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Evidence for Attentional Gradient in the Serial Position Memory Curve from Event-related Potentials

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Abstract

The occurrence of primacy versus recency effects in free recall is suggested to reflect either two distinct memory systems, or the operation of a single system that is modulated by allocation of attention and less vulnerable to interference. Behavioral and event-related brain potential (ERPs) measures were used to investigate the encoding substrates of the serial position curve and subsequent recall in young adults. Participants were instructed to remember lists of words consisting of 12 common nouns each presented once every 1.5 sec, with a recall signal following the last word to indicate that all remembered items should be written on paper. This procedure was repeated for 20 different word lists. Both performance and late ERP amplitudes reflected classic recall serial position effects. Greater recall and larger late positive component amplitudes were obtained for the primacy and recency items, with less recall and smaller amplitudes for the middle words. The late positive component was larger for recalled compared to unrecalled primacy items, but it did not differ between memory performance outcomes for the recency items. The close relationship between the enhanced amplitude and primacy retrieval supports the view that this positive component reflects one of a process series related to attentional gradient and encoding of events for storage in memory. Recency effects appear to index operations determined by the anticipation of the last stimulus presentation, which occurred for both recalled and unrecalled memory items. Theoretical implications are discussed.

Introduction

Serial Position Memory

The U-shaped serial position curve is one of the most well-established recall memory findings (Murdock, 1962; Robinson & Brown, 1926; Ebbinghaus, 1913; Nipher, 1876). After a list of words is presented, recall performance is greater for items from the beginning (primacy effect) and end (recency effect) compared to items presented in the middle of a list (Capitani, Della Sala, Logie, & Spinnler, 1992; Atkinson & Shiffrin, 1968). The classic theoretical interpretation is that primacy memory effects occur for initial list items that are encoded and relatively well rehearsed, thereby promoting transfer from short-term storage to long-term memory. Subsequent retrieval is enhanced compared to items in the middle of the list, as these items are not rehearsed as strongly as the initial items. Recency effects occur because the just-presented list items are encoded in the short-term store and are immediately available for output when the end of the list signals that retrieval is required (Shiffrin & Atkinson, 1969; Glanzer & Cunitz, 1966). Experimental manipulations of stimulus presentation speed that affect only

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primacy items and postlist interference tasks that affect only recency items strongly support this view (Lewandowsky & Brown, 2005; Glanzer, 1966; Murdock, 1962). An alternative interpretation is that, because initial items have minimal interference from preceding items and final items have no interference from subsequent items, both primacy and recency effects reflect the operation of a single memory system (Wixted & Ebbesen, 1991; Crowder, 1982).

An influential model of serial position memory effects posits an attentional primacy gradient. During encoding the amount of attention devoted to each stimulus is reduced across successive serial positions, such that each successive stimulus receives less attention than the previous one (Brown, Preece, & Hulme, 2000; Page & Norris, 1998). Hence, items presented at the beginning receive more attention and produce a stronger neural trace. As a result, retrieval for stimuli presented first is better compared to stimuli in the subsequent positions. An alternative theoretical mechanism for producing both primacy and recency effects is interference (Nairne, 1988; Melton, 1963). An initial memory trace is sensitive to interference so that the stimulus memory traces for middle items are subject to more interference as additional subsequent items are presented. Thus, initial items have no interference from preceding items and final items have no interference from subsequent items so that retrieval performance is enhanced as primacy and recency positions are less affected by interference.

Memory and Event-related Potential Effects

Event-related potential (ERP) assessment of recall memory was initially conducted to determine whether P300 amplitude was associated with recall performance (Fabiani, Karis, & Donchin, 1986, 1990; Karis, Fabiani, & Donchin, 1984). Lists of words presented sequentially and ERPs were recorded. In some lists, one of the words was presented either in smaller or larger font size than the other words so that stimulus distinctiveness would affect encoding and facilitate recall memory. Distinct word stimuli that were subsequently recalled elicited larger P300 components during encoding than those that were not recalled. However, P300 amplitude was directly affected by the rehearsal strategy, such that component amplitude was larger for subsequent recall when participants used rote rehearsal (Fabiani et al., 1990). When participants employed an elaborative strategy for memorization, the variance in the P300 amplitude was not associated with subsequent recall. Taken together, these findings suggested that some aspect of the P300 amplitude reflects the strength of neural activity related to memory modification (Donchin, 1980).

Serial Position Memory and Event-related Potential Effects

Serial position effects assessed with ERP methods have typically employed memory scanning recognition rather than recall procedures. After memorizing a list of items, a probe stimulus is presented with the instruction to indicate whether that item was from the memory set. A robust finding is that probe stimuli from the last serial position produce shorter response times and larger P300-like components than those from the middle (Crites, Devine, Lozano, & Moreno, 1998; Patterson, Pratt, & Starr, 1991). The results are consistent with behavioral serial position findings that suggest retrieval is affected by how the stimulus items are encoded and accessed when recall is engaged (Craik & Lockhart, 1972). Neuroimaging studies also indicate that retrieval of previously studied events reactivates brain regions active during encoding of the same events (Nyberg, Habib, McIntosh, & Tulving, 2000). Taken together, behavioral and neuroimaging studies agree with ERP findings that serial position effects from recognition tasks appear to depend on the strength of memory formed during encoding and storage processes.

These proposed recognition mechanisms are likely to be operating when probe assays of serial position are used to elicit ERPs, with relatively large P300 amplitudes obtained for recency items rather than earlier probes (Chao & Knight, 1996; Patterson et al., 1991). Indeed, P300 amplitude increases linearly from probe stimuli of the initial to ending list items, suggesting that recognition primacy and recency effects reflect different processing mechanisms (Golob & Starr, 2004). To date, the majority of studies have assessed serial position in the auditory modality, with no evidence currently available that similar recognition serial position ERP effects occur for visual probes. Given that serial position effects could be modality dependent (Murdock & Walker, 1969; Murdock, 1968), how visual stimulus ERPs may vary across serial position is unclear.

ERPs and serial position at the time of encoding have been studied, with participants instructed to use elaborative learning strategy to chunk the words in groups comprised of three or five items (Rushby, Barry, & Johnstone, 2002). ERP comparisons were made between recalled and unrecalled words for each segment of the serial position curve corresponding to primacy, middle, and recency areas. The major finding was that early ERPs were modulated according to serial position and subsequent recall: Primacy recall was associated with increased P1 and P2 amplitudes, whereas recall at the middle positions only demonstrated increased P1 amplitude. Although behavioral recall performance varied in the typical way for both primacy and recency positions, ERPs were modulated only by primacy effects and did not reflect recency effects. Indeed, no consistent P300 amplitude effects were obtained for free recall across serial positions. It is important to note that participants were specifically instructed to utilize different elaborative strategies across two sessions. In one session, they formed sentences from three words, and in the other they formed sentences from five words. However, the results were analyzed and reported on the basis of the summation of these two strategies. These ERP serial position findings, therefore, do not directly address the primacy versus recency memory issue.

Present Study

The present study extends previous ERP serial position tasks by obtaining behavioral and ERP measures in the classic word list recall task and averaging separately over correctly recalled and unrecalled items for each portion of the list. It is hypothesized that the electrophysiological correlates of serial position should exhibit selective modulations for items presented in the primacy and recency positions compared with the items presented in the middle of a memory set. Theories based on behavioral findings suggest that primacy effects result from more attention allocation to items presented in the beginning of a list compared to the subsequent items (Farrell & Lewandowsky, 2002; Page & Norris, 1998). One approach to investigate the link between allocation of attention and primacy effect is to characterize how the P3 component varies across memory for serial position items. If primacy effects index greater allocation of attention, the P3 amplitude elicited by items initially presented should be larger compared to items presented in other positions. The present study was explicitly designed to assess encoding processes that determine successful retrieval in free recall. It is hypothesized that retrieval of more recently presented items indexes the maintenance of items in working memory to promote subsequent access in the absence of interference or delay (Green, 1986; Shiffrin & Atkinson, 1969). If recency operations are unrelated to encoding and reflect maintenance of items in short-term memory, then little difference should be obtained between ERPs from the recency and middle items.

Methods

Participants

A total of 30 (17 women, 13 men) university students served as subjects ($M = 20.8$, $SD = 2.7$ years) and received course credit or were paid for their participation. All subjects had normal or corrected-to-normal vision, reported being free of neurological and psychiatric disorders, and provided written informed consent.

Stimuli

Stimuli consisted of 240 words with high frequency (28.1 per million) selected from Kučera and Francis (1967). The stimuli varied in length between five and seven letters and were organized into 20 lists of 12 words each. The study word lists were randomly ordered and counterbalanced across subjects using five different orders. Each list was constructed to eliminate random occurrence of conceptually related words grouped in serial positions. All stimuli were presented on a monitor 100 cm in front of the participant. Each word was presented at the center of the screen in red lowercase letters (Arial 28 font) on a black background. A separate pool of 12 words was used for the practice test.

Procedure

Figure 1 illustrates the experimental paradigm. A single word was presented for a duration of 250 msec and an interstimulus interval of 1500 msec, with each of the 12 words in each list presented only one time. Before each list, three presentations of the characters XXXX occurred; after the last word of each list, the same character string was presented to signal stimulus recall. Participants were instructed to memorize the words for a recall test that would immediately follow. The subjects were not required to use any specific encoding strategies and were instructed to adapt methods that would produce maximal retrieval. Participants then were instructed to write the words just presented in any order on a sheet of paper. Recall time was 60 sec and the recall sheet was collected at the end of this time. After a brief rest, the next recall list was presented in the same fashion until all 20 lists had been viewed in about 2.5 hr. The number of lists presented was determined by extensive pilot work, with 20 word lists found to be the maximum before excessive fatigue occurred.

Recording Conditions

Electroencephalographic (EEG) activity was recorded from 19 electrodes that included Fz, Cz, Pz, F1/2, F3/4, F7/8, C3/4, T7/8, P3/4, P7/8, O1/2, referred to balanced linked earlobes, with a forehead ground and impedance at 10 kΩ or less. Additional electrodes were placed at the outer left canthus and below the left eye to measure electrooculographic (EOG) activity with a bipolar recording. The bandpass was 0.01–30 Hz (6 dB octave/slope), and the EEG was digitized at 4.0 msec per point for 1024 msec, with a 100-msec prestimulus baseline. Waveforms were averaged off-line, and trials on which the EEG or EOG exceeded ±100 μV were rejected. An EOG correction procedure was employed to remove any remaining artifact (Semlitsch, Anderer, Schuster, & Presslich, 1986).

Results

Data Analysis

The behavioral and ERP data were analyzed statistically in the same general fashion. Each dependent variable was obtained for each of the 1 to 12 serial positions. ERP waveforms from each serial position for each subject were averaged over the single trials from words that were correctly recalled and those that were unrecalled (i.e., not correctly recalled). The mean behavioral values and ERPs from serial positions 1–3, 4–6, 7–9, and 10–12 for the recalled and unrecalled words from each list for each subject were then used for subsequent analyses and will be termed serial position blocks 1, 2, 3, and 4, respectively. This approach was adopted to facilitate their presentation and statistical evaluation after preliminary analyses of list positions 1 to 12 did not differ substantially from the grouping of averages into four blocks.

To assess possible differential signal-to-noise contributions to the ERP averages after artifact rejection, the number of trials for each ERP average from each subject within the four serial position blocks for each memory outcome was determined. The mean number of trials in each serial position block for the recalled items was 27.8, 18.6, 17.6, 20.8, and for the unrecalled items was 11.9, 18.6, 16.2, 12.7, respectively. A two-factor (2 recall outcomes × 4 serial position blocks) analysis of variance (ANOVA) found more trials obtained for the recalled than unrecalled words, reliable differences among the serial positions, and a significant interaction ($p < .05$, in all cases). However, the correlation coefficients (r) between behavioral memory performance and the number of ERP trials across subjects for serial blocks 1 to 4 for the items recalled were 0.73, 0.75, 0.71, 0.52 and for the items unrecalled were 0.84, 0.76, 0.65, 0.64, respectively. Thus, the relationship between memory performance and the number of trials was consistent across serial position trial blocks regardless of recall outcome.

Statistical analyses were used to characterize serial position effects in several ways: First, a repeated measures ANOVA was performed, with Greenhouse–Geisser corrections applied to the *df* for factors with more than two levels and the corrected probability reported. A one-way ANOVA (4 serial position blocks) was applied to the proportion of recalled items, as the proportion of unrecalled stimuli was the complement of the recalled items. For the ERP data, a three-factor (2 memory outcomes × 4 serial position blocks × 3 midline electrodes) ANOVA was applied. Second, the memory outcomes were assessed separately with two-factor (4 serial positions × 3 midline electrodes) ANOVAs. These subanalyses were adopted to isolate recall memory effects directly. Third, primacy (serial positions 1 vs. 2) and recency (serial positions 3 vs. 4) effects were evaluated using Scheffé's planned comparison procedure using the associated Memory type × Serial position interaction error term. Fourth, Newman–Keuls post hoc mean comparisons also were used to assess memory outcome and serial position effects again using the interaction error term. Finally, hemispheric differences were assayed by excluding data from the midline, frontal (Fp1, Fp2), and occipital (O1, O2) electrodes. However, as suggested by the amplitude topographies (Figures 5 and 7), no hemispheric differences or interactions were obtained among memory outcome, serial position, and hemisphere. This issue will not be considered further.

Behavioral Performance

Figure 2 illustrates the mean percentage of recalled items for each serial position block. A one-factor (4 serial position blocks) ANOVA indicated that the proportion of words correctly recalled differed among the blocks [$F(3, 87) = 18.9$, $p < .001$]. Planned comparisons for the primacy effect found greater recall for serial position 1 compared to serial position 2 [$F(1, 29) = 70.6$, $p < .00001$]. Similarly, a strong recency effect was obtained, with serial position 3 recall proportion much smaller than serial position 4 [$F(1, 29) = 31.5$, $p < .00001$]. Post hoc assessment found that the proportion of recalled words in serial position block 1 differed from blocks 2 and 3 ($p < .001$ in each case), and that serial position block 4 differed from blocks 2 and 3 ($p < .001$, each case). Proportion recalled also differed between serial position blocks 1 and 4 ($p < .05$); blocks 2 and 3 did not differ from each other ($p > .75$). Thus, the behavioral recall data demonstrated a serial position curve.

Event-related Potential Serial Position Recall Effects

Figure 3 illustrates the grand averages for the recalled and unrecalled words for each serial position block from the midline electrodes. Waveform measures were defined as the negative and positive area voltage within early 250–500 msec and late 500–750 msec latency windows, respectively, obtained from each electrode. This approach was based on visual assessment of the data and previous ERP memory studies that found early and late waveform effects (Curran & Friedman, 2004;Doyle & Rugg, 1992;Paller, Kutas, & Mayes, 1987).

Early (250–500 msec) Window—

Figure 4 illustrates the early window mean negative area voltage for the recalled and unrecalled words from the midline electrodes as a function of serial position block from the midline electrodes. Figure 5 illustrates the topographic distribution of the area voltage within the window. Recalled items produced more negativity than unrecalled items overall [$F(1, 29) = 4.4$, $p < .05$]. The serial position factor yielded an overall main effect [$F(3, 87) = 4.0$, $p < .02$]. Negative amplitude area increased in magnitude from the frontal to parietal (i.e., the waveform became less negative) electrode locations [$F(2, 58) = 26.2$, $p < .01$]. No reliable interactions were obtained.

Assessment of the individual electrodes found marginally more negativity for recall relative to unrecalled words for each of the midline electrodes ($p < .10$ in all cases). Reliable serial position effects were obtained for the Fz [$F(3, 87) = 4.91$, $p < .01$] and Cz [$F(3, 87) = 3.09$, $p < .05$] electrodes. Planned comparisons yielded a significant primacy effect at Fz, as correctly recalled items in serial position block 1 produced less negative area than serial position block 2 [$F(1, 29) = 5.2$, $p < .05$]. Unrecalled items yielded no primacy ($F < 1$, $p > .85$) or recency ($F = 1.8$, $p > .15$) serial position effects. Planned comparisons found a reliable primacy effect at Cz for correctly recalled items, as serial position block 1 produced less negative area than serial position block 2 [$F(1, 29) = 6.04$, $p < .05$]. Unrecalled items yielded no primacy ($F < 1$, $p > .75$), with a marginal recency serial position effect obtained [$F(1, 29) = 3.3$, $p < .10$]. Post hoc assessment found that the recalled serial position block 2 was significantly different from the unrecalled serial position block 4 for data from Fz ($p < .01$) and less strongly for Cz ($p < .05$). Thus, the early negativity demonstrated overall recall effects, with reliable primacy effects obtained from the frontal and central electrodes.

Late (500–750 msec) Window—Figure 6 illustrates the early window mean positive area voltage for the recalled and unrecalled words as a function of serial position block from the midline electrodes. Figure 7 illustrates the topographic distribution of the area voltage measure within the window. The same ANOVA structure used for the early window was applied to the later 500–750 msec positive amplitude data. Recalled items produced larger positive areas than unrecalled items [$F(1, 29) = 15.3$, $p < .001$]. The overall serial position block factor was not significant [$F(3, 87) = 1.8$, $p > .15$]. Positive area increased in magnitude from the frontal to parietal (i.e., the waveform became larger from the frontal to parietal) electrode locations [$F(2, 58) = 24.3$, $p < .00001$]. More important, serial position interacted with electrode, such that data from the frontal and central electrodes did not demonstrate strong serial position effects, whereas the parietal electrode produced clear serial position effects [$F(6, 174) = 3.8$, $p < .02$].

Assessment of the individual electrodes revealed that recalled items had larger positive areas than unrecalled items for the Fz [$F(1, 29) = 10.3$, $p < .01$], Cz [$F(1, 29) = 14.3$, $p < .001$], and Pz [$F(1, 29) = 11.2$, $p < .005$] electrodes. Moreover, the positive area voltage data from the Pz electrode demonstrated a significant overall effect of serial position block [$F(3, 87) = 4.00$, $p < .02$]. Planned comparisons on the Pz data revealed a primacy effect, as recalled items in serial position block 1 had more positive voltage area than serial position block 2 [$F(1, 29) = 4.41$, $p < .05$]. Unrecalled items yielded no primacy serial position effects ($F = 1$, $p > .30$). Recalled items produced no reliable recency area differences between serial positions 3 and 4 ($F = 2.7$, $p > .10$). However, unrecalled items evinced a reliable recency difference between positions 3 and 4 [$F(1, 29) = 5.53$, $p < .05$]. Thus, primacy and recency effects differed for the positive area measures from recalled and unrecalled memory items.

Discussion

The present study employed ERPs to examine serial position memory effects. Recall performance produced a serial position curve, with a greater percentage of words found for the primacy and recency items than for middle serial positions. The main ERP results were: (1) Early negative amplitude areas (250–500 msec) demonstrated a relatively weak recalled versus unrecalled difference, and memory outcome did not interact with serial position block. (2) Larger late positive amplitude areas (500–750 msec) were obtained for the correctly recalled compared to the unrecalled items. (3) Larger areas over the parietal sites for this measure were found in the primacy serial positions for recalled compared to unrecalled items, whereas recency area measures did not differ between memory outcomes.

The findings indicate that negative–positive modulations at the primacy position reflect the encoding strength and whether a word will be recalled correctly. Although the P3 component may not be a direct index of storage processes, memory for items that elicit a P3 is better than items that do not elicit a P3, even under task conditions that require immediate or delayed retrieval (Golob & Starr, 2004; Paller, McCarthy, & Wood, 1988). The close relationship of P3 amplitude and delayed retrieval also supports the view that the component is one of the series of processes that reflect the encoding of events for storage in memory. With respect to recency effects, no distinction between recalled and unrecalled items was observed, as these behavioral outcomes were both associated with a robust P3. Furthermore, recall performance for the primacy items was greater than recall at the recency position. Taken together, these P3 results support a distinction between primacy and recency memory operations during encoding.

Recall Event-related Potential Primacy Effects

Previous studies have demonstrated a strong relationship between encoding processes and subsequent retrieval (Guo, Duan, Li, & Paller, 2006; Awh, Vogel, & Oh, 2006; Friedman & Trott, 2000; Craik & Lockhart, 1972). The primacy effect from serial position recall reflects this association, as recall for items in the beginning of the list is greater even though early items are vulnerable to decay and interference from later items (Murdock, 1968). The primacy gradient model postulates that items presented in the beginning of a list receive more attention during the encoding stages of processing than later items (Farrell & Lewandowsky, 2002; Page & Norris, 1998). In a homogenous sequence, each new item is less surprising and the strength of attention declines across successive trials (Brown et al., 2000; Lewandowsky & Murdock, 1989). The link between attention and depth of encoding therefore produces stronger retrieval performance for items presented in the initial compared to subsequent serial positions. The mediating effect of attention on enhanced recognition is further supported when subjects study the items with full attention compared to those with divided attention (Yonelinas, 2001). These findings also are consonant with results that suggest words studied with full attention are recognized with more confidence and associated with greater P300 amplitude (Curran, 2004).

Primacy position encoding effects were associated with larger late positive amplitudes relative to items in the middle serial positions, with the ERP waveforms for correctly recalled primacy items larger than unrecalled items. Hence, the strength of encoding underlies successful storage of information into memory and can index subsequent retrieval. In the primacy position, the cognitive and neural processes associated with these functions were dissociated predominately in the positive-going deflection of ERP waveforms. P300 amplitude is affected by attentional resources with relatively easy tasks yielding larger components than difficult tasks (Polich, 2003; Wickens, Kramer, Vanasse, & Donchin, 1983). During retrieval of the initial list items that were relatively easy to encode and store compared to other items, enhanced positive amplitude for primacy items was obtained, which is perhaps related to P300 activity. The late positive amplitude may index memory trace strength formed during encoding. Indeed, increases in memory load reduce P300 amplitude in a manner that suggests fewer attentional resources are engaged because of increased task demands to process these items (Kok, 2001; Wijers, Mulder, Okita, & Mulder, 1989; Gomer, Spicuzza, & O'Donnell, 1976). Retrieval did not produce amplitude variation of the early ERP components, which is inconsistent with findings that primacy recall is associated with increased P1 and P2 amplitudes (Rushby et al., 2002).

Recall Event-related Potential Recency Effects

The superior retrieval for items at the recency position appears to reflect maintenance and direct output of these items from short-term memory (Green, 1986). When participants are instructed to perform a distraction task or delayed free recall, the recency effect is strongly attenuated (Glanzer & Cunitz, 1966). In contrast, recency (but not primacy) is relativity unaffected by increasing list length or presentation rate (Postman & Phillips, 1965; Murdock, 1962). Behavioral and computational studies have delineated storage and retrieval processes of recency memory, although the neural activity elicited for recency items is unclear (Botvinick & Plaut, 2006; Crowder, 1993; Lewandowsky & Murdock, 1989).

Consistent with the behavioral results, larger late positive amplitude was found for the recency for both recalled and unrecalled items. This outcome stands in contrast to the primacy gradient hypothesis, which predicts that recency position items receive less attention and more interference than items in preceding positions. As list presentation progresses, rehearsal of previous items and memory overload disturbs encoding of additional items. Encoding of items in the recency position should therefore yield a decrease in late positivity area. Given the observed larger ERP amplitude at the recency serial positions, participants likely knew when the memory set would end, so that recency items were associated with a temporal cue for recall. This hypothesis was explored only in subset of participants ($n = 11$) that were asked to guess the number of words in each list. Estimates ranged from 8 to 14 words per list, with two subjects reporting the exact number (12). The majority of these participants reported that they sensed the presentation of the last item or felt that the list was about to end. The enhanced positive amplitude may therefore reflect neural activity associated with anticipation of the last stimulus presentation, which would have occurred for both recalled and unrecalled memory items. This interpretation is consonant with ERP studies that find a similar enhanced positivity for cue stimuli that index cognitive shifts induced by such tasks as the Wisconsin Card Sorting Test (Watson, Azizian, & Squires, 2006; Barceló, Periáñez, & Knight, 2003).

As noted, the primacy ERP outcomes for recalled and unrecalled items were distinguishable, as the primacy effects differed but the recency effects were similar across both recalled and unrecalled items. The discrepancy may indicate that the enhanced positivity for primacy items reflects serial position encoding *and* memory storage, whereas recency items were limited to just encoding. This outcome is likely because the difference between recall memory for items in primacy and recency positions could stem from interference and memory overload (Oberauer, 2003; Cowan, Saults, Elliott, & Moreno, 2002). Hence, there may be greater flexibility during encoding of primacy items, whereas recency items are encoded less independently of previous storage operations. In the beginning of the list, there are few items competing for attention, and this process strengthens encoding and memory for the primacy items. However, rehearsal and interference from earlier items prevent in-depth encoding of items in the recency positions. In addition, items in the beginning of the list are unaffected by restrictions of memory capacity, whereas items in the recency positions would suffer from memory overload. These processes, therefore, could affect recency items, such that anticipation of the list ending would underlie the obtained ERP serial position effect.

Early Versus Late Effect

ERP correlates of memory have been demonstrated to consist of early and late components distinguished by their topography and temporal characteristics (Rushby et al., 2002; Paller et al., 1988). The early effect is a negative deflection commonly elicited by complex and meaningful stimuli (Halgren & Smith, 1987; Kutas & Hillyard, 1980), which begins about 300–400 msec post-stimulus onset and is maximal in the frontal electrode sites (Curran & Cleary, 2003; Curran, 1999). This component has been associated with learning, and declines with stimulus repetition as items become familiar (Smith & Halgren, 1987). Consistent with previous findings, the present study found relatively small negative deflections over frontal sites that were followed by larger positive voltage increases over parietal sites (Smith & Guster, 1993; Smith, Stapleton, & Halgren, 1986). The negative-going deflection was slightly larger for unrecalled compared to recalled items and did not differ between the recalled versus unrecalled items in other serial positions. These observations may indicate that encoding items at the primacy position is a two-part process that occurs during early and late intervals (Halgren & Smith, 1987). The early negativity may index the initial stage of encoding and the late positivity may reflect the strength of memory trace formed at that time. The functional relationship between the negative and late positive component is uncertain, but the pattern of ERP modulation appears to index distinct neural processes associated with encoding and memory formation.

Recency Versus Primacy Retrieval

In contrast to several earlier studies, the present study found that recall performance was superior for primacy rather than for the recency portion of the curve (Glanzer, 1971; Glanzer & Cunitz, 1966). The traditional interpretation for recency advantage is that these items are highly accessible and insensitive to decay. Recency effects can be impaired when participants are forced to perform a distracting task after the last item before the signal to begin recall (Glanzer & Cunitz, 1966). It is unlikely that the XXXX signal stimulus that occurred at the end of each memory set produced interference with recency retrieval. Indeed, the end-signal stimulus purposefully was included after extensive pilot testing by comparing conditions with and without an end-signal stimulus, with the strong observation that the absence of an end-signal stimulus to begin recall impaired retrieval for the very last item. In addition, and although findings differ, several studies suggest that the capacity of storage for primacy portion of the curve is greater than recency (Martin & Jones, 1970; Tulving & Colatla, 1970). Further, preliminary analyses of the separate 1–12 serial positions individually demonstrated a primacy relative to recency advantage. Thus, the present paradigm is consistent with previous findings and the dictates of the paradigm employed.

The relatively small discrepancy between the shape of the classic serial position curve and the present finding also may be related to the presentation and retrieval modality. The participants were presented with a visual word that was presumably encoded in a verbal form and behaviorally recorded in a written form. In the majority of classic serial position studies, participants were presented with auditory stimuli and received instructions to retrieve the items orally (Murdock, 1962, 1968). It therefore seems likely that different systems are employed for retrieving auditory compared to written retrieval, and that these differences can produce serial position curves so that retention of items in the primacy exceeded those in the recency position.

Functional Neuroimaging and Serial Position

Previous research implies a dual-storage model of primacy and recency, although link between these processes and its neural substrates is still speculative. The advent of functional magnetic resonance imaging (fMRI) has identified some of the brain mechanisms mediating the serial position curve (Karlsgodt, Shirinyan, van Erp, Cohen, & Cannon, 2005; Zhang et al., 2003). In general, the findings indicate a functional distinction for primacy and recency retrieval on the basis of anatomy and activation patterns. One fMRI study demonstrated that primacy probes generated activation in the left hippocampal regions, whereas recency probes increased activation in the inferior parietal lobe and premotor cortex (Talmi, Grady, Goshen-Gottstein, & Moscovitch, 2005). Additional fMRI evidence implicates the involvement of the hippocampus in long-term storage processes, such that hippocampal activation appears selective for primacy but not recency retrieval thereby enhancing long-term memory storage for primacy items (Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Schacter &

Wagner, 1999). This interpretation is consistent with the proposal that primacy items engage more rehearsal to increase long-term memory processing (Strange, Otten, Josephs, Rugg, & Dolan, 2002; Rundus, 1971). In contrast, recent memory items are stored on a temporary basis and activate areas that only contribute to short-term storage (Ranganath & D'Esposito, 2005; Konishi et al., 2002).

Conclusion

ERPs and neuroimaging experiments have suggested that distinct network regions are associated with serial position memory effects. These approaches are beginning to elucidate the neurobiological mechanisms, whereby the human brain encodes and retrieves information. The present findings support this perspective and help to characterize the neuroelectric activation stemming from encoding and memory processes underlying the serial position curve.

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References

Atkinson, RC.; Shiffrin, RM. Human memory: A proposed system and its control processes. In: Spence, KW.; Spence, JT., editors. The psychology of learning and motivation: Advances in research and theory. Vol. 2. New York: Academic Press; 1968. p. 89-195.

Awh E, Vogel EK, Oh SH. Interactions between attention and working memory. Neuroscience 2006;139:201–208. [PubMed: 16324792]

Barceló, F.; Periáñez, JA.; Knight, RT. A new ERP paradigm for studying individual differences in the executive control of attention. In: Reinvang, I.; Greenlee, MW.; Hermann, M., editors. The cognitive neuroscience of individual differences. Oldenburg: bis-Publishers; 2003. p. 47-62.

Botvinick MM, Plaut DC. Short-term memory for serial order: A recurrent neural network model. Psychological Review 2006;113:201–233. [PubMed: 16637760]

Brown GDA, Preece T, Hulme C. Oscillator-based memory for serial order. Psychological Review 2000;107:127–181. [PubMed: 10687405]

Capitani E, Della Sala S, Logie RH, Spinnler H. Recency, primacy, and memory: Reappraising and standardizing the serial position curve. Cortex 1992;28:315–342. [PubMed: 1395637]

Chao LL, Knight RT. Prefrontal and posterior cortical activation during auditory working memory. Cognitive Brain Research 1996;4:27–37. [PubMed: 8813410]

Cowan N, Saults JS, Elliott EM, Moreno M. Deconfounding serial recall. Journal of Memory and Language 2002;46:153–177.

Craik FIM, Lockhart RS. Levels of processing: A framework for memory research. Journal of Verbal Learning and Verbal Behavior 1972;11:671–684.

Crites SL Jr, Devine JV, Lozano DI, Moreno S. Event-related potentials and serial position effects in a visual probe recognition task. Psychophysiology 1998;35:293–304. [PubMed: 9564749]

Crowder RG. The demise of short-term memory. Acta Psychologica 1982;50:291–323. [PubMed: 7124433]

Crowder RG. Short-term memory: Where do we stand? Memory & Cognition 1993;21:142–145.

Curran T. The electrophysiology of incidental and intentional retrieval: ERP old/new effects in lexical decision and recognition memory. Neuropsychologia 1999;37:771–785. [PubMed: 10408645]

Curran T. Effects of attention and confidence on the hypothesized ERP correlates of recollection and familiarity. Neuropsychologia 2004;42:1088–1106. [PubMed: 15093148]

Curran T, Cleary AM. Using ERPs to dissociate recollection from familiarity in picture recognition. Brain Research, Cognitive Brain Research 2003;15:191–205. [PubMed: 12429370]

Curran T, Friedman WJ. ERP old/new effects at different retention intervals in recency discrimination tasks. Brain Research, Cognitive Brain Research 2004;18:107–120. [PubMed: 14736570]

Donchin E. Surprise!…Surprise? Psychophysiology 1980;18:493–513. [PubMed: 7280146]

Doyle MC, Rugg MD. Event-related potentials and recognition memory for low- and high-frequency words. Journal of Cognitive Neuroscience 1992;4:69–79.

Ebbinghaus, H. Memory. Rueger, HA.; Bussenius, CE., translators. New York: Teachers College; 1913. Original work published 1885

Eldridge LL, Knowlton BJ, Furmanski CS, Bookheimer SY, Engel SA. Remembering episodes: A selective role for the hippocampus during retrieval. Nature Neuroscience 2000;3:1149–1152.

Fabiani M, Karis D, Donchin E. P300 and recall in an incidental memory paradigm. Psychophysiology 1986;23:298–308. [PubMed: 3749410]

Fabiani M, Karis D, Donchin E. Effects of mnemonic strategy manipulation in a Von Restorff paradigm. Electroencephalography and Clinical Neurophysiology 1990;75:22–35. [PubMed: 1688770]

Farrell S, Lewandowsky S. An endogenous distributed model of ordering in serial recall. Psychonomic Bulletin & Review 2002;9:59–79. [PubMed: 12026954]

Friedman D, Trott C. An event-related potential study of encoding in young and older adults. Neuropsychologia 2000;38:542–557. [PubMed: 10689032]

Glanzer M. Encoding in the perceptual (visual) serial position effect. Journal of Verbal Learning and Verbal Behavior 1966;5:92–97.

Glanzer M. Short-term storage and long-term storage in recall. Journal of Psychiatric Research 1971;8:423–438. [PubMed: 4939382]

Glanzer M, Cunitz AR. Two storage mechanisms in free recall. Journal of Verbal Learning and Verbal Behavior 1966;5:351–360.

Golob EJ, Starr A. Serial position effects in auditory event-related potentials during working memory retrieval. Journal of Cognitive Neuroscience 2004;16:40–52. [PubMed: 15006035]

Gomer FE, Spicuzza RJ, O'Donnell RD. Evoked potential correlates of visual item recognition during memory scanning tasks. Physiological Psychology 1976;4:61–65.

Green RL. Sources of recency effects in free recall. Psychological Bulletin 1986;99:221–228.

Guo C, Duan L, Li W, Paller KA. Distinguishing source memory and item memory: Brain potentials at encoding and retrieval. Brain Research 2006;1118:142–154. [PubMed: 16978588]

Halgren E, Smith ME. Cognitive evoked potentials as modulatory processes in human memory formation and retrieval. Human Neurobiology 1987;6:129–139. [PubMed: 3305439]

Karis D, Fabiani M, Donchin E. “P300” and memory: Individual differences in the von Restorff effects. Cognitive Psychology 1984;16:117–216.

Karlsgodt KH, Shirinyan D, van Erp TG, Cohen MS, Cannon TD. Hippocampal activations during encoding and retrieval in a verbal working memory paradigm. Neuroimage 2005;25:1224–1231. [PubMed: 15850740]

Kok A. On the utility of P3 amplitude as a measure of processing capacity. Psychophysiology 2001;38:557–577. [PubMed: 11352145]

Konishi S, Uchida I, Okuaki T, Machida T, Shirouzu I, Miyashita Y. Neural correlates of recency judgment. Journal of Neuroscience 2002;22:9549–9555. [PubMed: 12417679]

Kučera, H.; Francis, WN. Computational analysis of present-day American English. Providence: Brown University Press; 1967.

Kutas M, Hillyard SA. Reading senseless sentences: Brain potentials reflect semantic incongruity. Science 1980;207:203–205. [PubMed: 7350657]

Lewandowsky S, Brown GDA. Serial recall and presentation schedule: A micro-analysis of local distinctiveness. Memory 2005;13:283–292. [PubMed: 15948613]

Lewandowsky S, Murdock BB. Memory for serial order. Psychological Review 1989;96:25–57.

Martin M, Jones GV. Negative recency and measurement of primacy memory. British Journal of Psychology 1970;70:441–443. [PubMed: 486880]

Melton AW. Implications of short-term memory for a general theory of memory. Journal of Verbal Learning and Verbal Behavior 1963;2:1–21.

Murdock BB. The serial position effect of free recall. Journal of Experimental Psychology 1962;64:482–488.

Murdock BB. Modality effects in short-term memory: Storage or retrieval? Journal of Experimental Psychology 1968;77:79–86. [PubMed: 5663602]

Murdock BB, Walker KD. Modality effects in free recall. Journal of Verbal Learning and Verbal Behavior 1969;8:665–676.

Nairne JS. A framework for interpreting recency effects in immediate serial recall. Memory & Cognition 1988;16:343–352.

Nipher FE. On the distribution of numbers written from memory. Transactions of the Academy of St Louis 1876;3:79–80.

Nyberg L, Habib R, McIntosh AR, Tulving E. Reactivation of encoding-related brain activity during memory retrieval. Proceedings of the National Academy of Sciences, U S A 2000;97:11120–11124.

Oberauer K. Understanding serial position curves in short-term recognition and recall. Journal of Memory and Language 2003;49:469–483.

Page MPA, Norris D. The primacy model: A new model of immediate serial recall. Psychological Review 1998;105:761–781. [PubMed: 9830378]

Paller KA, Kutas M, Mayes AR. Neural correlates of encoding in an incidental learning paradigm. Electroencephalography and Clinical Neurophysiology 1987;67:360–371. [PubMed: 2441971]

Paller KA, McCarthy G, Wood CC. ERPs predictive of subsequent recall and recognition performance. Biological Psychology 1988;26:269–276. [PubMed: 3207786]

Patterson JV, Pratt H, Starr A. Event-related potential correlates of the serial position effect in short-term memory. Electroencephalography and Clinical Neurophysiology 1991;78:424–437. [PubMed: 1712278]

Polich, J. Overview of P3a and P3b. In: Polich, J., editor. Detection of change—Event-related potential and fMRI findings. Boston: Kluwer Academic Press; 2003. p. 83-98.

Postman L, Phillips LW. Short term temporal changes in free recall. Quarterly Journal of Experimental Psychology 1965;17:132–138.

Ranganath C, D'Esposito M. Directing the mind's eye: Prefrontal, inferior and medial temporal mechanisms for visual working memory. Current Opinion in Neurobiology 2005;15:175–182. [PubMed: 15831399]

Robinson ES, Brown MA. Effect of serial position on memorization. American Journal of Psychology 1926;37:538–552.

Rundus D. Analysis of rehearsal processes in free recall. Journal of Experimental Psychology 1971;89:63–77.

Rushby JA, Barry RJ, Johnstone SS. Event-related potential correlates of serial-position effects during an elaborative memory test. International Journal of Psychophysiology 2002;46:13–27. [PubMed: 12374643]

Schacter DL, Wagner AD. Remembrance of things past. Science 1999;285:1503–1504. [PubMed: 10498535]

Semlitsch HV, Anderer P, Schuster P, Presslich O. A solution for reliable and valid reduction of ocular artifacts applied to the P300 ERP. Psychophysiology 1986;23:695–703. [PubMed: 3823345]

Shiffrin RM, Atkinson RC. Storage and retrieval processes in long-term memory. Psychological Review 1969;76:179–193.

Smith ME, Guster K. Decomposition of recognition memory event-related potentials yields target, repetition, and retrieval effects. Electroencephalography and Clinical Neurophysiology 1993;86:335–343. [PubMed: 7685267]

Smith ME, Halgren E. Event-related potentials elicited by familiar and unfamiliar faces. Electroencephalography and Clinical Neurophysiology (Supplement) 1987;40:422–426. [PubMed: 3480159]

Smith ME, Stapleton JM, Halgren E. Human medial temporal lobe potentials evoked in memory and language tasks. Electroencephalography and Clinical Neurophysiology 1986;63:145–159. [PubMed: 2417815]

Strange BA, Otten LJ, Josephs O, Rugg MD, Dolan RJ. Dissociable human perirhinal, hippocampal, and parahippocampal roles during verbal encoding. Journal of Neuroscience 2002;15:523–528. [PubMed: 11784798]

Talmi D, Grady CL, Goshen-Gottstein Y, Moscovitch M. Neuroimaging the serial position curve. A test of single-store versus dual-store models. Psychological Science 2005;16:716–723. [PubMed: 16137258]

Tulving E, Colatla V. Free recall of trilingual lists. Cognitive Psychology 1970;1:86–98.

Watson TD, Azizian A, Squires NK. Event-related potential correlates of extradimensional and intradimensional set-shifts in a modified Wisconsin Card Sorting Test. Brain Research 2006;1092:138–151. [PubMed: 16696954]

Wickens C, Kramer A, Vanasse L, Donchin E. Performance of concurrent tasks: A psychophysiological analysis of the reciprocity of information-processing resources. Science 1983;221:1080–1082. [PubMed: 6879207]

Wijers AA, Mulder G, Okita T, Mulder LJ. Event-related potentials during memory search and selective attention to letter size and conjunctions of letter size and color. Psychophysiology 1989;26:529–547. [PubMed: 2616701]

Wixted JT, Ebbesen EB. On the form of forgetting. Psychological Science 1991;2:409–415.

Yonelinas AP. Consciousness, control, and confidence: The 3 Cs of recognition memory. Journal of Experimental Psychology: General 2001;130:361–379. [PubMed: 11561915]

Zhang DR, Li ZH, Chen XC, Wang ZX, Zhang XC, Meng XM, et al. Functional comparison of primacy, middle and recency retrieval in human auditory short-term memory: An event-related fMRI study. Cognitive Brain Research 2003;16:91–98. [PubMed: 12589893]

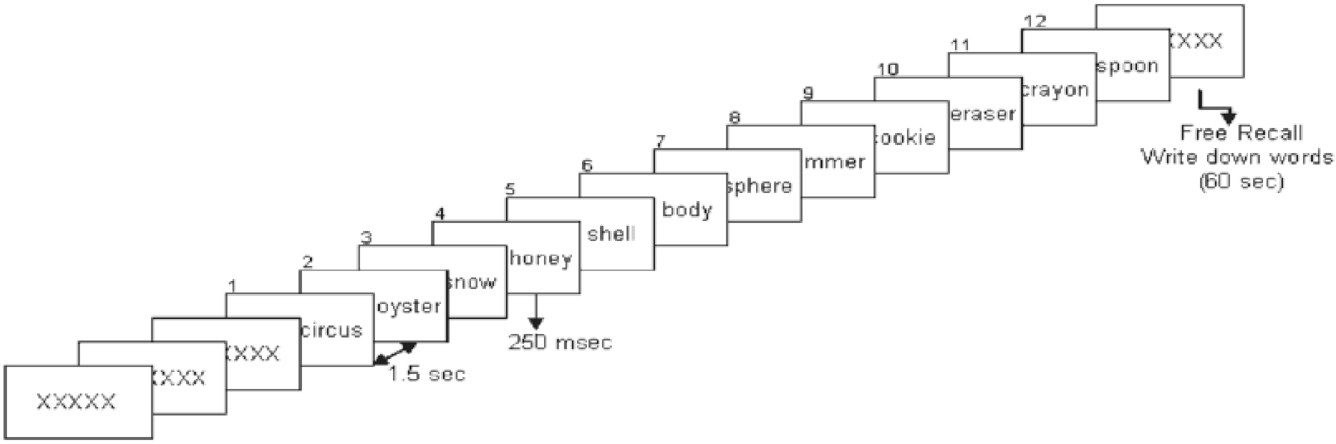

Figure 1.

Schematic illustration of the experimental design with an example of word list. This procedure was repeated for 20 different word lists.

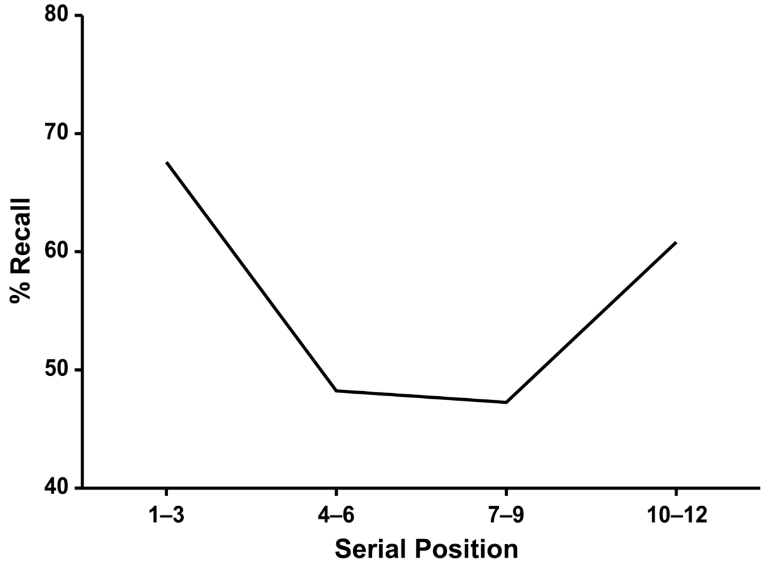

Figure 2.
Mean percentage of recalled item as a function of each serial position block (*n* = 30).

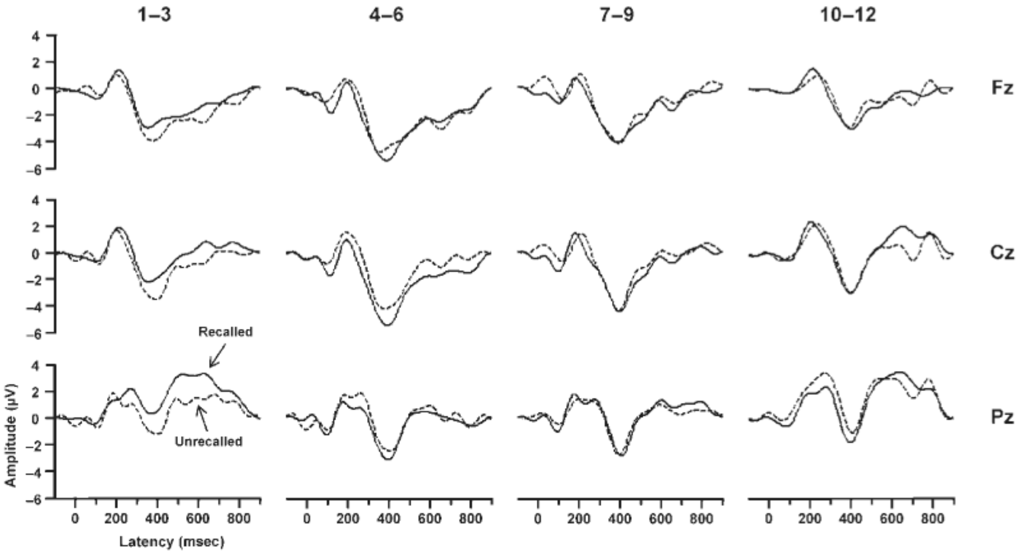

Figure 3.

Grand-averaged event-related potentials for the recalled and unrecalled words from each serial position block at the midline electrodes.

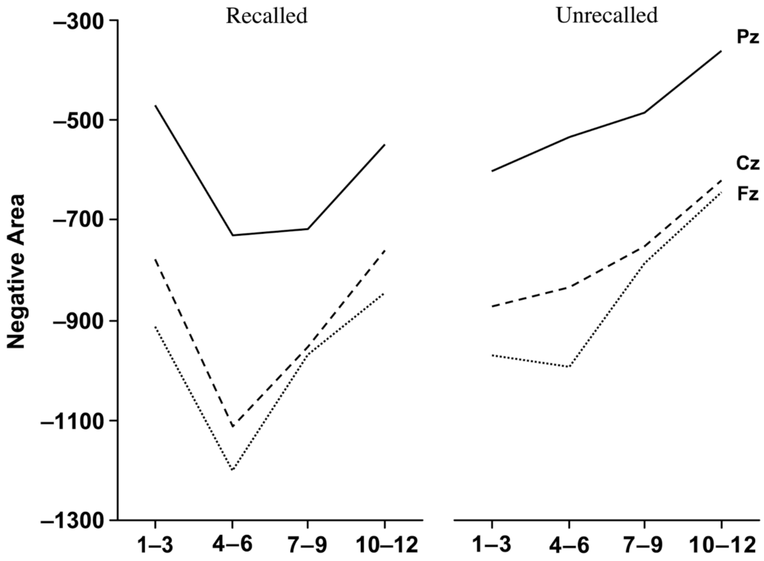

Figure 4.

Mean recalled (left) and unrecalled (right) early negative amplitude as a function of serial position block for the midline electrodes.

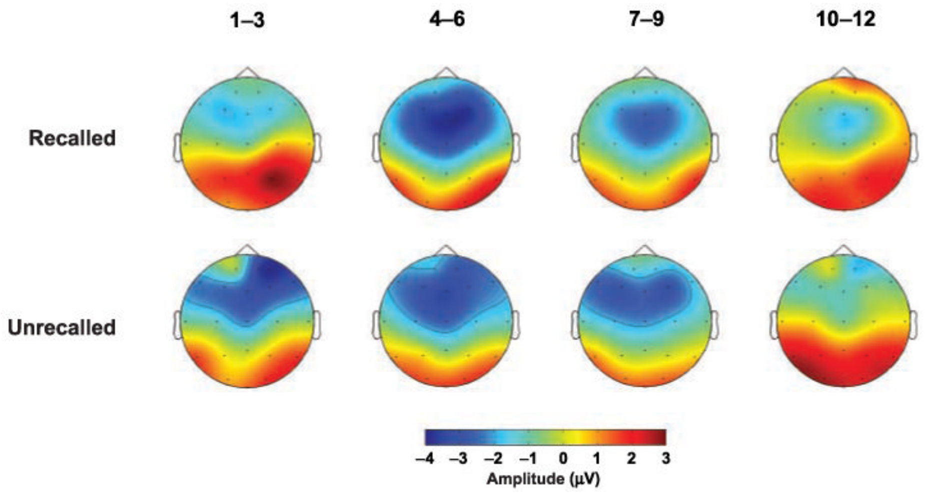

Figure 5.

Topographic maps illustrating the area voltage distribution from the (early) 250–500 msec latency window for recalled and unrecalled items as a function of serial position block from all scalp electrodes.

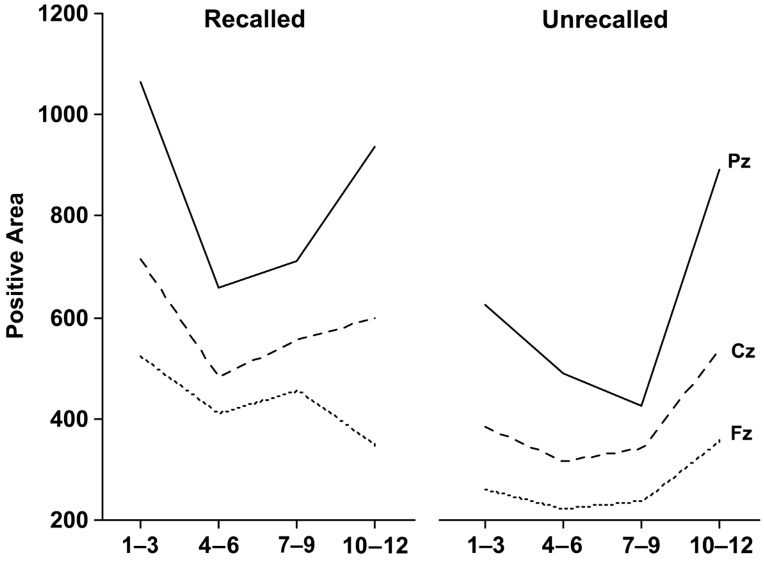

Figure 6.
Mean recalled (left) and unrecalled (right) late positive amplitude as a function of serial position block from the midline electrodes.

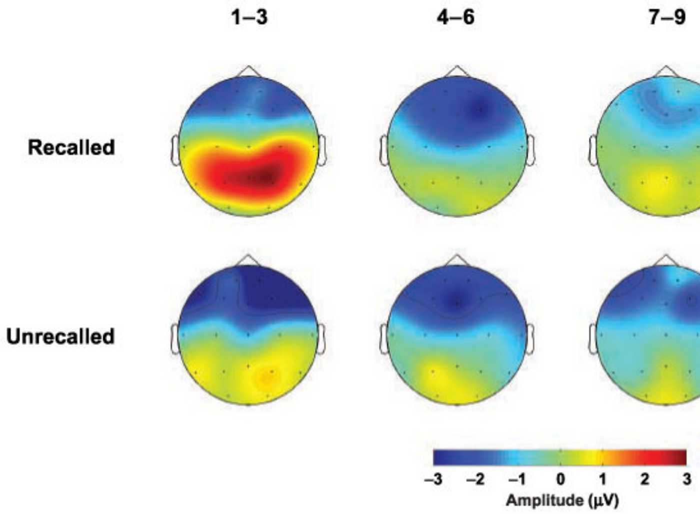

Figure 7.

Topographic maps illustrating the area voltage distribution from the (late) 500–750 msec latency window for recalled and unrecalled items as a function of serial position block from all scalp electrodes.