Serial Position Effects in Auditory Event-related Potentials during Working Memory Retrieval

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Abstract

■ It is established that recall of an item from a list of sequentially presented items is sensitive to the item's position in the memorized list. However, little is known about the brain mechanisms that mediate these serial position effects. Studies of working memory retrieval using event-related potentials report amplitude reductions during retrieval (auditory cortical N100, neocortical late positive wave [LPW]) as memory load increases. We tested the hypothesis that N100 and LPW amplitudes to probes are also affected by serial position. Event-related potentials were recorded from subjects performing an auditory working memory task. A set of one or five digits was memorized, then subjects classified a probe digit as either present or absent from the memory set. A control task was also given. Amplitudes of the N100 and LPW were reduced in the 5-item versus the 1-item set. In the 5-item set N100 amplitude was significantly larger for the initial (1st) serial position, relative to Positions 2–5, while linear increases in LPW amplitude were seen across serial positions (5th > 1st position). A control task without memorization showed no N100 or LPW amplitude changes with set size or serial position. The findings reveal that the N100 and LPW are influenced differently by serial position during working memory retrieval: N100 shows a primacy effect and LPW demonstrates a recency effect. The results suggest that primacy and recency effects may be mediated by different brain regions at different times during memory retrieval. ■

INTRODUCTION

The term *working memory* refers to the process of temporarily storing information in memory, and includes the ability to manipulate the stored information (Baddeley, 1992). The temporary storage and manipulation of information is a necessary element in more sophisticated capabilities such as reasoning, planning, and language comprehension.

Working memory is typically divided into encoding, maintenance, and retrieval phases. Sternberg (1966) introduced a behavioral paradigm to study working memory retrieval. First, subjects encoded a list of memory set items presented sequentially, such as letters or digits. Then, following a short delay a probe item was delivered and subjects indicated if the probe was (in-set) or was not (out-of-set), a member of the memory set by pressing one of two buttons. Reaction times increased linearly with increases in memory load, and the reaction time versus memory load slopes were equivalent between in-set and out-of-set probes.

It was originally proposed that the linear reaction time versus set size function implied a serial comparison process between the probe and each item in the memory set, with a fixed amount of time (~40 msec) for each comparison (Sternberg, 1966). Subsequent studies provided results that were difficult to reconcile with a serial, exhaustive model (see Dosher & Sperling, 1998). One important finding showed that reaction times to in-set probes usually vary as a function of their serial position within the sequence of memory set items (McElree & Dosher, 1989; Monsell, 1978; Ratcliff, 1978; Burrows & Okada, 1971). Probe reaction times are shortest for items presented last in the memory set sequence (recency effect), progressively increase across earlier positions, and sometimes exhibit reductions when matching the first item that was presented (primacy effect). The serial-exhaustive search model predicted equivalent reaction times across serial positions because the entire list is scanned before a response is selected, regardless of the probe's serial position. Models that incorporate a parallel comparison between probes and memory set items (e.g., Murdock, 1971) or are based on trace strength (e.g., Ratcliff, 1978) can account for serial position effects by including parameter values that covary with serial position.

Event-related potentials recorded while subjects performed the Sternberg task show two components that display changes as a function of memory load during retrieval. When auditory stimuli are presented the N100 component, a prominent negative wave generated in the auditory cortex having a peak latency ~100 msec after stimulus presentation, exhibits linear amplitude reductions in response to increases in memory load (Golob & Starr, 2000; Conley, Michalewski, Starr, 1999; cf. Kaufman, Curtis, Wang, & Williamson, 1992). Probes also elicit a sustained late positive wave (LPW, often called P300) that is maximal at parietal electrode sites and is

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likely generated by several neocortical areas, including the posterior parietal cortex (Rypma & D'Esposito, 2000; Starr & Barrett, 1987). The LPW typically exhibits latency increases, and sometimes amplitude reductions, in response to increased memory load (e.g., Pelosi, Hayward, & Blumhardt, 1995; Kramer, Strayer, & Buckley, 1991; Pratt, Michalewski, Barrett, & Starr, 1989; Ford, Pfefferbaum, Tinklenberg, & Kopell, 1982). Larger LPW amplitudes have been observed for auditory probes matching the last memory set item, relative to the remaining serial positions (Chao & Knight, 1996; Patterson, Pratt, & Starr, 1991). In a picture recognition task, a recency effect was also observed in a portion of the LPW (Crites, Devine, Lozano, & Moreno, 1998).

The present study examines the N100 and LPW components as a function of serial position to evaluate neurobiological processes associated with retrieval using a factor, serial position, which is important in the development of current theories of working memory retrieval. Experiments tested the hypothesis that the overall reduction in N100 and LPW amplitudes with increased memory load is related to averaging across serial positions, the number of which covaries with set size. N100 and LPW amplitudes were predicted to be larger for the recency and/or primacy positions. Although a few studies have examined the LPW as a function of serial position, the current study extends these findings by detailing the LPW in a typical auditory Sternberg task using verbal material.

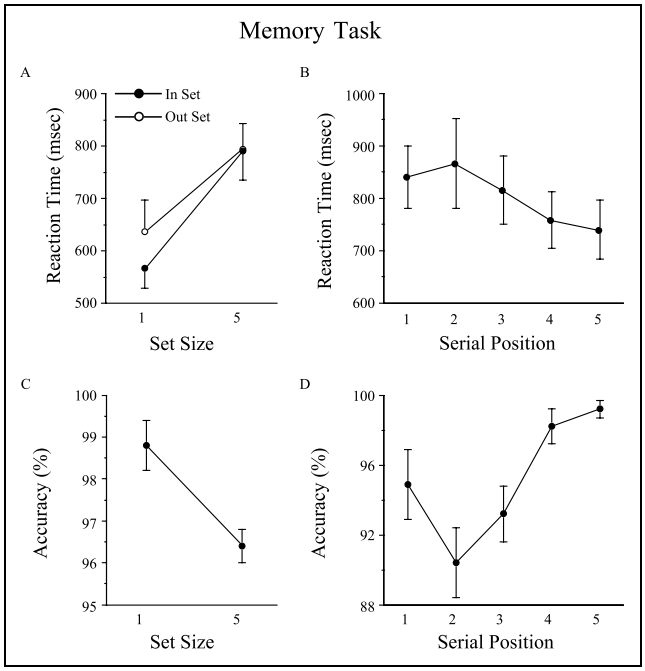

Figure 2. Behavioral results from Experiment 1. Reaction time as a function of memory set size (A) and serial position (B) in the 5-item memory set. Reaction time was significantly longer for the 5- versus 1-item memory set. Reaction time was also significantly different as a function of serial position, which indicates a recency effect. Accuracy as a function of memory load (C) and serial position (D). Accuracy was significantly reduced for the 5- versus 1-item memory set and showed a significant recency effect across serial positions. Error bars indicate standard error.

RESULTS

Experiment 1

Behavior

A schematic diagram of the task is presented in Figure 1. Reaction time as a function of set size is shown in Figure 2A. There was a significant difference in reaction time between 1- and 5-item set sizes, $F(1,11) = 60.4$; $p < .0001$. Mean slope of the reaction time versus set size function was 47.1 ± 6.6 msec/item. There was also a significant difference between in-set and out-of-set probes, $F(1,11) = 5.2$; $p < .05$, with faster reaction times for in-set probes (see Table 1). Although differences between in-set and out-of-set probes were primarily seen for the 1-item set size, the Set Size × Probe Type interaction did not attain significance.

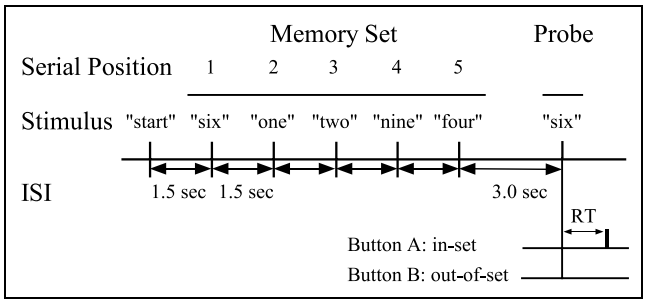

Figure 1. Schematic diagram of experimental paradigm. Each block contained 20 trials (10 in-set, 10 out-of-set), with a 3.0-sec intertrial interval (ISI).

There was a significant difference in accuracy between 1- and 5-item set sizes, $t(11) = 3.2$; $p < .01$, with greater accuracy for the 1-item set size (Figure 2C). Percentage of trials without a response for 1- and 5-item sets were 0.5% and 1.8%, respectively.

Reaction time as a function of serial position for in-set probes in the 5-item set size is shown in Figure 2B. Reaction times were significantly different across serial positions, $F(4,44) = 5.9$; $p < .01$. Post hoc testing indicated significant differences between Position 1 versus Positions 4 and 5, Position 2 versus Positions 4 and 5, and Position 3 versus Position 5. These results indicate a recency effect, with faster reaction times for probes having positions toward the end of the memory set relative to earlier positions. A significant primacy effect for reaction time was not observed, a result that may be related to rehearsal during the long retention period.

Similarly, reaction times in the 5-item set to out-of-set probes were analyzed as a function of the last trial a

Table 1. Amplitudes and Latencies of Event-related Potentials to Probes

	Amplitude (μV)				*Latency (msec)*			
	In-Set		*Out-of-Set*		*In-Set*		*Out-of-Set*	
	1 Item	*5 Item*	*1 Item*	*5 Item*	*1 Item*	*5 Item*	*1 Item*	*5 Item*
N100[a,b]	−9.1	−6.4	−8.3	−7.3	123	134	128	130
P200	5.1	4.9	5.9	5.3	213	215	204	218
N200[a,b]	−0.8	−3.6	−0.7	−3.4	276	298	278	299
P300[a,b]	5.1	2.8	4.4	2.0	342	368	337	368
LPW[a,b]	7.5	5.4	6.6	3.7	406	529	453	538
Reaction time	N/A	N/A	N/A	N/A	566	790	636	792

Note: All values were measured from the Cz electrode site except for the LPW, which was measured from Pz.

[a]Significant main effect for set size (amplitude).

[b]Significant main effect for set size (latency).

particular out-of-set probe digit was present in a memory set (negative recency effects: 1 trial back, 2 trials back, 3–9 trials back). There was a significant effect for negative recency position, $F(2,22) = 4.4$; $p < .03$, with mean reaction times of 852, 786, and 799 msec for 1 trial back, 2 trials back, and 3–9 trials back, respectively. Post hoc testing indicated that reaction times for probes 1 trial back were significantly slower than 2 and 3–9 trials back.

There were significant differences in accuracy among in-set serial positions (see Figure 2D), $F(4,44) = 5.8$; $p < .01$. Post hoc testing indicated significant differences between Position 2 and Positions 4 and 5, and Position 3 versus Position 5, results consistent with a recency effect. As with reaction time, a significant primacy effect was not observed. For out-of-set probes, there were no significant differences in accuracy across negative recency positions ($p < .06$). Because there were too few samples of 3–9 back probes to accurately measure event-related potentials, there will be no further discussion of negative recency effects.

Event-related Potentials

Grand average potentials to probes (in-set and out-of-set combined) from all electrode sites are shown in Figure 3. Note that N100 amplitude is largest at the Cz electrode, while the LPW is largest at the Pz electrode. Inset shows a close-up view of the Cz electrode site. Probes elicited transient components having peak latencies of ∼130 msec (N100), ∼210 msec (P200), ∼280 msec (N200), and ∼350 msec (P300). The longer N100 latency, relative to pure tones, is due to the use of speech stimuli. There was also a sustained positive slow wave, termed the late positive wave (LPW), that began at ∼200 msec, peaked between 600 and 800 msec, and returned to baseline at ∼1000 msec. The tracings in Figure 3 illustrate the two main electrophysiological findings under consideration in this study. First, amplitude of the N100 component decreased with increased working memory load (N100 1-item set > N100 5-item set). Second, the LPW decreased in amplitude with increased working memory load, especially between 200 and 600 msec after stimulus presentation.

Serial Position Effects

N100. Average potentials for each of the five serial positions for in-set probes were constructed. Potentials for serial Positions 1, 3, and 5 are shown in Figure 4A. N100 amplitude for Position 1 is ∼2 μV larger than Positions 3 and 5. A one-way repeated measures analysis of variance (ANOVA) evaluating serial position (1st,

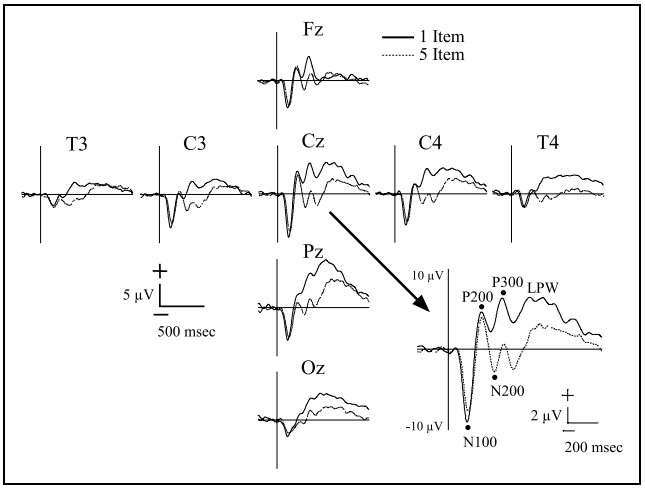

Figure 3. Event-related potentials to probes at all electrode sites for 1- and 5-item memory sets. Inset from Cz site shows measured components. Potentials were low-pass filtered (DC—16 Hz).

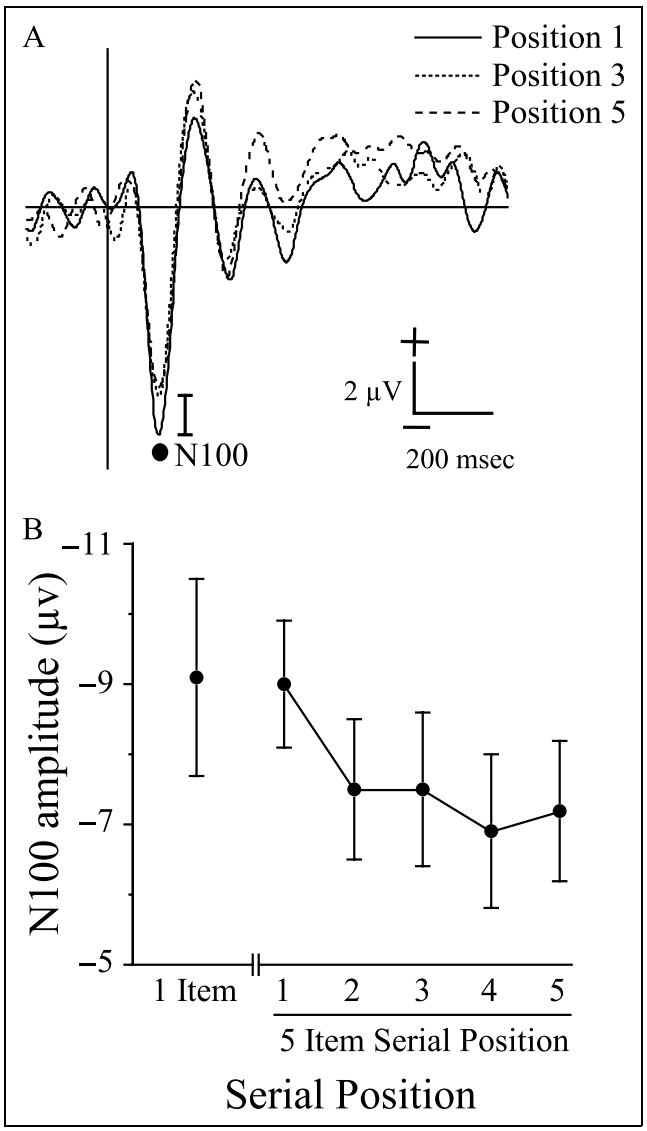

Figure 4. N100 component as a function of serial position. (A) Potentials to in-set probes that were presented in the 1st, 3rd, and 5th serial positions of the memory set (bandpass filtered 1–16 Hz). (B) Plot of N100 amplitudes for in-set probes in the 1-item memory set and across serial positions in the 5-item memory set. N100 amplitudes were equivalent for the 1-item set and the 1st serial position of the 5-item set, and had significantly smaller amplitudes for serial Positions 2 through 5. Error bars indicate standard error.

3rd, 5th) indicated a significant difference in N100 amplitude across serial position, $F(2, 22) = 6.8$; $p < .01$. A planned comparison using a Helmert contrast showed a significant difference between Position 1 and Positions 2 through 5, $F(1,11) = 32.3$; $p < .001$. A one way ANOVA among serial Positions 2 through 5 indicated no significant differences across these serial positions ($p > .80$). Mean N100 amplitudes across serial position are plotted in Figure 4B. For comparison, N100 amplitude for in-set probes from the 1-item set size is also shown. Note that N100 amplitude for in-set probes in the 1-item set is nearly identical to the amplitude for serial Position 1 in the 5-item set (−9.1 μV and −9.0 μV, respectively). Taken together, the results show that N100 amplitude was largest for probes that were memorized at Position 1, and that there were no differences between probes memorized at later serial positions (Positions 2–5).

There were no significant differences in N100 latency across serial position (1st, 3rd, 5th).

P200, N200, and P300. The P200, N200, and P300 components coincided with the beginning of the LPW. bandpass filtering between 1 and 16 Hz attenuated the LPW to allow measurement of the P200, N200, and P300 components.

Separate one-way repeated measures ANOVA tests assessing serial position (1st, 3rd, 5th) for the P200, N200, and P300 components showed no significant amplitude differences across serial position. There were also no significant differences across serial position for P200, N200, and P300 latency.

LPW. Four separate ANOVA tests (one per site: Fz, Cz, Pz, Oz) assessed LPW amplitude using the factors of serial position (1, 3, 5) and window (200–399, 400–599, 600–799, 800–999 msec). For LPW amplitude at Fz, Cz, and Oz sites showed no significant effects. At Pz, the site with maximal amplitude of the LPW, there were significant effects for serial position, $F(2,22) = 5.3$; $p < .03$, and window, $F(3,33) = 4.8$; $p < .02$. The Serial Position × Window interaction was not significant. The same results were found when all five serial positions were included.

Potentials from the Pz electrode for serial Positions 1, 3, and 5 are shown in Figure 5A, and mean LPW values for each window as a function of serial position are shown in Figure 5B. The monotonic increases in LPW amplitude across serial position for the 200–399, 400–599, and 600–799 windows suggests a linear increase in LPW. Trend analysis over the five serial positions indicated significant linear trends for the 200–399 msec, $F(1,44) = 11.0$; $p < .01$, 400–599 msec, $F(1,44) = 22.0$; $p < .01$, and 600–799 msec, $F(1,44) = 18.8$; $p < .01$, windows. There was not a significant linear trend for the 800–999 msec window, and quadratic trends for all windows were nonsignificant. Slopes of linear curves fit to the group mean values were 0.61 ($r = .92$), 1.04 ($r = .88$), and 0.98 ($r = .96$) μV/serial position for the 200–399, 400–599, and 600–799 msec windows, respectively.

In summary, the LPW results show linear changes across serial position that last between ~200 and ~800 msec. The scalp potential changes appear to be spatially restricted because linear changes as a function of serial position were found only at the Pz electrode site.

Memory Load: One-Item versus Five-Item Sets

N100. Event-related potentials to probes are shown in Figure 6 for in-set (A) and out-of-set (B) probes. Mean

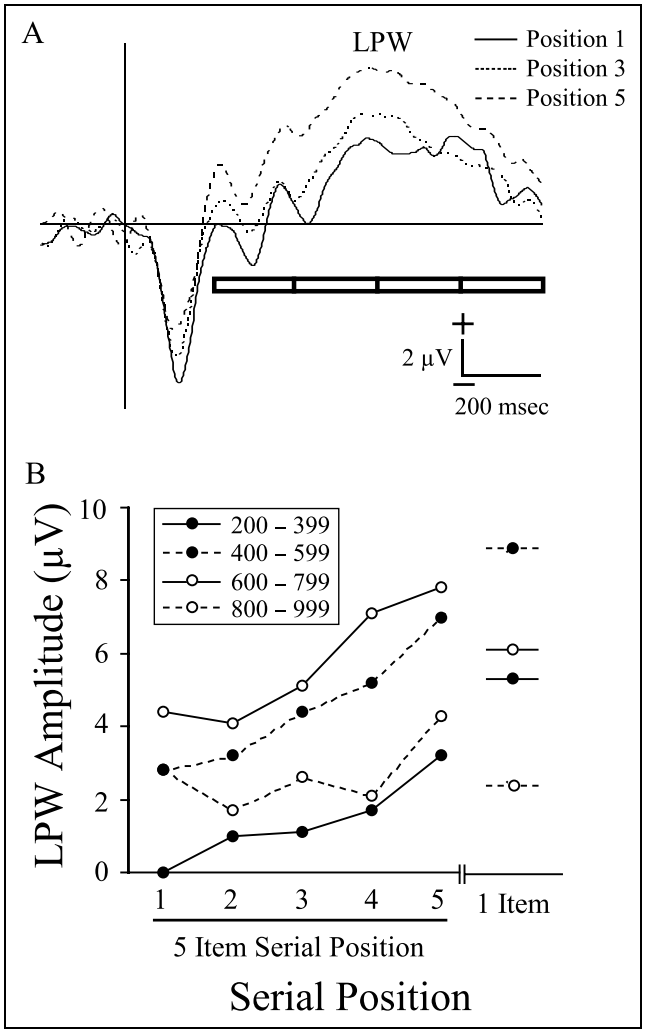

Figure 5. LPW component as a function of serial position. (A) Potentials to in-set probes that were presented in the 1st, 3rd, and 5th serial positions of the memory set. (B) Plots of LPW amplitudes from four 200-msec windows (starting 200 msec after probe presentation) as a function of serial position. LPW amplitudes for probes in the 1-item memory set are also presented for comparison.

amplitude and latency values are shown in Table 1. Separate ANOVAs assessed N100 amplitude and latency with factors of probe type (in-set, out-of-set) and set size (1 item, 5 item). For N100 amplitude there was a significant effect for set size, $F(1,11) = 14.0$; $p < .01$, but no significant effect for probe type. Although the difference in N100 amplitude between 1- and 5-item set sizes was larger for in-set probes (~3 μV) versus out-of-set probes (~1 μV), the difference did not attain significance ($p > .10$).

There was a significant difference in N100 latency across set size, $F(1,11) = 12.5$; $p < .01$, but no significant effects of probe type or Probe Type × Set Size interaction.

P200, N200, P300. Mean amplitude and latency values for the P200, N200, and P300 components are presented in Table 1, and potentials for in-set and out-of-set probes are shown in Figure 6. For the P200 component there were no significant effects of set size, probe type, or Probe Type × Set Size interaction for either amplitude or latency measures. There were significant differences across set size for N200 amplitude, $F(1,11) = 22.4$; $p < .001$, and latency, $F(1,11) = 10.3$; $p < .01$. There were no significant differences in N200 amplitude or latency for probe type or for the Probe Type × Set Size interaction. There were significant differences in P300 amplitude, $F(1,11) = 9.5$; $p < .01$, and latency, $F(1,11) = 9.6$; $p < .01$, across set size. There were no significant differences in P300 amplitude or latency for probe type or the Probe Type × Set Size interaction.

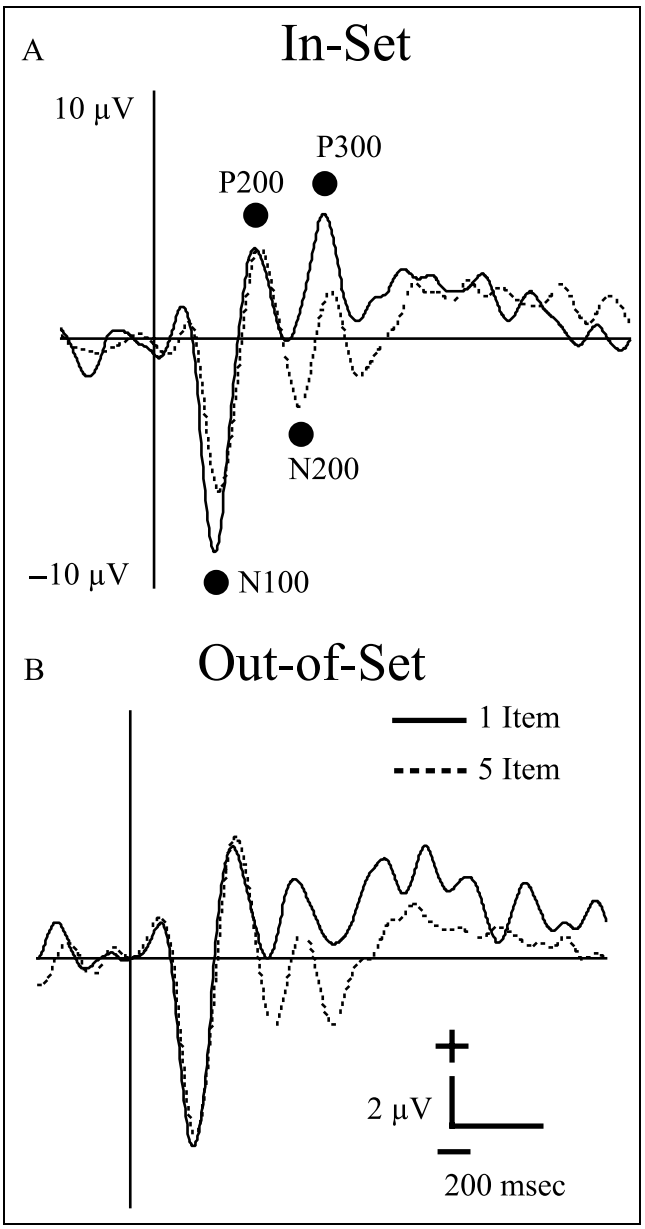

Figure 6. Grand average potentials (1–16 Hz) in the 1- and 5-item memory sets for in-set (A) and out-of-set (B) probes. The N100, N200, and P300 components had significantly smaller amplitudes and longer latencies for the 5-item memory set relative to the 1-item memory set.

LPW. Initial characterization of the scalp distribution of the LPW showed amplitude reductions with increased memory load at the Cz, Pz, and Oz sites, with a maximum amplitude at Pz.[1] LPW amplitudes to in-set and out-of-set probes were analyzed with a 2 (probe type) × 4 (window) × 2 (set size) ANOVA test at the Pz site. Potentials are shown in Figure 7 for in-set (A) and out-of-set (B) probes, with the corresponding window amplitudes (C, D). There were significant main effects for window, $F(3,33) = 8.9$; $p < .01$, and set size, $F(1,11) = 11.3$; $p < .01$. There were also significant effects for the Window × Set Size, $F(3,33) = 6.2$; $p < .01$, and Probe Type × Window × Set Size interactions, $F(3,33) = 4.0$; $p < .03$. Post hoc testing indicated significant set size differences for in-set probes only for the two windows between 200 and 600 msec. For out-of-set probes all four windows, 200–1000 msec, had significant differences between set sizes. These results indicate that LPW amplitudes at the Pz site in the 5-item set were less than the 1-item set, but the difference between set sizes had a longer duration for out-of-set probes (200–1000 msec), relative to in-set probes (200–600 msec).

For comparison with previous reports, the LPW was also analyzed by defining a peak amplitude and latency at the Pz site for each probe type and set size after bandpass filtering (0.1–16 Hz) (see Table 1). There was a significant effect of set size on LPW amplitude, $F(1,11) = 18.9$; $p < .01$, and latency, $F(1,11) = 24.5$; $p < .001$.

In summary, at ~100 msec after probe presentation N100 amplitude was less negative with increased set size. No amplitude or latency changes were seen for the P200 component. Then, beginning ~250 msec after probe presentation amplitudes of the N200, P300, and LPW were less positive with increased set size. Within these same time periods (~100 msec, ~250–400 msec) latency increases in N100, N200, and P300 were observed following increases in memory load.

Experiment 2

Subjects were given the same stimulus sequences as in Experiment 1, but were asked to ''listen to the numbers'' in the memory set, and to classify the probes as ''even or odd numbers,'' rather than in-set or out-of-set.

Behavior

Reaction time as a function of set size is shown in Figure 8A. Reaction time was analyzed using the factors of set size (1, 5) and probe type (in-set, out-of-set). There were no significant reaction time effects for set size, probe type, or Probe Type × Set Size interaction. For the accuracy measure, there were no significant effects of set size, probe type, or for the Probe Type × Set Size interaction (Figure 8C).

In Figure 8 reaction time (C) and accuracy (D) across serial positions are plotted. There were no significant differences across serial position for either reaction time or accuracy.

Event-related Potentials

Event-related potentials to probes in Experiment 2 are shown in Figure 9. As with Experiment 1 there were prominent N100 and P200 components (A, B); however, the N200, P300, and LPW (C, D) components were not readily apparent in Experiment 2.

One-Item versus Five-Item Sets

N100. Separate 2 (probe type: in set, out-of-set) × 2 (set size: 1, 5 item) ANOVA tests were conducted for N100 amplitude and latency. There were no significant effects for probe type, set size, and Probe Type × Set Size interaction.

P200. There were no significant effects for probe type, set size, or Probe Type × Set Size interaction for either P200 amplitude or latency.

LPW. Although a prominent LPW was not observed as in Experiment 1 (compare Figure 7A and B with Figure 9C and D), there was a small positive waveform beginning ~300 msec after stimulus presentation at posterior sites in Experiment 2. This waveform was assessed using a 4 (windows) × 2 (set size) ANOVA performed on the grand average probes (in-set and out-of-set combined) from the Pz site. There were no significant differences for window or set size, and the Window × Set Size interaction was not significant. Individual one-sample *t* tests were conducted to determine if the window amplitudes were significantly different from 0 μV (8 *t* tests: 2 [set sizes] × 4 [windows]). Significant differences were seen only in the 5-item set size for windows 600–799 and 800–999 msec. Thus, although there may be a small amplitude, late-developing slow wave in the control task, a large amplitude LPW having different amplitudes for 1- and 5-item memory loads was observed only when subjects were required to compare the probe with the memory set.

Serial Position Analysis

N100. Serial position data are shown in Figure 9 with tracings for the 1st, 3rd, and 5th serial positions in the 5-item set shown in (E), and mean values are plotted in (F) along with the results from Experiment 1 for comparison. A one-way repeated measures ANOVA across serial position (1st, 3rd, 5th) showed no significant change in N100 amplitude across serial position. Similarly, there were no significant changes in N100 latency across serial position.

P200. Separate ANOVA tests showed that P200 amplitude and latency did not change significantly across serial position.

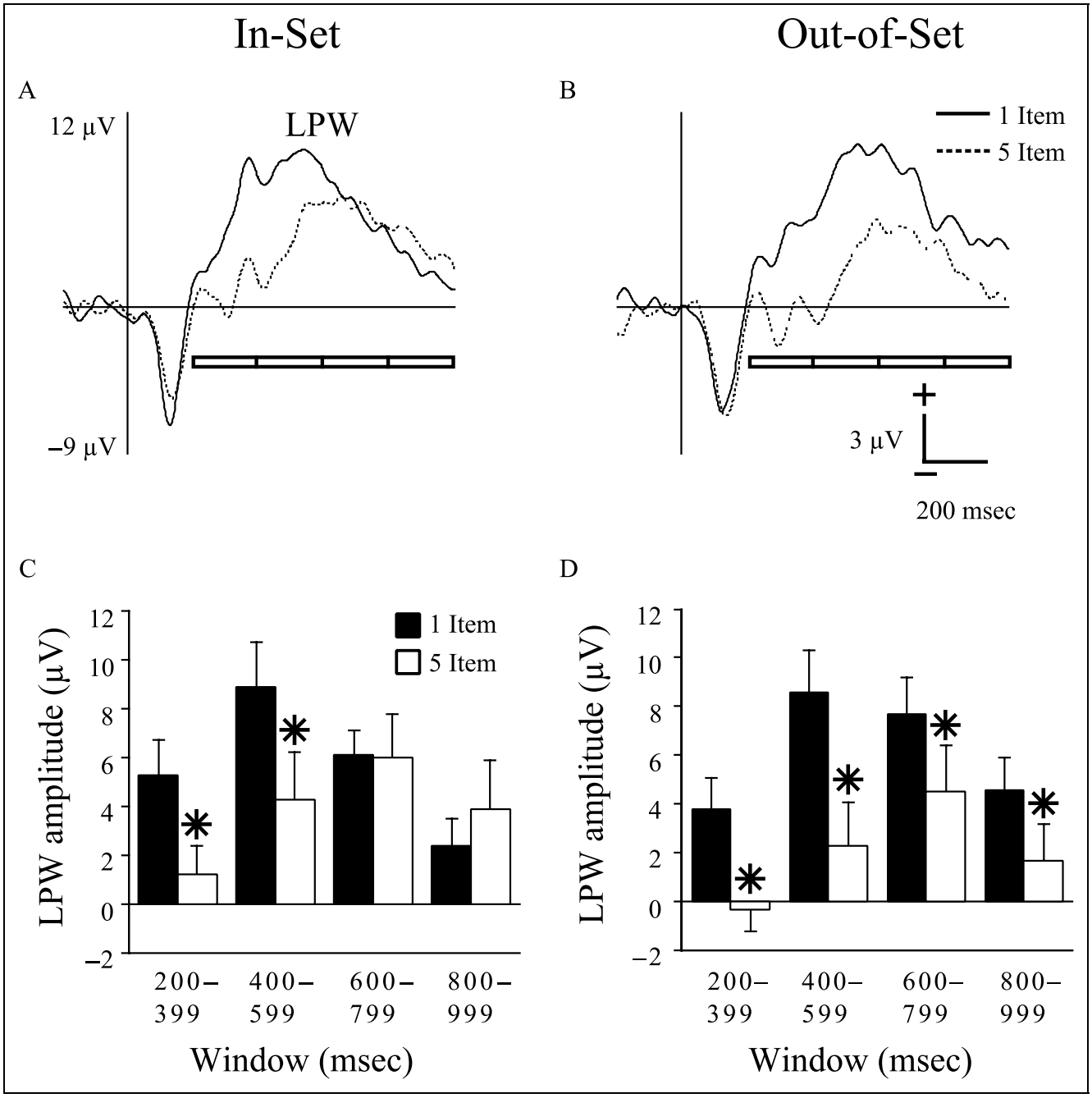

Figure 7. Grand average potentials (DC—16 Hz) to probes in 1- and 5-item memory sets. Potentials for in-set (A) and out-of-set (B) probes (DC—16 Hz) show amplitude differences between 1- and 5-item memory sets, with larger LPW amplitudes in the 1-item memory set. LPW amplitudes for 1- and 5-item memory sets are shown for in-set (C) and out-of-set (D) probes. Error bars show standard error.

LPW. Because the above analysis showed that for most windows the LPW was not significantly different from 0 μV, serial position analysis of the LPW was not conducted.

DISCUSSION

In the present study N100 and LPW amplitudes during retrieval from working memory were assessed as a function of memory load and serial position. The main results were as follows: (1) N100 and LPW amplitudes were significantly larger for 1-item memory loads relative to 5-item memory loads, (2) in the 5-item set N100 amplitudes were larger for the 1st serial position (primacy effect) relative to the remaining positions, and (3) in the 5-item set the LPW exhibited linear amplitude increases from the 1st (smallest amplitude) to 5th (largest amplitude) serial position. These changes were

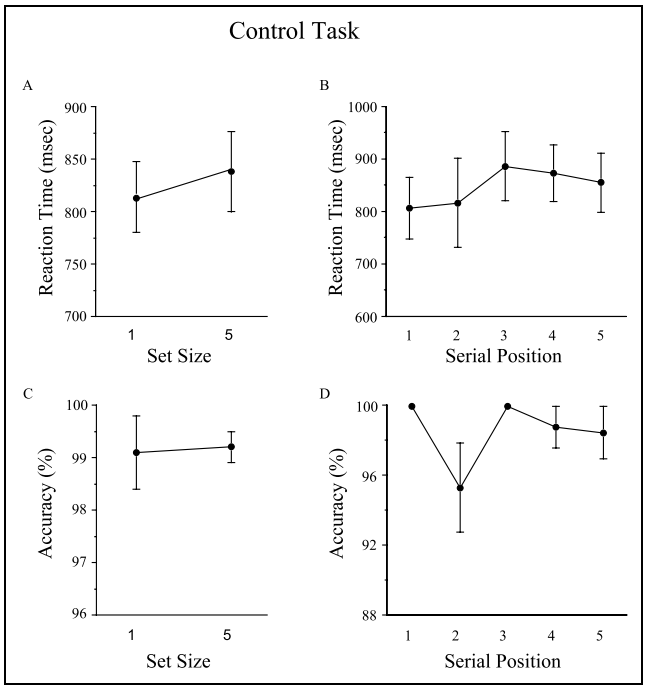

Figure 8. Behavioral results from Experiment 2 (control task). Reaction time as a function of set size (A) and serial position (B). Unlike Experiment 1, reaction time was not significantly different as a function of set size or serial position. Accuracy as a function of set size (C) and serial position (D). Error bars indicate standard error.

not observed in a control task that did not require subjects to memorize and recall the memory set items.

Auditory Cortex Activity during Memory Retrieval

Recent imaging studies in humans support the proposal that certain areas of sensory cortex activated during encoding are reactivated during memory retrieval (Nyberg, Habib, McIntosh, & Tulving, 2000; Persson & Nyberg, 2000; Wheeler, Petersen, & Buckner, 2000). Animal studies also show that auditory cortical neurons can differentially respond during the encoding, maintenance, and retrieval phases of working memory (Sakurai, 1994; Gottlieb, Vaadia, & Abeles, 1989), and that auditory association cortex is necessary for retention of auditory information in working memory (Colombo, D'Amato, Rodman, & Gross, 1990). Taken together, these results suggest that auditory cortical areas participate in a network that supports working memory for auditory information. The finding that N100 amplitude to probes covaries with memory load is consistent with the notion that sensory areas contribute to retrieval because the neural generators of the N100 have been localized to the primary/secondary auditory cortex (Zouridakis, Simos, & Papanicolaou, 1998; Pantev et al., 1995; Liegeois-Chauvel, Musolino, Badier, Marquis, & Chauvel, 1994). In addition, decreases in N100 amplitude following increases in memory load have also been reported during encoding (Golob & Starr, 2000; Conley et al., 1999), which also suggests similar patterns of auditory cortical activation during encoding and retrieval as a function of memory load.

N100 amplitudes during encoding showed no significant effect as a function of serial position (Golob & Starr, 2000), a result that was replicated in the present study (data not shown). Thus, differences in N100 amplitude during retrieval, as a function of serial position, do not reflect the initial N100 response during encoding. Instead, N100 serial position effects during retrieval may reflect additional processes involved in maintenance, retrieval, or both but not encoding. Accordingly, primacy effects may be due, in part, to processes taking place after encoding. Significant differences in N200 and P300 amplitude and latency for set size but not serial position also suggest somewhat different mechanisms for memory load versus serial position effects.

Although a significant primacy effect was seen for N100 amplitude, primacy effects were not observed for reaction time. There are several considerations relevant to the interpretation of this difference. First, the N100 peaks relatively early during the retrieval process (~130 msec), with ~500 or ~700 msec elapsing between the N100 peak and mean reaction time (for 1- and 5-items sets, respectively). Thus, many intervening processes can occur after the N100, but before the behavioral response, that could also influence behavior and, correspondingly, reduce the association between N100 amplitude and reaction time. Second, reaction time and N100 amplitude were not directly compared; instead, statistical significance was determined by separate comparisons for reaction time and N100 amplitude. Additional study, such as single-trial analysis, would be required to directly evaluate the association between serial position, N100 amplitude, and reaction time. Taken together, these considerations suggest that N100 amplitude differences for probes memorized in the primacy position reflects activity from one neural source that may be associated with primacy, but additional study is needed to directly support this possibility.

The absence of serial position differences to probes in the control task indicates that larger N100 amplitudes for the 1st serial position in the memory task are not due to sensory refractory effects (Näätänen & Picton, 1987). Serial position differences do not appear to be related to the time since memorization because probe N100 amplitudes for the 1-item set were greater than the last (5th) serial position in the 5-item set, even though the retention interval was equivalent. Moreover, N100 amplitudes for the 1st serial position in the 5-item set were almost identical to N100 amplitudes in the 1-item set, even though the time between item memorization and probe presentation was greater for the 1st serial position in the 5-item set. Equal N100 amplitudes for the 1-item set and the 1st serial position in the 5-item set also suggests that differences between the 1st and later serial positions are not due to intervening stimuli after memorization.

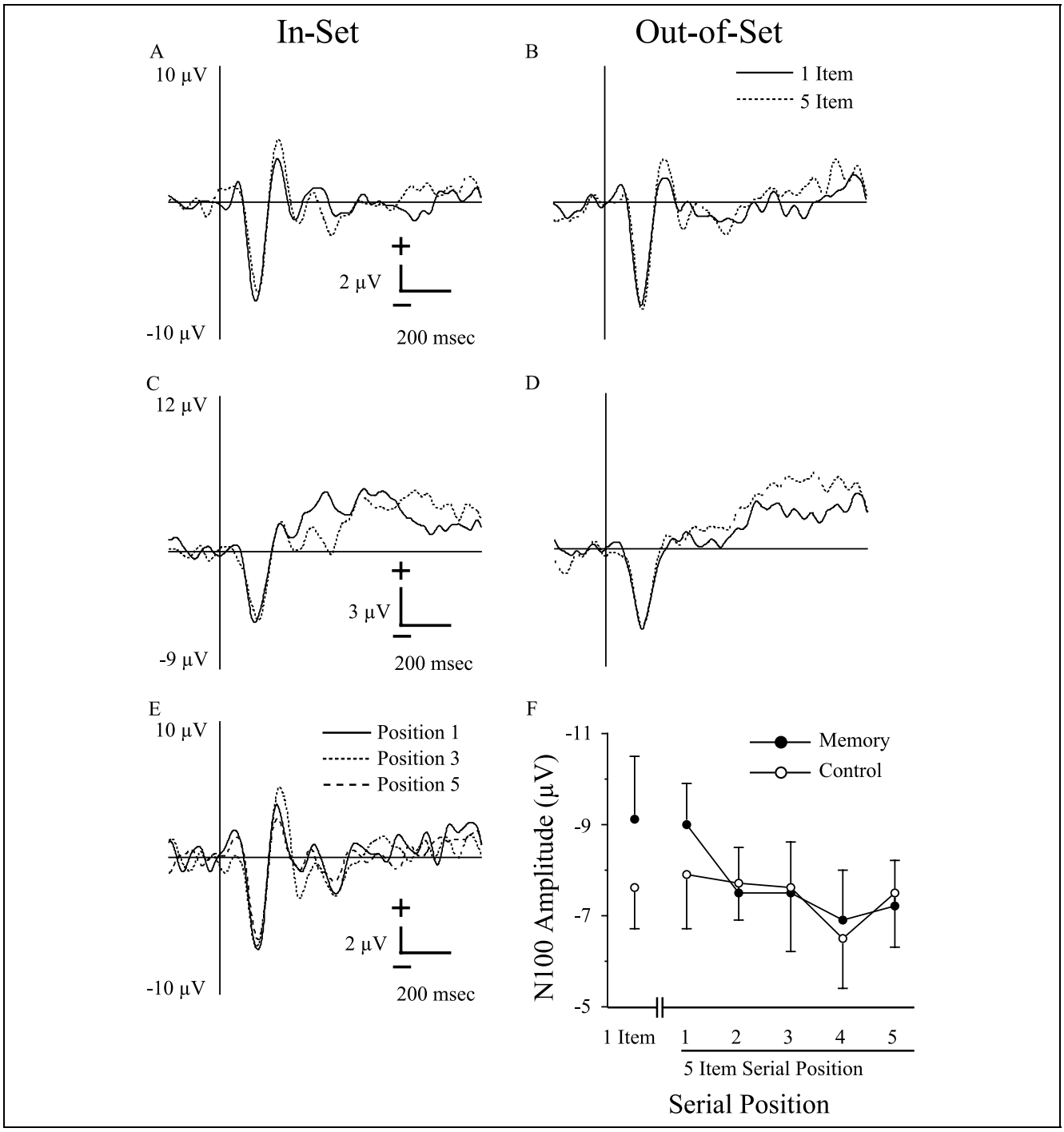

Figure 9. Potentials to probes in Experiment 2 (control task). Bandpass filtered potentials (1–16 Hz) to in-set (A) and out-of-set (B) probes. In-set and out-of-set status of probes was not relevant to the even/odd number classification task, but in-set and out-of-set averages were compiled for comparison with Experiment 1. Low-pass filtered potentials (DC–16 Hz) for in-set (C) and out-of-set (D) probes, illustrating the absence of a notable LPW (compare with Figure 7A and B). N100 tracings (E) and amplitude plots (F) as a function of serial position in Experiment 2. There were no significant effects of serial position on N100 amplitude or latency. Panel F shows N100 amplitudes in Experiment 1 (memory task) and Experiment 2 (control task). Note that N100 amplitudes were larger in the memory task versus control task in the 1-item set size and the 1st serial position of the 5-item set. Error bars indicate standard error.

Differences in N100 amplitude across serial positions may contribute to the overall differences between 1- and 5-item set sizes. Although overall reductions in N100 amplitude are also observed with increasing memory load for out-of-set probes, N100 amplitude differences for out-of-set probes may also be present as a function of negative recency (i.e., the number of trials since an out-of-set probe was present in a memory set).

Previous studies examining serial position effects during retrieval from working memory (Chao & Knight, 1996,

1997) reported no significant changes in auditory N100 amplitude across serial positions. There are several possibilities for the difference between these results and the current study. First, based on reaction time and accuracy measures, the task appeared to be more difficult than the task in the present experiment, a result possibly due to the use of nonverbal stimuli (environmental sounds), which are often difficult to encode verbally (Chao & Knight, 1996). A prominent negative frontal slow wave was also observed in the Chao & Knight (1996) studies, but not in the present study, which may have influenced N100 amplitude measures. The proportion of in-set versus out-of-set probes also differed between studies (80/20 in-set vs. out-of-set in Chao and Knight, 50/50 present study), with the 80/20 proportion potentially inducing a response bias toward in-set responses. Further study would be required to assess the contribution of these factors to differences between studies.

Late Positive Wave during Memory Retrieval

The finding that LPW amplitude decreased with greater memory load is consistent with previous studies (e.g., Kramer et al., 1991; Pratt et al., 1989). Peak latency of the LPW appeared to increase in the 5-item set versus the 1-item set; however, the entire LPW waveform did not appear to shift to the right for the 5-item set relative to the 1-item set (see Figure 7). Instead, analysis using the window measures showed that LPW amplitudes were reduced in the 5-item set, especially between ~200 and 600 msec poststimulus, which led to an apparent increase in LPW latency. This suggests that LPW latency differences between memory loads are reflected by changes in neural activity, synchronization, or both among the neurons that generate the LPW, especially between ~200 and 800 msec after probe presentation. Latency differences would be apparent because amplitude reductions ''cut out'' the peak seen in the 1-item set, leaving an apparent peak in the 5-item set having a longer latency. A similar argument has been proposed based on individual differences in LPW morphology (Pelosi et al., 1995).

Studies of verbal working memory using PET or fMRI show that posterior parietal lobe activation increases as a function of memory load (reviewed in D'Esposito, 2001; Cabeza & Nyberg, 2000). Because changes in LPW amplitude with memory load were restricted to the Pz site, the LPW results are compatible with the idea that posterior parietal activity contributed to the LPW component. Starr and Barrett (1987) provided further evidence of parietal involvement in the LPW by reporting that subjects with impaired working memory due to left parietal lesions had attenuated LPW amplitudes.

Three other studies have examined LPW/P300 amplitude as a function of serial position in similar working memory tasks (Chao & Knight, 1996, 1997; Patterson et al., 1991). These studies showed a significant recency effect for an LPW between ~350 and 750 msec after probe presentation, but did not report linear amplitude changes as a function of serial position. As discussed above, there were procedural differences between experiments that may relate to the somewhat different pattern of LPW amplitudes as a function of serial position.

Relation of N100 and LPW to Psychological Models of Working Memory Retrieval

In direct access analytic models the strength of memory traces of memorized items is proportional to performance accuracy and reaction time (Ratcliff, 1978; Norman & Wickelgren, 1969; Wickelgren & Norman, 1966). Recency of item presentation, relative to the probe, is thought to be an important determinant of memory trace strength. Declines in trace strength can occur over time, following interference of later items, and can also be modified by rehearsal (Dosher & Sperling, 1998; Seamon & Wright, 1976). Mean reaction time findings often indicate a primacy effect (i.e., shorter reaction times) that is limited to the 1st serial position in addition to recency effects (Monsell, 1978; Juola & Atkinson, 1971), and researchers have suggested a parameter reflecting the influence of primacy and recency to jointly model trace strength at a given serial position (Murdock, 1985).

The present findings suggest four potential neurophysiological characteristics related to memory trace strength. First, the N100 amplitude changes as a function of serial position suggest that primacy effects are restricted to the first serial position. Second, the influence of recency appears be graded across all serial positions because monotonic reductions in LPW amplitude were observed from the 5th through 1st serial position. The different pattern of primacy and recency effects across serial positions is consistent with mathematical models that incorporate constants for primacy and recency effects, with a brief influence of primacy and a more sustained influence of recency (Murdock, 1985; Wickelgren & Norman, 1966). Third, the event-related potential results suggest different time courses for the primacy and recency effects. Primacy effects were evident ~100 msec after probe presentation, while recency effects began ~200 msec after probe presentation. Fourth, the N100 and LPW are thought to be generated by different neuroanatomical locations. The N100 is generated in the primary/secondary auditory cortex (Zouridakis et al., 1998; Pantev et al., 1995). Although the neural generators of the LPW are unknown, the results are more consistent with activity in posterior cortical areas, rather than in the auditory cortex.

In the context of parallel process models (e.g., Murdock, 1971) amplitudes of the N100 and the LPW may be associated with the rate of information processing leading to the decision of in-set or out-of-set membership. In parallel models, probes are compared with all serial positions simultaneously, but the processing rates of

the serial positions are assumed to vary (Townsend & Ashby, 1983). Decisions for in-set probes are achieved once information accumulates to a criterion level, with faster processing rates leading to faster in-set decisions. Progressive reductions in processing rate are assumed, from the last serial position (e.g., 5th) toward the 1st, often with somewhat faster rates for the 1st position to reflect primacy. Decision times for out-of-set probe membership are determined by the serial position having the slowest processing rate (Townsend & Ashby, 1983). As with trace strength models, the different time courses and probable anatomical generators of the N100 and LPW suggest different aspects of processing rate may be mediated by different brain areas at different times following probe delivery.

The amount of probe information that the N100 is capable of indexing is fundamentally limited by the acoustic development of the probe stimulus. In the present experiment, voicing of the probes lasted 500 msec, while the peak latency of the N100 was ~130 msec. Thus, changes in peak N100 amplitude as a function of set size or serial position occurred before pronunciation of the entire word was complete. In principle, information conveyed by the N100 component could be sufficient to classify a probe as either definitely in-set, definitely out-of-set, or uncertain. These possibilities depend on the amount of information contained by the first phoneme of the probe, which is presented before the peak of the N100 component, relative to a comparison set of digits. An out-of-set decision could be reached when the first phoneme does not match any of the first phonemes of memory set items. In-set decisions could also be made at the time of the N100 provided the initial phoneme of a probe is unique among the entire set of potential memory set items. Additional information beyond the first phoneme would be needed if the first phoneme matches both an in-set and an out-of-set digit (e.g., ''six'' vs. ''seven'').

In the present study in-set and out-of-set probe averages were constructed from probes without regard to similarities or differences in the initial phonemes of the probes. Only three of nine digits (''one,'' ''eight,'' and ''nine'') had unique phonemes at the beginning of the word. Thus, if probe event-related potentials were averaged according to the initial phonemes it is possible that differences in N100 amplitude would be observed for definite in-set, definite out-of-set, and uncertain (in-set or out-of-set) probes. A stronger association between reaction time and N100 amplitude may also be present for definite in-set versus uncertain probes.

Conclusions

The present results show that N100 and LPW amplitudes decrease with increased memory load. When examined across serial positions, N100 amplitude had a primacy effect, and LPW amplitude exhibited a recency effect. These results suggest that (1) the influence of primacy and recency contribute to overall differences in N100 and LPW amplitude, respectively, with changes in memory load; (2) when processing probe information neural correlates of primacy (N100) can be present before neural correlates of recency (LPW); (3) primacy and recency effects can be generated by different cortical regions (N100—auditory cortex, LPW—posterior neocortical regions); and (4) primacy and recency effects observed in event-related potentials are consistent with trace strength and parallel models of working memory retrieval.

METHODS

Subjects

Subjects were UC Irvine undergraduate students (mean age = 21.3 ± 2.1 years, range: 19–26), and received course credit for their participation. Subjects were excluded if they had a history of epilepsy, head trauma, or major psychiatric condition. All subjects were right-handed, reported no hearing deficits, and signed informed consent forms. Experiments were performed in accordance with a protocol approved by the UC Irvine Institutional Review Board.

Behavioral Task

Experiment 1

Twelve subjects performed a modified Sternberg working memory task (Sternberg, 1966). Stimuli were digitized from a male voice (~500 msec duration, ~50 dB nHL) and presented from two speakers in front of the subject. Subjects were seated in a comfortable chair and held a small keypad containing four response buttons.

Each trial contained a start cue, a list of sequentially presented digits (memory set), and a probe digit (Figure 1). The memory set contained either one or five digits. Subjects determined if the probe was or was not present in the memory set, and pressed one of two buttons to indicate their choice. Speed while maintaining high levels of accuracy was stressed. Each block contained 20 memory trials (intertrial interval = 3.0 sec), and all trials within the block had the same number of items in the memory set. Memory set and probe digits were randomly determined, and the probability of in-set and out-of-set probes for each block was .50/.50. In the 5-item memory set in-set probes were drawn equally from each serial position in the memory set (p = .20/position, two probes/serial position in each 20-trial block).

Subjects were given 2 (n = 9 subjects) or 3 (n = 3 subjects) blocks of the 1-item set size and 10 blocks of the 5-item set. Each 1-item block was given either before or after five 5-item blocks, and the order was counterbalanced across subjects. For the in-set probe serial position analysis, this yielded a maximum of 20 sweeps for the subaverage of each serial position (10 blocks, 2 sweeps/serial position), with most subjects having 16–20 sweeps.

Experiment 2

Ten subjects participated in Experiment 2, none of which were in Experiment 1. The same sequences of digits was presented as in Experiment 1 (memory set, probe), but subjects were instructed to only ''listen to the numbers'' in the memory set. The probe digit was then classified as either an even or an odd number by pressing one of two buttons to indicate their choice. Experiment 2 controlled for the physical sequence of stimuli, the presence of a binary decision, and preparation and execution of a button press response.

Electrophysiological Recordings

Subjects were seated inside a sound-attenuating, electrically shielded chamber. Eight Ag/AgCl recording electrodes (Fz, Cz, Pz, Oz, C3, C4, T3, T4) were placed on the scalp according to the 10/20 system (Jasper, 1958). Electrode impedances were < 5 kΩ, and reference electrodes were placed on the left and right mastoid in a linked configuration. Two electrodes were placed above and below the left eye to monitor eye movements, and a ground electrode was placed on the forehead. The EEG and EOG were continuously digitized at 500 Hz with a bandpass of DC 100 Hz. An eye blink correction algorithm was then used to correct for artifacts (Gratton, Coles, & Donchin, 1983), and individual sweeps were sorted and averaged according to stimulus type (in-set or out-of-set; serial position).

Data Analysis

Behavioral measures included RT, relative to the onset of probe stimuli, and accuracy. Accuracy was expressed as the percent of correct responses among all trials with a response. The number of trials without a button press was also noted.

The EEG was digitally filtered using FFT and inverse FFT procedures. There were two filter settings, depending on the component of interest. For the N100, P200, N200, and P300 components bandpass filters were set at 1–16 Hz (12 dB/octave) to attenuate slow shifts. For the LPW, filters were set at DC 16 Hz. Peak latencies were calculated relative to stimulus onset, and peak amplitudes were defined relative to a 100-msec prestimulus baseline period. Component peaks were defined as follows: N100 (maximum negativity 80–180 msec), P200 (maximum positivity 150–250 msec), N200 (maximum negativity 175–350 msec), and P300 (maximum positivity 250–400 msec). The LPW was measured by calculating the mean event-related potential amplitude in four nonoverlapping 200-msec windows (200–399, 400–599, 600–799, and 800–999 msec). A secondary analysis defined a single LPW peak to compare with previous reports.

For comparisons between grand average in-set and out-of-set probes between the 1- and 5-item sets two blocks were used for each average. Only the 5-item blocks that were immediately before or after a 1-item block were used to equate S/N ratios between the 1- and 5-item set sizes.

Statistical Analysis

Data were analyzed using *t* tests and repeated measures ANOVA with the Greenhouse–Geisser correction to control Type I error when appropriate. Adjusted *p* values were reported, with $p < .05$ considered significant. Analysis included the factors of set size (1-, 5-item memory sets), probe type (in-set vs. out-of-set), electrode site, and window for the LPW. Except when noted, in-set and out-of-set probes were analyzed separately. Post hoc testing used Tukey tests, with significance set at $p < .05$.

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Note

1. For the midline sites a 2 (set size) × 4 (site) × 4 (window) ANOVA test showed a significant main effect of set size, $F(1,11) = 11.0$; $p < .01$, with larger amplitudes for 1- versus 5-item sets, and electrode site, $F(3,33) = 4.0$; $p < .04$. Site x window, $F(9,99) = 6.0$; $p < .01$, and Set Size × Site, $F(3,33) = 5.1$; $p < .03$, and Set Size × Site × Window interactions, $F(9,99) = 4.0$; $p < .03$, were also significant. Similar results were seen for lateral sites (T3, T4, C3, C4). Although LPW amplitudes were larger for right hemisphere sites in the grand average (Figure 3), this was due to three subjects with very large LPW amplitudes at C4/T4, and did not result in a significant difference between hemispheres ($p = .39$). Separate ANOVA tests for each midline site revealed significant main effects for set size at Cz, $F(1,11) = 14.1$; $p < .01$, Pz, $F(1,11) = 11.2$; $p < .01$, and Oz, $F(1,11) = 6.4$; $p < .03$, sites. There were also significant differences between windows at Pz, $F(3,33) = 8.9$; $p < .001$, and Oz, $F(3,33) = 7.3$; $p < .01$. At Pz there was also a significant Window × Set Size interaction, $F(3,33) = 6.2$; $p < .01$. There were no significant differences at the Fz site for set size, window, or the Set Size × Window interaction.

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