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Brain potentials before and during memory scanning

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Abstract

Brain potentials were recorded from 10 normal subjects engaged in a 3-item auditory verbal short-term memory task. A fixed interval (3 s) between the last memory item and the probe was compared to a random interval (1.8–4.2 s with a mean of 3 s). Subjects indicated by button press whether the probe was or was not a member of the memory-set. The same 3-item task was also presented as a counting task and required a button press to the 'fourth stimulus' (the probe). The amplitudes of several slow potential shifts preceding and following the probe, and the amplitudes and latencies of the accompanying short duration components (N100, P200) were measured. When the probe appeared at a fixed interval, the amplitude of a slow negative potential in the 300 ms period preceding the probe was slightly larger in the memory than in the counting task. When the probe appeared at a random interval in the memory task, the slow negative shift preceding the probe was absent. Another slow negative shift that peaked at approximately 376 ms after the probe was present in the memory tasks but was absent in the counting task. The amplitude of a late positive shift that peaked at approximately 700 ms after the probe was not different within the memory tasks, or between the memory and counting tasks. N100 amplitude but not P200 amplitude was larger in the memory task when the probe occurred at a fixed than at a random interval. These results suggest that the amplitude of a slow negative shift preceding the probe was related primarily to a temporal expectancy for the appearance of the probe and to a lesser extent to memory processes. In contrast, a slow negative shift that followed the probe occurred only during the memory tasks.

Keywords: Auditory short-term memory; Event-related potentials; Contingent negative variation

1. Introduction

Several electrophysiological studies of short-term memory function have used versions of a procedure originally described by Sternberg (1966, 1969) to document specific potential changes during the memorization, the retention of memorized items and the scanning of the memory store (e.g. Roth et al., 1975; Okita et al., 1985; Wijers et al., 1989; Ruchkin et al., 1990; Lang et al., 1992). In this procedure, stimulus items are presented for memorization followed by a probe item that the subject must classify as a member or not a member of the memory-set. Reaction times (RTs) to probe items increase linearly with the size of the memory-set. A prominent late positive potential that follows the probe by approximately 400 ms has been related to memory scanning processes (e.g. Pratt et al., 1989) since the peak latency of this potential lengthens with increased set size. However, the slope of the function relating the latency of this late positivity to memory load can vary widely among subjects (Pelosi et al., 1995) and the amplitude of this positive shift has no consistent relationship to memory load (Pratt et al., 1989). In contrast, a negative shift that occurs just prior to the late positive potential does increase in amplitude in an orderly manner with memory load (Okita et al., 1985; Wijers et al., 1989), suggesting a relationship to memory scanning processes.

The interval between the last item in the memory-set and the appearance of the probe is the period when rehearsal of the memorized items is presumed to occur. Roth et al. (1975) described a frontal slow negative shift appearing in the period before the probe that paradoxically decreased as the memory load (set size) increased. They considered that this negative shift was related to an expectancy for the appearance of the probe, a contingent negative variation (CNV), rather than to specific memory processes. In their study, the last item of the memory-set was followed, 1.5 s later, by a brief tone that alerted the

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subject to the impending appearance of the probe in 1.0 s. The pairing of the brief warning tone followed by the probe closely resembles the paired stimulus (S1-S2) paradigm used to elicit the standard CNV (e.g. McCallum, 1988). In contrast, in the Ruchkin et al. (1990) study, there was no warning signal between the last memory item and the probe. They described both an initial parietal positive wave followed by a frontal negative shift, both of which increased in amplitude with memory load, findings compatible with memory processes rather than with expectancy. Lang et al. (1992) showed that both stimulus modality and the type of rehearsal strategy had significant effects on the amplitude and scalp distribution of a slow negative shift that preceded the probe. With items presented in the auditory modality, the negative shift was largest frontally and began at the first memory item whereas, when items were presented visually, the negative shift was largest in the posterior temporal region and began only at the last memory item. When the auditory modality was employed for presentation, the scalp distribution of the negative shift was also affected by the rehearsal strategy. Larger negative shifts occurred in frontal leads with auditory rehearsal and larger shifts appeared in posterior leads with visual imagery. The findings in both the Lang et al. (1992) and Ruchkin et al. (1990) studies suggest that the slow potential shifts appearing before the probe are related to memory processes rather than to expectancy and that these memory processes are influenced by the modality of presentation and rehearsal strategy.

The present study examined the negative shifts that occurred before and after the probe as a function of the temporal certainty of the appearance of the probe relative to the last item of the memory-set. Loveless and Sanford (1974) showed that when the S2 stimulus in an S1-S2 pairing was made temporally uncertain the amplitude of the CNV was compromised. We manipulated the interval between the probe and the last item of the memory-set from fixed to random to test whether the amplitudes of the negative shifts were affected or not. We also studied the effects of changing the task from one that required memorization to one that required a response based on the classification of the probe as the 'fourth stimulus in the sequence', i.e. a counting task, to distinguish the role of memorization of the items versus tracking the number of items. Behavioral measures (RTs, accuracy), measures of the slow negative shifts that preceded and followed the probes, and measures of the evoked potential components to the probes (N100, P200, N200, and a late positivity or P300) were used to evaluate the tasks.

2. Methods

2.1. Subjects

Ten right-handed subjects (4 women, 6 men), ages 21–40 years (mean 26.8 years), participated in the study. Subjects had no hearing complaints or neurological problems. Individuals were recruited for the study, signed informed consent forms, and were tested according to university guidelines for approved projects involving human subjects.

2.2. Experimental procedures

2.2.1. Memory task

In a modified version of the Sternberg paradigm (Starr and Barrett, 1987), subjects were presented with a list of auditory stimuli which contained 3 items to memorize (separated by 1.2 s) followed by a probe item. Auditory digits were spoken in a male voice synthesized by a BBC microcomputer. The auditory digits were presented at a normal conversation level (60 dB nHL) from speakers in front of the subject. A small response box containing two buttons separated by 2 cm was placed in the subject's preferred hand. Handedness was determined by the hand used for writing and was the right side for all of the subjects. Subjects were instructed to press the right button with the thumb to in-set probes or the left button to out-of-set probes 'as quickly and accurately as possible'. The items presented were drawn from a repertoire of nine possible stimuli (digits 1–9). The probability that the

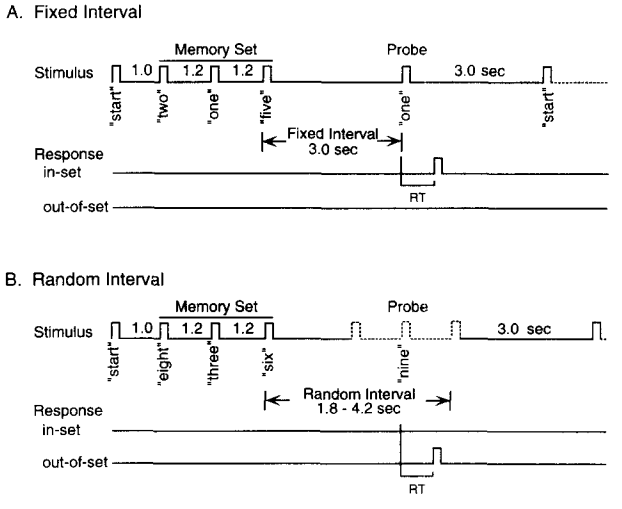

Fig. 1. Sample stimulus sequence in one trial of the memory task containing a 3-item memory-set. The stimulus sequence begins with the word 'start', followed by the items to be memorized ('two'; 'one'; 'five') and then the probe. The response of the subject classifying the probe as in-set along with the speed of response (RT) is indicated below the stimulus sequence. The temporal relationship of the sequence is indicated in seconds. Note that in the fixed interval condition (A), the interval between the last memory item and the probe was constant (3 s), whereas in the random interval condition (B), the interval between the last memory item and the probe varied, ranging from 1.8 s to 4.2 s with a mean of 3 s. The same stimulus sequence was used in the counting task with the probe ('the fourth stimulus') occurring at a fixed interval as in (A).

probe was a member of the memory-set was 0.5. The beginning of each trial was signalled by the spoken word 'start', 1.0 s before the first item of the memory-set. Two different conditions in the timing of the appearance of the probe were used (Fig. 1): (1) a fixed interval condition (3 s between last memory-set item and probe stimulus); and (2) a random interval condition (a Gaussian distribution of intervals between last memory item and the probe, ranging from 1.8 to 4.2 s with a mean of 3 s). The items contained in each trial were presented with the following restrictions: (a) the same probe digit was not allowed to occur on consecutive trials, and (b) not more than 3 consecutive in-set or out-of-set probes were permitted to occur in sequence. The memory item selected as the probe (positive) for the in-set trials was drawn from a position within the memory-set (i.e. first, second, or third) that was equally probable.

2.2.2. Counting task

In this task, subjects were presented with the same stimulus sequence as above containing 3 digits and the probe followed at a fixed interval of 3 s. Subjects were instructed to press the right button with the thumb 'without delay as soon as you hear the fourth stimulus', i.e. the probe. Subjects were instructed to keep track mentally of the number of items presented after the word 'start' and to respond at the fourth item. The effects of a random interval in the counting task were not examined.

2.3. Testing session

Subjects were seated in a comfortable chair in a sound-attenuated and electrically-shielded chamber. The subjects were instructed to keep their eyes open and to look at a fixation spot straight ahead. They were asked to refrain from blinking during the test period. Each task consisted of two blocks of 20 trials each, so that a total of 40 trials was acquired in each of the 3 conditions. The testing session started with the counting task. Then, subjects were tested in the memory task with the fixed interval and finally in the memory task with the random interval. The subjects, when questioned after the experiment, were aware that the time when the probe was presented differed in the two memory tests. There was a 3 min break after each task. Before the counting task and again before the initial memory task the subject was given 10 practice trials. The testing session lasted about 1 h. The counting task was presented first so that subjects would not memorize the specific items as they were subsequently instructed to do during the memory tasks.

2.4. Brain and muscle (EMG) potential recordings, RT

Disc electrodes (Ag/AgCl disc electrodes, 1 cm diameter) were placed over midline sagittal (Fz, Cz, and Pz) and lateral scalp positions (C3′ and C4′ were located 1 cm anterior to C3 and C4, respectively) and were referenced to linked electrodes at A1 and A2. Eye movements were monitored by electrodes situated above and at the lateral lower lid of right eye. Electrode impedances measured between scalp sites were below 3 kΩ. Muscle potentials (EMG) of the thenar muscles of the right hand were recorded between an electrode over the belly of the opponens muscle of the thumb and an electrode over the tendon at the metacarpophalangeal joint of the thumb. The potentials were differentially amplified (200 000 times for EEG; 100 000 times for the eye channel) using filter settings between 0.01 and 100 Hz (3 dB down). The muscle potentials were amplified 20 000 times and filtered (3 dB down) between 30 and 10 000 Hz. The BBC microcomputer controlled the presentation of the stimulus sequence and recorded reaction time from probe onset to the button press. A second computer digitized (256 points/channel) the brain and muscle potentials. The analysis epoch was 2.24 s and included a pre-stimulus baseline period of 0.91 s. Individual trials were saved in computer memory and later stored to disk for off-line analysis.

2.5. Data reduction and analysis

The single trials to the probes were averaged using two methods of signal alignment: (1) stimulus onset and (2) EMG onset. Only those trials with correct responses were included in the averages. If a trial was compromised by potentials from eye blinks, a compensatory adjustment of potentials was made (Gratton et al., 1983). Adjusted trials were examined and added to the average if the blink artifacts were removed. Trials from the in-set (positive) and out-of-set probes (negative) were pooled to compute the averages. EMG-locked averages were computed by aligning EMG onsets (rectified) from single trials to the 1.40 s point of the 2.24 s digitized trace. This alignment position corresponded to a point 0.49 s after stimulus onset (0.91 s (baseline) + 0.49 s = 1.40 s). For this alignment, the digitized data from trials with EMG onsets less than or equal to 0.49 s were shifted to the right, whereas trials with EMG onsets greater than 0.49 s were shifted to the left. The digitized points displaced off the time base by this procedure were discarded from the averaging procedure. The missing data points were filled with data copied point-by-point from the start of the waveform if it was shifted to the right or from the end of the waveform if shifted to the left. The points in a region before and after EMG onset were not affected by the method of point replacement. With the most rapid EMG onsets (<200 ms), the initial portion of the trace was modified (approximately 300 ms). These modified data points were included as part of the 400 ms period used to define the baseline in the EMG-locked averages.

The components in the averaged potentials were of two types: (1) sustained slow potential shifts and (2) short duration components superimposed on these slow shifts

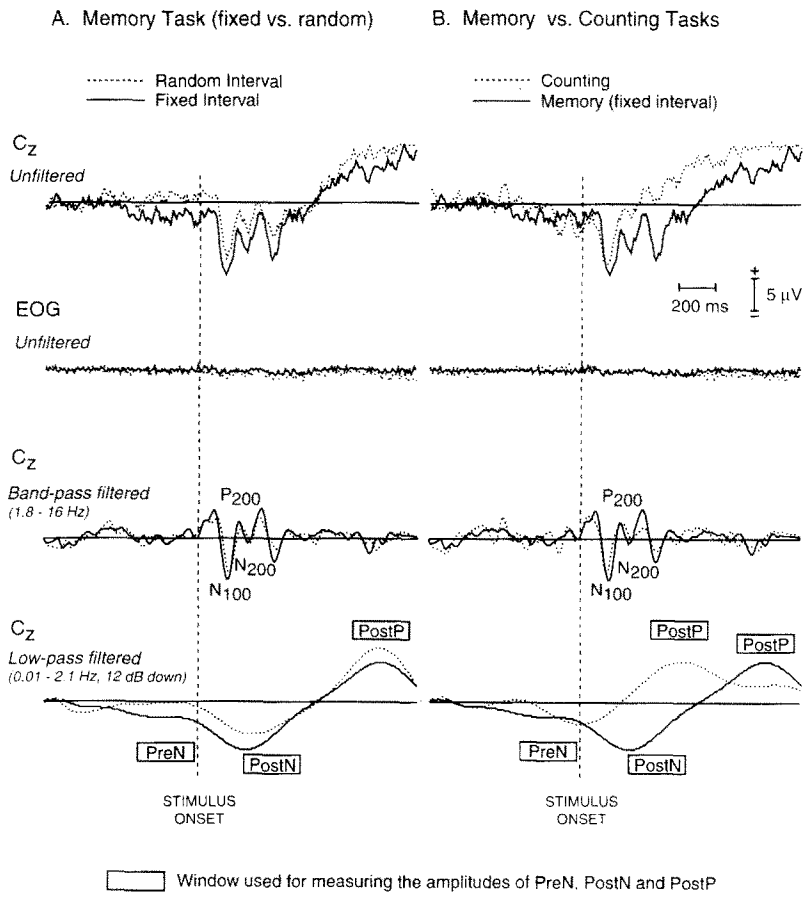

Fig. 2. Stimulus-locked averages from a single subject recorded from the Cz scalp site and the EOG channel. The slow potentials are labelled as pre- or post-stimulus (Pre or Post) and by their polarity (P or N for positive or negative, respectively). The short duration components are identified by polarity and approximate latency in ms. The averaged potentials in the upper traces were filtered in two ways: (1) from 1.8 to 16 Hz (middle traces) to attenuate the slow potentials for measurement of the short duration components; and (2) from 0.01 to 2.1 Hz (bottom traces) to attenuate the short duration components for measurement of the amplitudes of the slow potentials. The windows over which the averaged amplitude of the slow potentials were computed are represented by the open boxes. The placement and duration of these windows were based on the regions of significant differences between the two conditions defined by *t* tests (for correlated means). In this and subsequent figures positive is up and a horizontal line is drawn through the averaged pre-stimulus baseline period.

(Fig. 2). The slow potentials were labelled relative to stimulus onset (pre- or post-stimulus onset) and by polarity (positive or negative). Short duration components (N100, P200, and N200) were labelled by polarity and approximate latency in milliseconds.

The averaged potentials were filtered in two ways to measure amplitudes and latencies of various components and slow potentials. An example from one individual is shown in Fig. 2 to demonstrate the procedures used. The averaged potentials were bandpass filtered using FFT and inverse FFT procedures. Waveforms were filtered from 1.8 to 16 Hz to define the peak amplitudes and latencies of short duration components in the absence of slow potential shifts. The averaged waveforms were also low-pass filtered (zero-phase-shift digital filter, 0.01–2.1 Hz, 12 dB down) to measure the amplitude of the sustained slow potentials in the absence of the short duration components. These filter settings were selected on the basis of visual inspection of the averaged waveforms as satisfactory for separating the short duration components from the slow potential shifts. For stimulus-locked averages, the amplitudes of the short duration components were measured relative to the pre-stimulus baseline (average amplitude in a 500 ms period beginning 910 ms before stimulus onset). Peak latencies were measured from stimulus onset to the maximum polarity of a particular component. The relatively slow digitizing rate (approximately 114 samples/s) may not have been optimal for resolution of the peaks of N100 and P200 but was probably adequate for the relative comparison of these components among experimental conditions.

The placement and duration of the time periods for the measurement of slow shifts were based on significant differences of point-by-point *t* tests (for correlated means) between the averaged waveforms in the various tasks. Thus, the amplitudes of the slow negative potential shifts in the stimulus-locked averages were computed in two time domains showing multiple sequential point-by-point differences: (1) a 300 ms window preceding stimulus onset relative to baseline (average amplitude in a 120 ms period at the beginning of the averaged epoch) and (2) a 300 ms window beginning 245 ms after the stimulus rela-

tive to baseline (average amplitude in the 910 ms pre-stimulus period). The amplitude of the positive slow potentials after stimulus onset was defined in a 300 ms window centered on the maximum point relative to the baseline (average amplitude in the 910 ms pre-stimulus period). The amplitudes of the slow potential shifts in the EMG-locked averages were defined in two windows: (1) a 100 ms window immediately preceding EMG onset and (2) a 400 ms window beginning 500 ms before EMG onset. Both window measures were made relative to the average amplitude in a 400 ms period at the beginning of the averaged epoch. The use of a window measure for slow potential shifts provided a more stable estimate of the magnitude of the change than sampling a single point.

Analysis of variance procedures for repeated measures were used to evaluate the measures of amplitude and latency. The effects of interval (fixed versus random) on the memory tasks were analyzed in a two-factor ANOVA (interval × electrode). Separate analyses were conducted for the slow negative pre-stimulus shift, the post-stimulus slow negative potential, the late positive potential, and the short duration components (N100, P200, and N200). The electrode factor consisted of the midline sites Fz, Cz and Pz; the analyses of the slow pre-stimulus shift and the slow potentials synchronized to EMG onset included the midline and the lateral sites C3′ and C4′ in the electrode factor. Task effects between memory (fixed interval condition) and counting were analyzed in a two-factor ANOVA (task × electrode). Separate analyses for pre- and post-stimulus potentials and short components were performed to evaluate measures of amplitude and latency. Reaction time and accuracy were separately analyzed in a one-way ANOVA to examine the effects of interval (fixed versus random) on the two memory tasks and the effects of task (fixed interval memory versus counting). The Greenhouse-Geisser correction was applied and differences at $P < 0.05$, or better, were considered significant. Post-hoc differences among the means were carried out using the Newman-Keuls procedure.

3. Results

3.1. Memory task: effects of interval

3.1.1. Behavioral performance

RTs and accuracy (percentage correct) for both memory tasks in the fixed and random interval conditions are summarized in Table 1. RTs were significantly longer in the random interval condition than in the predictable, fixed interval condition (707 ms versus 657 ms, $P = 0.01$, respectively). There was no difference in accuracy between these two conditions (Table 1).

3.1.2. Stimulus-locked averages, slow potentials

Stimulus-locked grand averages for probes are shown in Fig. 3. In the fixed interval condition, a slow negative shift (PreN) began at least 500 ms before the onset of the probe and continued for up to 400 ms after the probe onset. In the random interval condition the pre-stimulus negative shift was essentially absent but a negative shift was still present in the post-stimulus period. These slow wave shifts were more apparent after low-pass filtering which attenuated the transient N100, P200, and N200 components (Fig. 2). The pre-stimulus negative shift was significantly larger overall in the fixed interval condition than in the random interval condition ($P < 0.01$). In the fixed interval condition, the distribution of the slow negative shift preceding the probe was posterior-central with significantly ($P < 0.01$) larger amplitudes at Cz ($-1.59\,\mu V$) and Pz ($-1.68\,\mu V$) than at Fz ($-0.44\,\mu V$); analysis of the small pre-stimulus amplitudes in the random interval condition indicated that none of the differences among the midline sites were significant. Differences in the amplitude of the pre-stimulus slow potential

Table 1

Means ± SD of the behavioral measures, RT (ms) and accuracy (percent correct), and component measures for peak latency (ms), peak or average amplitude (μV) at Cz for the stimulus-locked average potentials in the memory (fixed, random) and counting (fixed interval) tasks

	Counting task	Memory task	
	Press-on-probe	Fixed interval	Random interval
RT[a]	296 ± 52	657 ± 84	707 ± 115
Accuracy[b]	100	95	95
N100 amp.[c]	−3.06 ± 1.6	−3.32 ± 1.6	−2.73 ± 1.5
N100 lat.	178 ± 1.6	184 ± 12.4	183 ± 7.6
P200 amp.	1.73 ± 1.4	2.09 ± 1.7	1.99 ± 1.5
P200 lat.	262 ± 13.7	253 ± 11.3	261 ± 13.6
N200 amp.[d]	−1.00 ± 0.8	−2.09 ± 2.2	−2.17 ± 1.9
N200 lat.	322 ± 28	325 ± 26	342 ± 32
PostP amp.	3.68 ± 1.8	4.47 ± 3.0	4.25 ± 2.2
PostP lat.[e]	671 ± 87	774 ± 143	794 ± 85
PreN amp.[f]	−1.13 ± 0.8	−1.59 ± 1.1	0.12 ± 1.2
PreN C_{contra}/C_{ipsi}	−0 49/−0.53	−0.91/−1.09	0.08/0.12
PostN amp.[g]	1.42 ± 1.1	−1.80 ± 2.3	−1.94 ± 2.8

amp., amplitude; lat., latency; PostP, post-stimulus positive slow potential; PreN, pre-stimulus negative slow potential (300 ms window just before stimulus); C_{contra}/C_{ipsi} refer to the recording sites C3′/C4′; PostN, post-stimulus negative slow potential (300 ms window beginning 245 ms after stimulus).

[a]RT ($P < 0.01$) for memory interval (random > fixed); RT ($P < 0.001$) for task (memory [fixed interval] > counting).

[b]Accuracy ($P < 0.001$) for task (counting > memory [fixed interval]).

[c]N100 amplitude ($P < 0.05$) for memory interval (fixed > random).

[d]N200 amplitude ($P < 0.05$) for task (memory [fixed interval] > counting).

[e]PostP latency ($P < 0.05$) for task (memory [fixed interval] > counting).

[f]PreN amplitude ($P < 0.05$) for task (memory [fixed interval] > counting).

[g]PostN amplitude ($P < 0.001$) for task (memory [fixed interval] > counting).

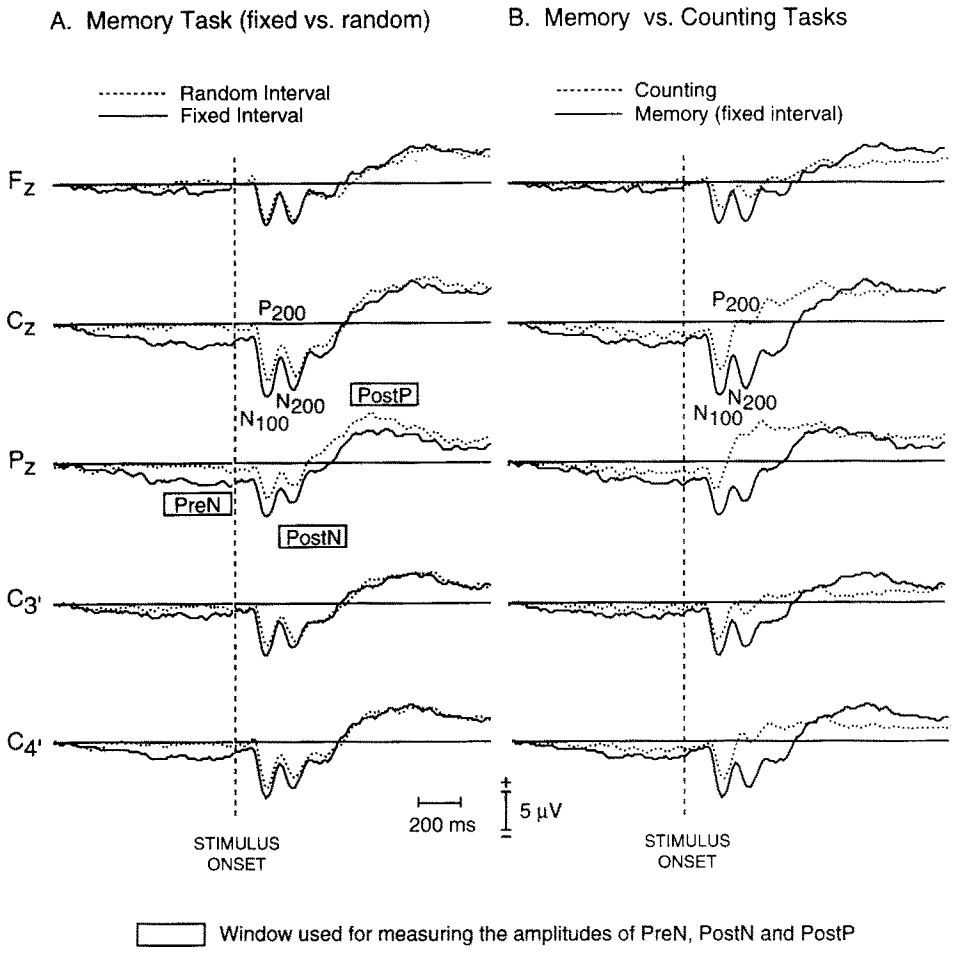

Fig. 3. Overlaid, stimulus-locked grand-averages from midline and lateral electrode sites as a function of condition (left column, fixed interval versus random interval in memory scanning task; right column, fixed interval in the memory task versus fixed interval in the counting task). The filter settings were 0.01–16 Hz. Note in the left column, the slow negative shift preceding stimulus onset (PreN) in the fixed interval condition and the absence of the negative shift in the random interval condition. In the right column, the pre-stimulus negative shift (PreN) was attenuated in the counting task compared to the memory task. The post-stimulus negative shift (PostN) evident in the memory task was absent in the counting task.

between the lateral electrodes at C3′ (−0.91 μV) and C4′ (−1.09 μV) in the fixed interval condition did not reach significant levels; similarly, differences at lateral sites C3′ (0.08 μV) and C4′ (0.12 μV) in the random interval condition were not significant.

The amplitudes of the slow negative shift after the onset of the probe (PostN) were not significantly different between the fixed and random conditions (Table 1). The post-stimulus negative shift had a central-frontal distribution with significantly ($P < 0.01$) larger potentials at Cz (−1.87 μV) and Fz (−1.02 μV) than at Pz (0.24 μV) (pooled across interval). The central-frontal distribution of the post-stimulus negative shift distinguishes it from the central-parietal distribution of the pre-stimulus negative shift.

The amplitudes of the late positive slow wave (PostP) did not differ significantly between the fixed and random interval conditions (Table 1). The distribution of the late positive slow wave was posterior-central maximal with significantly larger ($P < 0.05$) amplitudes (pooled across interval) at Cz (4.36 μV) and Pz (4.48 μV) than at Fz (3.18 μV).

3.1.3. Short duration components

N100 amplitudes (Fig. 3) measured after removal of the slow negative shift by high-pass filtering were significantly ($P < 0.05$) larger overall when the probe appeared at a fixed interval than at a random interval (e.g. value at Cz, −3.19 μV versus −2.65 μV, respectively). N100 had a central distribution; the potentials at Cz were larger than the potentials at either Fz or Pz sites ($P < 0.05$) for both the fixed and random interval conditions. N100 latency, and the amplitudes and latencies of P200 and N200, did not differ significantly between the two memory conditions using fixed or random intervals (Table 1).

3.2. Fixed interval memory task compared to a counting task

3.2.1. Behavioral performance

Reaction times in the counting task ('press on the fourth stimulus') were significantly faster than in the memory task (296 ms versus 657 ms, $P < 0.001$, respectively). The accuracy in the counting task was 100% and was higher ($P < 0.001$) than for the memory task (95%).

3.2.2. Stimulus-locked averages, slow potentials

The superimposed grand averages during the counting and memory (fixed interval) tasks are shown in Fig. 3. A negative shift preceding the stimulus (PreN) was present for both tasks, whereas the negative shift after the stimulus (PostN) was present in the memory task but, in the counting task, was either absent or replaced by the earlier appearance of the slow positive shift. The amplitude (Table 1) of the pre-stimulus negative shift was significantly ($P < 0.05$) larger in the memory task than in counting task (mean values at Cz, $-1.59\,\mu$V versus $-1.13\,\mu$V, respectively). The scalp distribution in the counting task was central-posterior with significantly ($P < 0.01$) larger potentials at Cz ($-1.13\,\mu$V) and Pz ($-0.85\,\mu$V) than at Fz ($-0.01\,\mu$V). Lateral differences in the amplitudes of the pre-stimulus negative shift at C3′ ($-0.49\,\mu$V) and C4′ ($-0.53\,\mu$V) did not reach significant levels in the counting task.

The amplitude of the post-stimulus negative shift was significantly ($P < 0.001$) larger in the memory than the counting task (mean values at Cz, $-1.80\,\mu$V versus $+1.42\,\mu$V, respectively). In the counting task, this potential had a distribution which was parietal-central and positive in polarity. The latency of the late slow wave peak (PostP) was significantly ($P < 0.05$) shorter in the counting than in the memory task (mean values at Cz, 671 ms versus 774 ms, respectively).

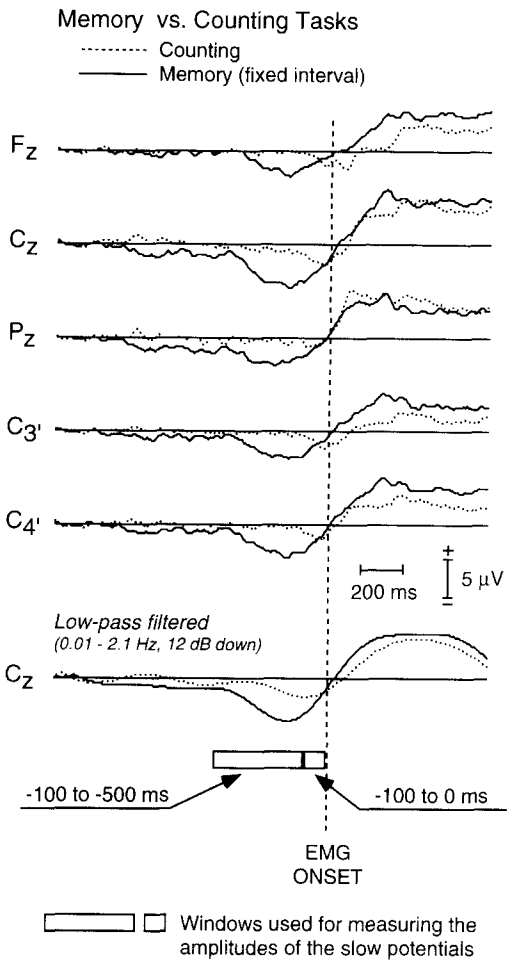

Fig. 4. EMG-locked grand averages in the counting and memory tasks. Note the presence of a negative shift 500–100 ms before EMG onset in the memory compared to the counting task. The filter settings were 0.01–16 Hz except for the traces at Cz at the bottom. The negative shift in the memory task was the same negative shift that preceded the stimulus in the stimulus-locked averages in the memory task. There were no differences in the average amplitude of the negative shift in the 100 ms period immediately preceding EMG onset between these two conditions.

3.2.3. Short duration components

Peak latencies and amplitudes of the short duration components (N100, P200) measured after removal of the slow potential shift by high-pass filtering were not significantly different between memory and counting tasks (Table 1). However, N200 amplitudes were larger ($P < 0.05$) in the memory than in the counting task (mean value at Cz, $-2.09\,\mu$V versus $-1.00\,\mu$V, respectively).

3.2.4. EMG-locked averages

In the EMG-locked averages, a short-duration negative shift was evident in the counting task beginning approximately 200 ms before movement onset in contrast to the relatively longer duration of negative shift in the memory task that began 500 ms before EMG onset (Fig. 4). The amplitudes of the slow negative potential measured in a 100 ms window before EMG onset between the memory task with fixed interval and counting task were not significantly different (mean value at Cz, $-1.04\,\mu$V versus $-0.87\,\mu$V, respectively; Table 2). In contrast, the overall amplitudes in a 400 ms window beginning 500 ms before EMG onset were significantly ($P < 0.05$) larger in the memory task (fixed interval) than in the counting task (mean value at Cz, $-1.97\,\mu$V versus $-0.72\,\mu$V, respectively). The distribution of the long-duration negative shift was central dominant for both the memory and counting tasks; none of the differences between lateral sites in each task attained significant levels. A separate comparison of the pre-movement negative shift between the two memory tasks (fixed versus random interval), indicated that the differences in amplitude were not significant.

Table 2

Mean ± SD of amplitude (μV) for EMG-locked potentials in the memory (fixed interval) task and the counting task at Cz

	Counting task	Memory task
	Press-on-probe	Fixed interval
400 ms window beginning 500 ms before EMG onset		
Amp.[a]	−0.72 ± 0.6	−1.97 ± 1.8
C_{contra}/C_{ipsi}	−0.29/−0.23	−1.25/−1.35
100 ms window just before EMG onset		
Amp.	−0.87 ± 1.2	−1.04 ± 3.0
C_{contra}/C_{ipsi}	−0.65/−0.25	−0.56/−0.49

Amp., amplitude; C_{contra}/C_{ipsi} refer to the recording sites C3′/C4′.
[a]Average amplitude ($P < 0.001$) for task (memory [fixed interval] > counting).

4. Discussion

4.1. Slow potentials

The results of this study using a memory scanning task showed that the amplitude of a negative shift before the presentation of the probe was affected by the temporal certainty or uncertainty of the appearance of the probe. When the occurrence of the probe was made temporally uncertain, the amplitude of the negative shift preceding the probe was markedly attenuated and RT was slightly but significantly prolonged. These results are similar to those found in a study reported by Loveless and Sanford (1974) on CNV and RT. In that study regular and irregular foreperiods were used between the warning stimulus (S1, a 1000 Hz tone) and the response stimulus (S2, white noise). They found that CNV amplitudes were markedly decreased and RTs were increased when the duration of the foreperiod was irregular relative to a regular foreperiod. It is likely, therefore, that the negative potential appearing for several hundred milliseconds before the probe in a memory scanning task represents, to a large extent, an expectancy for the impending temporal appearance of the probe, as originally suggested by Roth et al. (1975). The scalp distribution of the pre-stimulus slow potential in the memory task when the probe occurred at a fixed interval was central-parietal maximal, which is also consistent with the distribution of the CNV reported in other studies (Ruchkin et al., 1986, 1987, 1988; Brunia et al., 1988; Frost et al., 1988). The lack of a significant difference in the amplitudes of the pre-stimulus slow negativity between the two lateral sites (C3′ and C4′) distinguishes this slow negative shift from the Bereitschaftspotential (BP) accompanying self-paced movement which is lateralized to the hemisphere contralateral to the responding hand (Vaughan et al., 1968; Deecke et al., 1969; McCallum, 1978).

The results of the present study also suggest that the slow negative potential shift preceding the probe was influenced by short-term memory functions since the negative shift was slightly, but significantly larger when subjects were engaged in the memory scanning task compared to the counting task. These findings support the proposal by Ruchkin et al. (1990) and Lang et al. (1992) that the negative potential preceding the probe reflects aspects of short-term memory function. Rehearsal of the memorized items using subvocal repetition or visual imagery is thought to occur in the period between the presentation of items for memorization and their recall (Baddeley et al., 1984). However, the difference in the amplitude of the negative shift before the probe in the memory versus the counting tasks in the present study cannot be unequivocally ascribed to memory processes since the two tasks were quite different in their level of difficulty as reflected by the 350 ms disparity in RTs (657 ms in memory task versus 296 ms in the counting task). Task difficulty, which is known to affect the amplitude of endogenous slow potentials such as the CNV (Delse et al., 1972), could also be the basis for the differences in amplitude observed for the potentials in the counting and memory tasks. Further studies of brain potentials in memory versus non-memory tasks when adjusted for level of difficulty would assist in distinguishing the factor of task difficulty from that of memory processing.

A second slow negative shift peaking at approximately 376 ms after the appearance of the probe was not affected by whether the appearance of the probe was certain or uncertain. The scalp distribution of this negative shift was frontal-central and different from the posterior scalp distribution of the pre-stimulus negative shift. When the task was changed from one which required keeping a mental record of the number of stimuli presented and responding to the probe as 'the fourth stimulus' to one which required memorization, this negative shift then appeared. These findings support the suggestion by others that the negative shift occurring after the probe is related to memory function (Okita et al., 1985; Wijers et al., 1989). It is in this period that the scanning of the memory store is occurring and when the identification of the probe as a member or not a member of the memory-set is made. Although it is logical to speculate that the negative shift peaking about 376 ms after probe onset represents activity in neural systems subserving processes such as scanning and/or matching of the probe to the memory-set items, the contribution of potentials related to the different motor response requirements of the memory and counting tasks needs to be considered. In the memory task the subjects chose between two buttons to classify the probes as in- or out-of-set. In the counting task only a single button press response was made at the occurrence of the fourth stimulus. Unpublished studies in our laboratory using the same memory scanning task but requiring a mental classification of the probes instead of a button press have shown no

differences in the potentials compared to those accompanying the two-alternative forced-choice button press response requirement. Thus, differences in the motor response requirements between the memory and counting tasks are unlikely to be the bases for differences in the potentials accompanying the two tasks. Our data do not allow us to address whether the degree of difficulty between the counting and memory tasks rather than the requirement for memory processing, per se, could account for the observed disparity of the brain potentials in the two tasks. For instance, there is a slow negative shift, processing negativity or Nd, that follows stimuli relevant for performance of a task (Naatanen, 1982) with a latency that is delayed in difficult versus easy discrimination tasks (Novak et al., 1992). Thus, a processing negativity could contribute to the late negative shift (250–550 ms) observed in the present studies during memory scanning but not during the counting task.

The amplitude of the slow positive potential shift that appeared after the probe was not significantly different between any of the tasks (fixed versus random probe interval in the memory tasks, memory versus counting tasks). There was a latency difference between the peak of the slow positive shift in memory and counting tasks perhaps due to differences in task difficulty (Polich, 1987; Czigler and Szenthe, 1988). In this regard, the slow positive shift appears to have little specificity to short-term verbal memory function but rather represents aspects of stimulus classification (e.g. a P300-like potential) and appears across a wide variety of tasks (Smith et al., 1970; Hillyard et al., 1971; Squires et al., 1973; Rohrbaugh et al., 1974).

4.2. Short duration components

The results of the present study showed that N100 amplitude was significantly larger in the memory task with fixed interval than with random interval, whereas there were no differences of N100 amplitude between the memory and the counting task. The definition of changes of N100 to relevant stimuli appearing with temporal uncertainty is consistent with prior observations of the effects of cognitive variables of attention (Hillyard et al., 1973), expectancy (McCarthy and Donchin, 1976; Hirata and Lehmann, 1990), and response preparation (Starr et al., 1995) on the amplitude of N100. The amplitudes of N100-P200 are not different for tones presented regularly every 2.0 s and for tones presented at intervals between 1 and 4.5 s (mean of 2 s) when auditory stimuli are presented without the requirement for stimulus classification (Nelson et al., 1969; Nelson and Lassman, 1977). The finding that the N200 component was significantly larger in the memory than the counting task may be accounted for by the overlap of this peak with the slow negative shift in the memory but not the counting task.

4.3. Pre-movement potentials

All of the tasks used in this study required the subject to make a motor response to the stimuli. When such a motor act is 'voluntary' and self-paced, a negative shift appears that is initiated many hundreds of milliseconds before the motor response (Kornhuber and Deecke, 1965). An analysis of the potentials preceding the motor response in this study showed a negativity in the memory task that began approximately 500 ms prior to the EMG response, whereas in the counting task the negativity began approximately 200 ms before the motor response. The amplitudes of the negative shift in the period immediately prior (100 ms) to EMG onset were not significantly different in the two tasks; this negative shift may reflect brain processes involved in motor response preparation that is 'obligatory', initiated in response to an auditory cue, and is to be distinguished from the negative shifts accompanying self-paced 'voluntary' movements. The additional negativity that extends back another 400 ms before the motor response in the memory but not the counting tasks appears to be the same negative shift that follows the probes in the stimulus-locked averages in the memory task. The negative shift was of relatively long duration so that the slight temporal adjustments introduced in the EMG-locked averages relative to the stimulus-locked averages would have very little effect on its amplitude or shape. It is of interest that even the low amplitude pre-stimulus slow negative potential shift can still be identified in the EMG-locked averages of both the memory and counting tasks (see Fig. 3, bottom traces). Since the order of the memory tasks (fixed, random) was the same for all the subjects after the counting task, the results may have been influenced by practice or subject fatigue and limited the interpretation of the findings. However, the high accuracy of the subjects and the relatively short testing time for each task, suggest that effects resulting from practice or subject fatigue were probably minimal.

The results of these studies demonstrated that the amplitude of a slow negative potential that appeared in the period between the last memory item and the probe in a memory scanning task was primarily affected by the temporal certainty for the appearance of the probe and, to a lesser extent, by memory processes. In contrast, a negative shift that occurred 250 and 550 ms after the probe was present during memory processing independent of the temporal certainty of the appearance of the probe but was absent in a counting task. The amplitude of a late slow positive potential, which peaked at 700 ms, was not different between the memory and counting tasks.

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