-term memory processes were engaged in a systematic manner using a variant of a paradigm described by Sternberg (1969). A list of items to be memorized were presented once every 1.2 sec. followed in 2 sec. by a probe item (Fig. 1A) that had an equal probability of being (an "inset" probe) or not being (an "out-of-set" probe) a member of the immediately preceding memory set. The subject indicated his/her classification of the probe by responding as soon as possible by pressing one of two buttons and accuracy and reaction times were recorded. The items were both verbal (numbers 1 to 9) and nonverbal (musical notes from middle C to D, one octave higher) presented in the auditory or visual modality. Blocks of twenty trials were presented containing the same number of items (one, three, or five), the same type of item (verbal or nonverbal), and in the same modality (visual or auditory).

Results

Normal subjects

Reaction time measures increased in a linear fashion as the number of items memorized increased. The slopes were approximately 50 msec/item for verbal items (Fig. 1D) and twice that, 100 msec/item, for musical notes. There were no significant differences in reaction times between inset and out-of-set probes.

The brain potentials accompanying the probes consisted of early sensory events (N100, P200) that differed in scalp distribution and amplitudes between auditory and visual modes of presentation. A late sustained positivity peaking at a modal latency of 450 msec of largest amplitude parietally accompanied the presentation of all of the different probes (Fig. 1A). We believe this potential reflects brain activities related to the scanning of the

Fig. 1. **A** A schematic representation of the short-term memory task used to measure brain potentials and behavior. For the memory items there is a small negative potential shift over the frontal region (left trace). For the probe there is a large positivity seen over the parietal region (right trace). **B** Brain potentials to probes in normals with (dashed line) and without (solid line) an intervening interfering auditory task. Note the attenuating effect of interference. **C** Brain potentials to probes in subjects normal (solid line) and in one patient with disordered auditory verbal short-term memory from a lesion of the left angular gyrus. Note the attenuation of the potential in the patient. **D** RT as a function of set size for young normals, old normals, patients with disordered auditory short-term memory from a lesion of the dominant angular gyrus (STM), and patients with Alzheimer's disease

contents of the short-term store. The latency of this component increased with set size at approximately a 30 msec/item rate, approximately half that defined for reaction times. Moreover the increase in latency of the parietal positivity with increases in set size was similar for all of the various types of memory items, differing again from reaction times.

There were features of this parietal positivity that could be correlated with short-term memory processes. First, the parietal positivity differed for inset and out-of-set probes: the former began at an earlier latency than to the out-of-set probes. This finding is compatible with the idea that scanning of the contents of the short-term store can be completed sooner for inset than for out-of-set probes. For instance, if scanning of the short-term store

followed a serial or even a random order then a match would be made for inset probes, on the average, halfway through the list. In contrast, a probe could be correctly classified as out-of-set only after the entire contents of the short-term store were scanned. Since reaction times do not differ between inset and out-of-set probes it is likely that the parietal positivity reflects an early stage in short-term memory processes that can distinguish between inset and out-of-set probes which is not realized by reaction time measures.

A second observation of note is that the amplitude of the parietal positivity to the inset probes is affected by its serial position within the list of items. Amplitudes were larger when the probe was the first or last item of the memorized list compared to the items in the middle of the list (Patterson et al., 1991). This serial position effect is both modality and item specific occurring only with verbal items presented in the auditory mode.

Finally, interference from competing stimuli, which is well known to decrease retrieval from the short-term store, is accompanied by a marked attenuation of the parietal positivity and a lengthening of the reaction time. These latter observations were made by Flora Swire when she had subjects perform an arithmetic task during the interval between the presentation of the last memory item and the probe. The late positivity was attenuated by more than half for verbal material presented in both the auditory and visual modalities (Fig. 1B) while reaction times increased by approximately 100 msec. These observations are relevant when considering the mechanisms underlying alterations of the probe evoked potentials that occurs in patients with disordered short-term memory.

Up to this point we have been concerned with the brain events accompanying the scanning of the short-term store. During memorization of the list of items a sustained low amplitude component appeared that was positive for visually presented digits and acoustically presented notes but negative or absent to acoustically presented digits. Recording from the frontal region showed that all items regardless of modality or type showed a progressive tendency to become negative as memorization progressed from the first to the fifth item in a list. Thus, during memorization there is a low amplitude potential, particularly to acoustically presented material, that is largest in the frontal derivations (Fig. 1A).

Patients

Two groups of patients have been studied: three patients with lesions of the left angular gyrus and impaired auditory short-term memory (Starr and Barrett, 1987) and twenty-five patients with a variety of dementing disorders. The first group of patients with disordered auditory short-term memory showed a selective attenuation or even absence of the parietal positivity to verbal probes presented in the auditory but not in the visual modality. The scanning rates of only the auditory short-term store, using their reaction times, was abnormal at 150 msec/item, almost three-fold greater than found in normals (Fig. 1D). The attenuation of the amplitude of the parietal

positivity (Fig. 1C) was similar to that, found by Flora Swire, in normal subjects engaged in an interfering task. It has been suggested that interference affects auditory verbal short-term memory functions by preventing "rehearsal" using articulatory processes. One does not have to repeat the items "out loud" for rehearsal to occur since rehearsal can occur through activation of neural representations of the phonetic output system. It may be that patients with the selective disorder of auditory verbal short-term memory have alterations in their articulatory rehearsal capabilities leading to deficits similar to that seen in normals exposed to interfering stimuli. The patients do not have a disorder of their short-term memory functions, per se, since verbal material presented in the visual modality can be successfully stored and retrieved and the accompanying parietal positivities were of normal amplitude.

In patients with dementing illness reaction time measures of the time required to scan the contents of the short-term store increased two fold compared to aged matched controls (Fig. 1D). In contrast, the amplitude and latency of the parietal positivity were unaffected. Thus, in dementia, short-term memory processes represented by the amplitude and latency of the parietal positivity accompanying the classification of the probes appears normal. It is the use of this information for behavior (i.e., accuracy and reaction times) that becomes abnormal.

In both groups of patients the long latency potentials accompanying the memorization of the list of items have not yet been analyzed. However, the short latency sensory events (N100) were no different than normal.

*Localization of brain structures that are active
during short-term memory processes*

The distribution of magnetic fields over the scalp during scanning of the auditory short store at the time of the parietal positivity to the probe (350–700 msec), showed outward fluxes over the left hemisphere and inward fluxes over the right hemisphere. These findings are compatible with activity arising from two dipolar sources localized deep in brain in the region of the medial temporal lobes. During memorization, at the time of the sustained

Table 1. Localization of brain activity during auditory processing of a verbal item

Memorization

- 100 msec — Sensory processing in primary auditory cortex, Heschl's gyrus
200–600 msec — Cognitive processes of attention or short-term memory, temporal cortex adjacent to Heschl's gyrus

Retrieval

- 100 msec — Sensory processing in primary auditory cortex, Heschl's gyrus
200–800 msec — Cognitive processes of memory scanning, medial temporal lobes
— Hippocampus

frontal negativity to acoustically presented digits (300–500 msec), activity could be localized to a dipole source in the region of auditory cortex adjacent to Heschl's gyrus. Even earlier, at 100 msec after the items' appearance, activity originating from a dipolar source in Heschl's gyrus was clearly evident. Thus a shifting sequence of activity could be defined accompanying the engagement of auditory short-term memory (Table 1): at 100 msec there is activity in primary auditory sensory cortex; at 300–500 msec, during the presentation of the items to be memorized, there is activity in auditory cortex adjacent to primary sensory cortex; finally at 300–700 msec during the presentation of probes and the scanning of the short-term store, there is activity in the medial portions of both temporal lobes.

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