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The N100 auditory cortical evoked potential indexes scanning of auditory short-term memory

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Abstract

Objective: To study activity of auditory cortex reflected by the N100 and P200 components of the auditory evoked potentials during memorization and scanning of short-term memory stores.

Methods: In a MEMORY task subjects classified a probe digit either as *a member* or *not a member* of a previously presented list of digits that varied in size from one, 3, 5 and 7 items. For comparison, subjects in a NUMBER task listened to a list of digits as in the MEMORY task but determined only whether the probe digit as *odd* or *even*. Evoked potentials to the presentation list and to probes were recorded from scalp electrodes and separately averaged for both tasks. The components peaking at approximately 100 ms (N100) and 200 ms (P200) that reflect activity of primary auditory cortex were identified and peak amplitudes and latencies were measured.

Results: For presentation set items, the amplitude of N100 was affected by set size in the MEMORY but not in the NUMBER task; N100 was larger for the one item set than for the 3, 5, and 7 item sets. P200 increased in amplitude in a linear manner for both the MEMORY and NUMBER tasks. For probe items, N100 but not P200 amplitude decreased in a linear manner as the number of items in the presentation set increased in the MEMORY but not in the NUMBER task. The linear change of N100 amplitude during memory scanning was particular to in-set but not to out-of-set probes. The amplitudes of both N100 and P200 were almost twice as large in probe digits than in the digits in the presentation set in both the MEMORY and NUMBER tasks.

Conclusion: Auditory sensory cortical activity in humans during an auditory short-term memory task shows dynamic changes during both memorization and memory scanning.

Keywords: Evoked potentials; Memory scanning; Auditory sensory cortex

1. Introduction

Short-term memory includes processes for coding, rehearsal, memorization, and the scanning of the memory store. For auditory short-term memory, left temporo-parietal cortical regions appear to be involved in encoding and storage while left frontal cortical regions appear to be related to rehearsal and recall (Warrington and Shallice, 1969; Warrington et al., 1971; Starr et al., 1991; Fiez et al., 1996; Smith et al., 1996). In this report, we will show that activity of the auditory sensory cortex, reflected by the amplitude of the N100 component of the auditory evoked potential (Hari et al., 1980; Rogers et al., 1990; Scherg and Picton, 1991), changed in an orderly manner as a function of memory load and probe type.

The latency and amplitudes of the N100 auditory evoked component have been traditionally considered to represent sensory processes reflecting physical attributes of the auditory stimulus such as intensity (Davis and Zerlin, 1966) and presentation rate (Davis et al., 1966). The auditory N100 amplitude has also been shown to be affected by cognitive processes such as attention (Davis, 1964; Picton and Hillyard, 1974), expectancy (Starr et al., 1997), and tasks involving short-term memory. Kaufman et al. (1991) showed that N100 magnetic fields recorded during an auditory short-term memory task changed in amplitude with memory load. Stanny and Elfner (1980) reported that the serial position of an in-set probe relative to the memorized list influenced N100 amplitude. Serial position effects on late slow wave potentials accompanying both memorization and memory scanning have also been described (Patterson et al., 1991; Chao and Knight, 1996).

In this report, we will present evidence that the amplitude of the N100 changed during both memorization and the scanning of the memory store as a function of memory load. In contrast, N100 amplitude did not change with the

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number of preceding auditory stimuli when memorization and memory scanning were not required and subjects only identified the probe as an odd or even number. These latter results provide evidence that auditory sensory cortex activity, as indexed by the amplitude of the N100 component, was involved during auditory short-term memory processes. In contrast, P200 amplitudes were not uniquely affected by memorization.

2. Methods

2.1. Subjects

Thirteen normal individuals (11 females and two males) without complaints of hearing or neurological disorders were tested. The mean age was 24.3 years; 12 subjects were right-handed and one subject was left-handed. Each subject signed an informed consent following the guidelines for approved projects involving human subjects.

2.2. Task procedures

A list of numbers followed by a probe item was acoustically presented. The stimuli were the numbers zero to twelve presented at a normal conversation level (60 dB nHL) from speakers in front of the subject. The digits were synthesized by a BBC micro-computer (Acorn) and spoken in a male voice. The digit stimuli were used in two tasks: (1) a short-term memory task (MEMORY) and (2) a number classification task (NUMBER). The procedure (Starr and Barrett, 1987) was the same for each task (Fig. 1). The word *start* was followed by a list of numbers. Stimuli were presented every 1.2 s. Three seconds after the last number a probe digit was presented. In the MEMORY task, the subject decided whether the probe item was or was not a member of the presentation list (in-set, out-of-set, respectively). In the NUMBER task the subject was told to ignore the presentation set and wait for the last number, the probe, and determine whether it was odd or even. Subjects indicated their response by pressing one of two adjacent reaction time buttons. The assignment of which button indicated probe type in the tasks (in-set or out-of-set in the MEMORY task; odd or even in the NUMBER task) was randomly determined for each subject. There was an equal chance that the probe was in-set or out-of-set in the MEMORY task, or as odd or even in the NUMBER task. The serial position of in-set probe items relative to the presentation set was evenly distributed across lists in both tasks. Presentation set sizes included one, 3, 5, and 7 items. The following additional restrictions were imposed on the construction of the digit lists: (1) no number in the presentation set was repeated; (2) a probe number was not allowed to repeat on more than 3 consecutive trials; and (3) probe type (in-set or out-of-set in the MEMORY task, odd or even in the NUMBER task) was limited to 4 consecutive trials for both tasks. Each task was presented on separate days in order to avoid one long test session. The order of the tasks and the order of the presentation set sizes within each task were randomly determined for each subject.

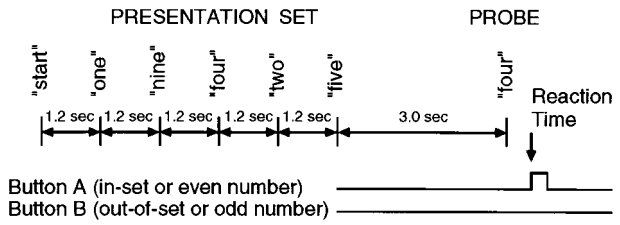

Fig. 1. Sample segment of the stimulus sequence for the 5-item MEMORY and NUMBER tasks. In the MEMORY task, the appropriate button press depended on whether the probe was *in-set* or *out-of-set*. In the NUMBER task, the appropriate button press depended on whether the probe digit was *odd* or *even*. In this example, a correct button press is indicated to an in-set probe in the MEMORY task or to an even number in the NUMBER task.

For each presentation set size subjects were presented 40 trials in the MEMORY task and 20 trials in the NUMBER task (MEMORY task total = 160 (4 set sizes × 40 trials); NUMBER task total = 80 (4 set sizes × 20 trials)). The total number of trials in the NUMBER task was sufficient for overall comparison with the MEMORY task but insufficient to define probe type effects (e.g. odd or even). Subjects were seated in a comfortable chair and were instructed to look straight ahead at a set of cross hairs in order to limit eye movements. They were encouraged to respond quickly and accurately. Practice for each task, using a 5 item presentation set, was given prior to data collection to insure that subjects understood the task and responded appropriately. Subject testing was performed in a sound attenuating and electrically shielded chamber.

2.3. Data collection

Brain electrical activity was recorded from Ag/AgCl scalp electrodes placed at midline Fpz, Fz, Cz, and Pz sites, and lateral locations C3 and C4; scalp sites were referenced to linked electrodes on the earlobes. Marked scalp sites were cleaned and lightly abraded; impedances measured between electrodes were less than 3 kΩ. Brain potentials were amplified (200 000) with a bandpass of 0.01–100 Hz (time constant = 16 s). Eye movement potentials were recorded from electrodes placed above and below the right eye, amplified (10 000) and filtered as above. Potentials to the presentation set were digitized for 0.96 s and included a 0.12 s prestimulus period (256 data points per channel with a dwell of 3.75 ms). Potentials to the probes were digitized for 2.8 s (256 data points and included a 1.12 s prestimulus period with a dwell of 11 ms). The sampling rate for the probe items was only sufficient for accurately identifying spectral components up to approximately 23 Hz.

2.4. Signal processing

Averages were computed from stored single trials to

correct responses. An adjustment procedure (modified after Gratton et al., 1990) was applied to trials with eye movement artifacts. The number of probe trials available for each set size averaged 31.0 ± 5.6 out of the 40 available for the MEMORY task and 16.7 ± 2.4 trials out of the 20 available for the NUMBER task. Averages were band-pass filtered (1.0–20 Hz) to attenuate very slow potential shifts and higher-frequency recording noise.

N100 was identified as a negative deflection occurring between 80 and 160 ms (mean = 120 ms) and P200 as a positive deflection between 180 and 260 ms (mean = 220 ms). Peak amplitude was computed relative to the average prestimulus period (1.12 s for probes, 0.12 s for presentation set items); component latencies were determined from stimulus onset to the peak maximum.

2.5. Statistical analyses

Analysis of variance (ANOVA) procedures for repeated measures were used to evaluate separately the behavioral measures (accuracy and RT) and the amplitudes of N100, P200, peak-to-peak amplitudes of N100–P200, and the latencies of N100 and P200.

Accuracy and RTs were separately analyzed in 3 factor ANOVAs for task (MEMORY vs. NUMBER), probe type (in-set, out-of-set), and presentation set size (one, 3, 5, and 7 items).

For the evoked potentials to the presentation set items, a 3-factor ANOVA was computed for the factors of task (MEMORY vs. NUMBER), set size (one, 3, 5, and 7 items), and electrode site (Fpz, Fz, Cz, Pz, C3, and C4). Serial position effects in the presentation sets (3, 5, and 7 items) were evaluated in a 3-factor ANOVA using the factors of task (MEMORY vs. NUMBER), position (first-, middle-, last-item), and electrode site (Fpz, Fz, Cz, Pz, C3, and C4).

For the probes, a 3-factor ANOVA was computed using the factors of task (MEMORY vs. NUMBER), presentation set size (one, 3, 5, and 7 items), and electrode site (Fpz, Fz, Cz, Pz, C3, and C4). A separate 3-factor ANOVA was computed for the MEMORY task for the factors of probe type (in-set, out-of-set), load (1, 3, 5, and 7 items) and electrode site (Fpz, Fz, Cz, Pz, C3, and C4).

For the comparison of the presentation set items to the probe items, a 4-factor ANOVA was computed for the factors of stimulus type (presentation items, probes), task (MEMORY vs. NUMBER), set size (one, 3, 5, and 7 items), and electrode site (Fpz, Fz, Cz, Pz, C3, and C4).

Differences at $P < 0.05$, or better, after Greenhouse–Geisser correction were considered significant. Post-hoc comparisons of the means were made with Tukey's test procedure. Residual errors were not computed to test for the normality of the distributions.

Trend analysis was employed to evaluate component measures as a function of presentation set size. Tests for linear and quadratic trends were conducted on the means separately for the MEMORY and NUMBER tasks when significant main effects for presentation set size were indicated. Regression procedures were applied to indicate the index (r^2) of fit of the means from significant trends (adjusted r^2, P-value).

3. Results

3.1. Behavior

Accuracy. The overall accuracy differences between the MEMORY and NUMBER tasks were not significant but both tasks were affected by set size ($P < 0.001$). Accuracy was reduced for the 5 and 7 item sets compared to the one and 3 item sets for both MEMORY and NUMBER tasks (Fig. 2, top). In the MEMORY task considered separately, significant probe type ($P < 0.02$) and load effects ($P < 0.001$) were indicated. Accuracy was generally higher to in-set (e.g. 97.7, 98.1, 95.3, and 93.5, for set sizes one, 3, 5, and 7, respectively) than for out-of-set probes (e.g. 93.5, 98.1, 92.7, and 89.8%, respectively). No significant interaction between probe type (in-set, out-of-set) and task load in the MEMORY task was indicated for accuracy.

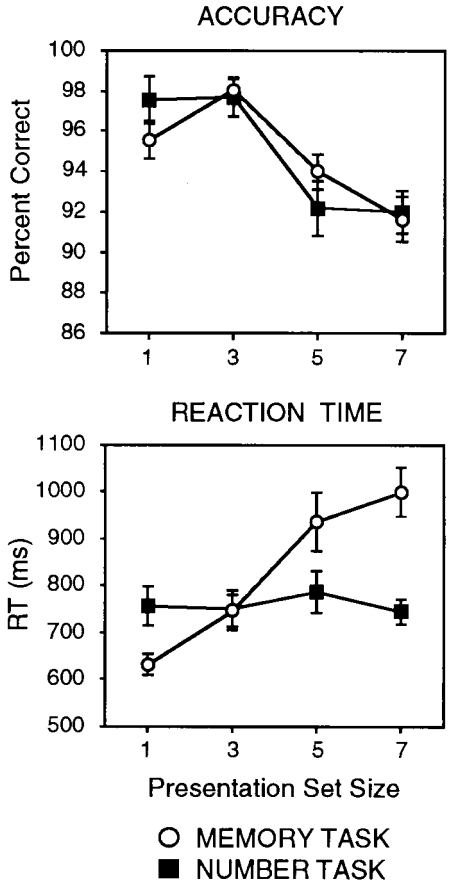

Fig. 2. Behavioral measures (means and standard errors) for all subjects for accuracy (above) and RT (below) as a function of set size for MEMORY and NUMBER tasks.

Reaction time. Reaction times to probes were faster ($P < 0.05$) in the NUMBER task (mean = 759 ms) than in the MEMORY task (mean = 827 ms). There was a significant ($P < 0.001$) interaction between experimental tasks and load (set size) for RT. In the MEMORY task, RT showed a linear relation with load ($P < 0.01$; $r^2 = 0.95$, $P < 0.02$) that was not present in the NUMBER task (Fig. 2, bottom). Effects for probe type or the interaction of probe type and load were not significant for RT in the MEMORY task.

3.2. Evoked potential components

The grand-averaged potentials recorded from Cz to the presentation set items and to the probes pooled across different set sizes and probe types independent of task are illustrated in Fig. 3. Components identified were N100 and P200 for both the probes and presentation set items; for the probes, P400, N500, and a sustained late positive wave, P500; and for the presentation set items, a sustained late negativity, N500. In this paper, we restricted analysis to the N100 and P200 components appearing in both the NUMBER and MEMORY tasks.

3.2.1. Presentation set items

Task and set size. N100 amplitude was significantly larger in the NUMBER than in the MEMORY task (−1.95 μV vs. −1.59 μV, respectively, $P = 0.05$; see Table 1). N100 showed a significant effect of set size in the MEMORY but not in the NUMBER task (task by set-size interaction, $P < 0.01$). Post-hoc comparisons in the MEMORY task showed that N100 was larger for the one item compared to the 3, 5, and 7 item sets (Fig. 4). In this and all subsequent figures, the averaged potentials are shown for the Cz electrode, the recording site with the largest amplitudes, and the graphs contain the pooled results from all recording sites. The changes in N100 amplitude as a function of set size were not significant for linear trend or quadratic trend. Serial position effects for N100 amplitude did not attain significant levels.

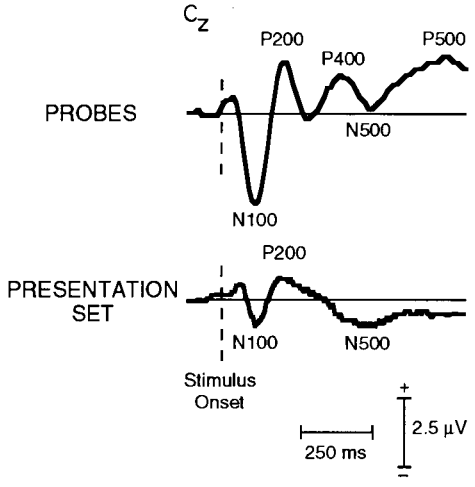

Fig. 3. Grand averaged evoked potentials for probes (above) and for presentation set items (below) at the Cz site. Stimulus onset is indicated by the vertical dashed lines and the average includes a 120 ms prestimulus period and an 840 ms poststimulus period. Components are labeled by polarity and approximate latency after stimulus onset.

P200 amplitudes were not significantly different in the MEMORY and NUMBER tasks. However, P200 amplitudes in both tasks were affected by set size (Fig. 4, $P < 0.05$). The task and set size interaction for P200 amplitude was not significant. For both tasks, a relationship between P200 amplitude and set size for linear trend was indicated (MEMORY, $P < 0.05$; $r^2 = 0.98$, $P < 0.006$; NUMBER, $P < 0.01$; $r^2 = 0.84$, $P = 0.05$).

There were no significant latency differences of N100 or P200 as a function of task, set size, or serial position in a set.

3.2.2. Probes

Task and set size. Overall N100 amplitude differences between the MEMORY and NUMBER tasks did not attain significant levels but there was a significant task by set size interaction ($P < 0.03$; Fig. 5 and Table 1). N100 amplitude decreased systematically with increased set size in the MEMORY but not in the NUMBER task (Table 1). In the MEMORY task, a linear relationship between N100 amplitude and set size was indicated ($P < 0.01$; $r^2 = 0.94$, $P < 0.03$).

Overall, P200 amplitude differences between the MEMORY (mean = 2.3 μV) and NUMBER (mean = 2.5 μV) tasks did not reach significant levels. A task by load interaction for P200 amplitude approached significant levels ($P < 0.06$). A separate analysis of P200 amplitude in the MEMORY task revealed a significant linear relationship with set size ($P < 0.01$; $r^2 = 0.80$, $P < 0.07$), whereas P200 amplitude in the NUMBER task did not display a significant linear trend with set size.

Probe type (in-set, out-of-set) in the MEMORY task. N100 amplitude in the MEMORY task was significantly ($P < 0.05$) larger to in-set than to out-of-set probes (Fig. 6). Significant linear relationships between N100 amplitude and set size were found for both in-set ($P < 0.01$) and out-of-set ($P < 0.01$) probe types. However, the relation of N100 amplitude and set size probes was significant and stronger in in-set probes ($r^2 = 0.98$, $P < 0.002$) than in out-of-set probes ($r^2 = 0.52$, ns). The interaction of probe type and load for N100 amplitudes did not reach significant levels.

Probe type did not significantly affect P200 amplitude. Further, no significant probe type effects involving N100 latency or P200 latency were indicated.

3.2.3. Presentation set and probe potentials

N100 amplitudes to probes were significantly larger than in presentation set items ($P < 0.01$) in both the MEMORY (e.g. Cz: presentation set item = −1.96 μV; probe = −4.92 μV) and NUMBER (e.g. Cz: presentation set item = −2.30; probe = −4.95; see Table 1) tasks. Fig.

Table 1
Mean amplitudes (μV) in the MEMORY and NUMBER task for presentation set items and probes as a function of load for N100, P200, and N100–P200 for all electrodes and for the Cz site. An average mean ($\bar{x}$) was computed across load.

Load	Memory task					Number task				
	1	3	5	7	$\bar{x}$	1	3	5	7	$\bar{x}$
N100										
All electrodes										
Prese ntation items	−2.67	−1.38	−1.15	−1.17	−1.59	−2.07	−2.13	−1.67	−1.94	−1.95
Probes	−4.35	−3.62	−3.25	−2.99	−3.55	−3.35	−3.69	−3.42	−3.42	−3.47
In-set	−4.76	−4.14	−3.46	−3.00	−3.84					
Out-of-set	−4.00	−3.10	−3.03	−2.98	−3.28					
Cz										
Presentation items	−3.28	−1.75	−1.37	−1.43	−1.96	−2.55	−2.54	−1.95	−2.17	−2.30
Probes	−5.93	−5.26	−4.50	−3.97	−4.92	−4.77	−5.41	−4.86	−4.75	−4.95
In-set	−6.42	−5.80	−4.85	−3.98	−5.26					
Out-of-set	−5.44	−4.73	−4.14	−3.97	−4.57					
P200										
All electrodes										
Presentation items	1.20	1.40	1.52	1.66	1.45	1.03	1.14	1.76	1.84	1.44
Probes	1.93	2.51	2.88	3.12	2.61	2.15	3.07	2.19	2.77	2.55
In-set	1.89	2.44	2.73	2.95	2.50					
Out-of-set	1.97	2.58	3.03	3.28	2.72					
Cz										
Presentation Items	1.69	1.64	1.82	1.96	1.78	1.45	1.45	2.25	2.28	1.86
Probes	2.38	3.74	3.92	4.10	3.54	3.21	4.31	3.00	3.82	3.59
In-set	2.61	3.64	3.82	4.20	3.57					
Out-of-set	2.87	3.80	4.38	4.57	3.91					
N100–P200										
All electrodes										
Probes	6.28	6.13	6.13	6.11	6.16	5.40	6.66	5.61	6.11	5.95
In-set	6.65	6.58	6.19	5.95	6.34					
Out-of-set	5.97	5.68	6.06	6.26	5.99					
Cz										
Presentation items	4.97	3.69	3.19	3.39	3.81	4.00	3.64	4.20	4.45	4.07
Probes	8.31	9.0	8.42	8.07	8.45					
In-set	9.03	9.44	8.77	8.18	8.86					
Out-of-set	8.31	8.53	8.52	8.54	8.48					

3 compares the grand average at Cz of all presentation items with all probes independent of task. N100 and P200 amplitudes were more than doubled when the same physical stimuli were presented as probes compared to when they were presented as memory set items.

There were no significant differences in the scalp distributions or latencies of the N100 or P200 evoked by probes and presentation set items.

4. Discussion

The results of this study showed that the amplitude of the N100 auditory evoked potential component both to presentation set items and to probe items during memorization and memory scanning were affected by the size of the presentation set. For presentation set items, N100 amplitude was largest for the one item task and then fell to a constant level for the 3, 5, and 7 item loads. For probes, N100 amplitude decreased in a linear fashion with set size. These changes were specific to short-term memory functions (MEMORY task) since N100 amplitudes to both presentation set items and to probes did not change in amplitude as a function of set size in the NUMBER task when subjects only classified the probes as odd or even. These results extend earlier studies indicating that activity of auditory sensory cortex during short-term memory function is sensitive to memory load (Kaufman et al., 1991). The bases for the failure of other studies to define changes of N100 amplitude with memory load (Knight et al., 1989; Pratt et al., 1989; Pelosi et al., 1992) are not apparent.

Not all of the changes of N100 amplitude defined in the MEMORY task can be ascribed to memory processes. N100 amplitude to the probes in both the MEMORY and NUMBER tasks increased an equivalent amount relative to the N100 evoked by the immediately preceding presentation set items. This increase of N100 amplitude to the probes may be related to central processes involved in preparation to make a motor response to the probes required for both tasks (Starr et al., 1997). We do not think that attention processes play a role in the increase of amplitude of N100 to probes in both tasks since attention was directed to the

presentation set items in the MEMORY task and was discouraged by instruction in the NUMBER task.

Changes of N100 amplitude to the probes during memory scanning are compatible with the proposition (Picton et al., 1978) that auditory cortex is involved in auditory short-term memory processes. Principles governing N100 amplitude include the number of auditory cortical neurons activated, the extent of their activation, the synchrony of their discharges, and the orientation of the equivalent dipole source relative to the recording arrays. Since amplitude and not the duration of the N100 component to the probes were affected during memory scanning, the observed changes were likely due to alterations in discharge rates and/or number of neural units active rather than altered neural synchrony. Another mechanism for affecting amplitude could have been a change in the orientation of the equivalent dipole(s) for N100, for which we have no data to resolve the issue.

P200 amplitude to probes in the MEMORY task increased in amplitude in a linear manner with memory load. Some of the P200 changes appeared to be a passive consequence of the changes in N100 amplitude. For instance, probe P200 amplitude relative to N100 (i.e. P200 minus N100), did not change as a function of task, set size, or type of probe. P200 amplitude to presentation items was affected in a generalized manner with load independent of

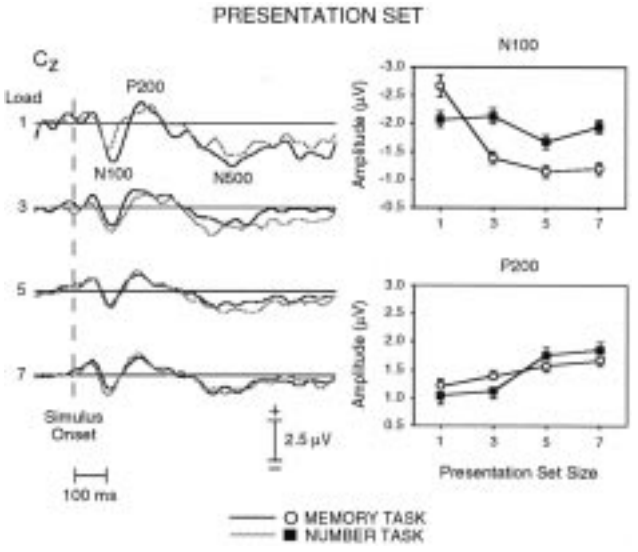

Fig. 4. Grand averaged evoked potentials to items in the presentation set as a function of load for the MEMORY and NUMBER tasks at Cz over 960 ms including a 120 ms prestimulus period. The average includes the N100, P200 and a late slow wave, N500. On the right, the amplitudes of N100 and P200 (but not N500) are plotted in the graphs and they represent the average amplitude pooled over the electrode site. Note that the amplitudes of N100 were largest for the one item set compared to the 3, 5 and 7 item sets in the MEMORY task whereas N100 was of comparable amplitude across all presentation loads for the NUMBER task. The N500 amplitude was not plotted but was clearly largest in the one item set in both the MEMORY and NUMBER tasks. In this and all subsequent figures, the averaged potentials are shown for the Cz electrode, the recording site with the largest amplitudes, and the graphs contain the pooled results from all recording sites.

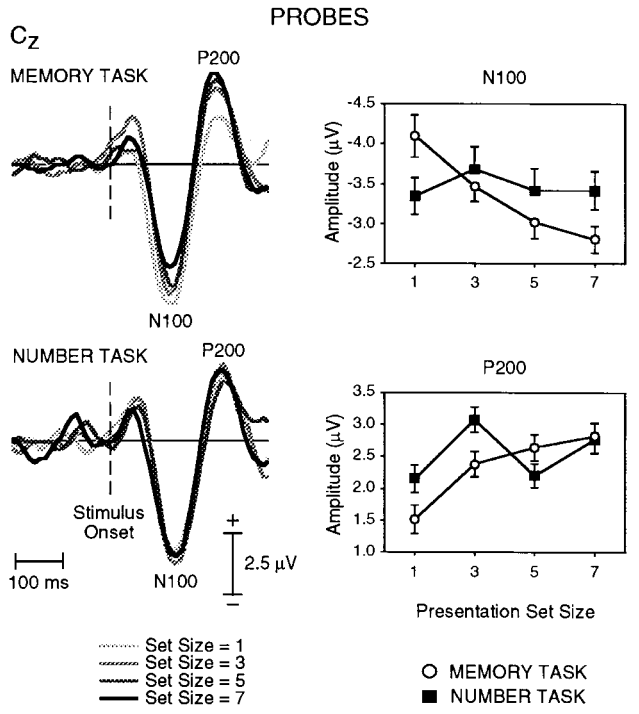

Fig. 5. Grand averaged evoked potentials to probes for the MEMORY and NUMBER tasks at Cz. The portion of the average shown includes only the prestimulus period and the time of occurrence of the N100 and P200 components. Means and standard errors for peak amplitudes of N100 pooled over electrodes are plotted as a function of set size on the graphs to the right. Note the amplitude decrement of N100 as a function of set size in the MEMORY task but not in the NUMBER task. P200 amplitude increased slightly as a function of set size in both tasks.

the N100 changes, increasing in size in both the MEMORY and NUMBER tasks.

In the present experiments, probe type affected the N100 amplitude; N100 was larger in in-set than out-of-set probes at all but the largest (7 item) memory loads. We suggest that the larger N100 response to in-set probes compared to out-of-set probes represents a form of sensory memory or priming.

A model that could account for some of these findings is that memorization of a list of acoustically presented items is accompanied by an increase in excitability of subsets of neurons specific for each item. This heightened excitability affects subsequent neuronal responses to these same items when they appear as probes. In our studies, in-set probes were equally likely to be in any of the positions of the memorized list so that, on average, in-set probes for each set size can be considered as representing the middle position of each of the lists. Thus, the average time between the in-set probe and its prior appearance in the memorized set was 2 s for a one item list, 3.2 s for a 3 item list, 4.4 s for a 5 item list, and 5.6 s for a 7 item list. The decrease of N100 amplitude in in-set probes with memory set size may be related to the time interval intervening between the appearance of a particular digit as a memory item and then again its appearance as a matching probe. We did not include

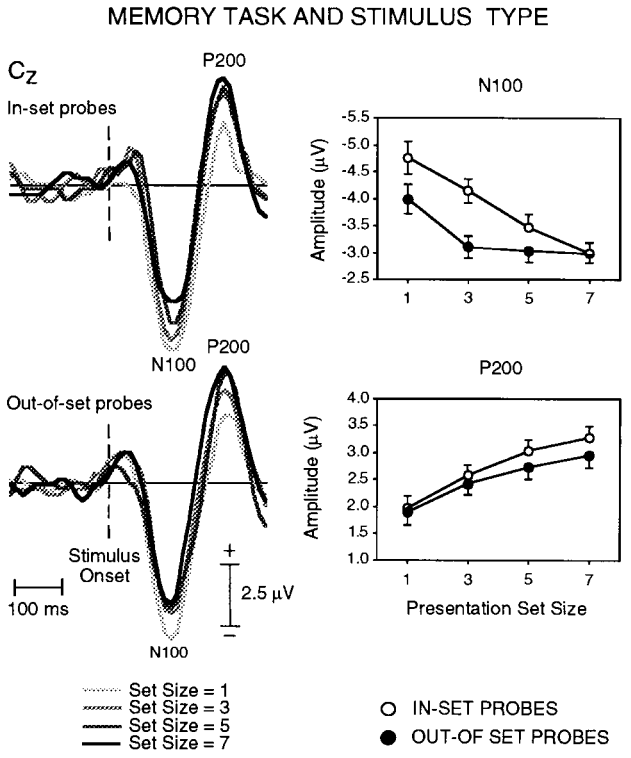

Fig. 6. Grand averaged evoked potentials for in-set and out-of-set probes are shown as a function of set size in the MEMORY task at Cz. The portion of the average shown includes only the prestimulus period and the time of occurrence of the N100 and P200 components. Means and standard errors for peak amplitudes of N100 pooled over electrodes are plotted as a function of set size on graphs to the right. N100 amplitude changed linearly with set size for in-set but not out-of-set probes.

memory lists of more than 7 items to test if the slope of the function relating to in-set N100 amplitude to memory load would asymptote once the capacity of short-term memory was exceeded.

The decrease of activity of auditory sensory cortex with increasing memory load could be one of the inputs utilized by behavioral systems to affect speed of response (Sternberg, 1966). Certainly, the linear functions relating memory load to both RT (64.8 ms/item) and to N100 amplitude (0.41 μV/item) suggest that RT and N100 may also be related. That activity of auditory sensory cortex can influence speed of motor response appears plausible when applied to classical studies of simple reaction times to auditory stimuli in which increasing sound intensity is associated with increasing N100 amplitude (Beagley and Knight, 1967) and decreasing RT (Chocholle, 1945). We suggest that the observed changes of N100 amplitude found in the present study during the scanning times of auditory short-term memory, may influence motor systems responsible for speed of response (RT). There are several levels at which auditory pathway activity can influence motor systems and include the brain-stem for middle ear muscle and startle responses (Carmel and Starr, 1964), subcortical areas for directional orienting responses, and cerebral cortex as occurs during sound induced motor seizures.

The results of these studies support the proposition that auditory sensory cortex participates in both sensory encoding and the cognitive processing of these sensory events (Naatanen and Picton, 1987). Auditory short-term memory is characterized by rapid and automatic features that may be most efficiently handled by combining sensory and memory features into sensory cortex.

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