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Authors

Golob, Edward J
Starr, Arnold

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Visual encoding differentially affects auditory event-related potentials during working memory retrieval

EDWARD J. GOLOB AND ARNOLD STARR

Institute for Brain Aging and Dementia, and Department of Neurology, University of California, Irvine, Irvine, California 92627, USA

Abstract

Previous working memory studies using auditory stimuli at both encoding and retrieval show amplitude decreases in event-related potentials (N100 and late positive wave, LPW) at retrieval as a function of memory load. This study tested if these effects are associated with phonological or semantic coding by presenting visual stimuli at encoding and auditory stimuli at retrieval. We hypothesized that event-related potentials associated with phonological but not semantic coding would be affected by modality differences at encoding and retrieval. Memory sets having one, three, or five visual digits were followed by auditory probes that subjects classified as present or absent from the set. Reaction time increased and LPW amplitudes decreased with increases in memory load, but there were no significant effects of memory load on N100 amplitude. Results suggest that with respect to brain activity that covaries with memory load, probe N100 amplitude is associated with phonological coding and LPW amplitude is associated with semantic coding.

Descriptors: Short-term memory, Priming, N100, P300

The process of encoding, storing, and retrieving information in working memory likely involves the coordinated use of various memory codes. Several findings suggest that in verbal working memory tasks both phonological and semantic codes can be used. First, phonological errors during recall and recognition are more common than orthographic-based errors, even when material is presented in the visual modality (Conrad, 1962, 1964). Second, greater phonetic similarity among memorized items is associated with more accurate item recall, and less accurate ordered recall (Baddeley, 1966; Conrad & Hull, 1964; Watkins, Watkins, & Crowder, 1974). Finally, recency effects, indicating greater accuracy for item(s) at the end of a sequentially memorized list, are more pronounced for acoustic stimuli compared with visual material (Corballis, 1966).

Neuroimaging and lesion studies have implicated a network of posterior parietal and prefrontal regions in the mediation of working memory (D'Esposito, 2001; Smith & Jonides, 1997; Vallar & Shallice, 1990). The auditory cortex may also be involved in memory retrieval when using acoustic stimuli (Colombo, D'Amato, Rodman, & Gross, 1990; Nyberg, Habib, McIntosh, & Tulving, 2000; Wheeler, Petersen, & Buckner, 2000). The involvement of auditory cortex and posterior

neocortical regions in working memory retrieval is supported by studies reporting an association between memory load and the amplitude of event-related potentials (ERPs) thought to be generated from these regions (Conley, Michalewski, & Starr, 1999; Golob & Starr, 2000, in press). In these studies, the auditory N100 component and a subsequent late positive wave (LPW) both showed amplitude reductions as memory load increased.

It is unclear what types of memory codes are associated with the ERP findings. One possibility is that ERP amplitude changes with memory load reflect a semantic code. Thus, amplitude changes with memory load would reflect the amount of item information at a symbolic level, independent of the physical stimulus used to convey the semantic information. An alternative hypothesis is that ERP amplitude changes reflect a phonological code that depends on the physical features of the stimuli. Acoustic cues presented during retrieval would then reactivate sensory cortex engaged during encoding (e.g., Damasio, 1989; Mesulam, 1998). Thus, a perceptual-based phonological code would require processing of the memorized stimuli by the auditory cortex during encoding as a necessary condition for subsequent changes in ERP amplitude to auditory cues during memory retrieval.

The present study was designed to distinguish these two possibilities of memory coding (semantic, phonological), as they relate to auditory ERP changes with memory load. Participants memorized lists of digits presented in the visual modality; memory was assessed in a recognition format using an auditory retrieval cue. If ERP amplitudes during retrieval reflect a semantic code, then reductions in ERP amplitude with increasing

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Address reprint requests to: Edward J. Golob, Ph.D., 154 Med Surge I, Department of Neurology, University of California, Irvine, Irvine, CA 92627, USA. E-mail: egolob@uci.edu.

memory load would be observed during retrieval regardless of the modality used during encoding. In contrast, if the ERP amplitudes reflect perceptual coding, then no changes in ERP amplitude would be expected during retrieval if the stimuli presented at encoding and retrieval have different modalities.

Methods

Participants

Participants were University of California, Irvine, undergraduate students ($n = 17$; mean age = 21.3 ± 2.1 , range: 19–26), and received course credit for their participation. All participants were right-handed, reported no hearing or visual deficits, and signed informed consent forms. Experiments were performed in accordance with a protocol approved by the University of California, Irvine, Institutional Review Board.

Behavioral Task

Participants performed a modified Sternberg working memory task (Sternberg, 1966) inside a sound attenuating, electrically shielded chamber. Visual stimuli were presented on a monitor ~ 0.75 m in front of the participant. White digits (10×4 –6 cm, depending on the digit, 48.7 cd/m, 500 ms duration) were presented on a black background. Auditory stimuli were digitized from a male voice (~ 500 ms duration, ~ 50 dB nHL) and presented from two speakers ~ 0.75 m in front of the participant. Participants were seated in a comfortable chair and held a small keypad containing four response buttons.

Each trial contained a visual start cue followed by a list of sequentially presented digits (memory set), and a probe digit. Interstimulus intervals between memory set items were 1.5 s, with a 3.0-s retention period before probe presentation. The memory set contained either one, three, or five digits. Participants determined if the probe was (in-set probe) or was not (out-of-set probe) present in the memory set, and pressed one of two buttons to indicate their choice with their right thumb. Participants were instructed to respond rapidly while maintaining high levels of accuracy.

Each block contained 20 memory trials and lasted 4.5 min. Order of set sizes was approximately counterbalanced across participants (5 or 6 participants per set size for the first, second, and third group of blocks). The intertrial interval following probe presentation varied with set size (9.0, 6.0, and 3.0 s for one, three, and five items, respectively) in order to fix the interstimulus interval between probes at 13.5 s for all set sizes. The purpose of equating the time between probe presentations across set sizes was to avoid differences in N100 amplitude among set sizes due to refractory effects rather than memory load (i.e., N100 amplitude is positively correlated with interstimulus intervals up to ~ 10 –15 s; Näätänen & Picton, 1987). All trials within a given block had the same number of items in the memory set, and the participant was informed of the set size before each block. Digits in each trial were randomly determined without repeats, and the probabilities of in-set and out-of-set probes were each .50. In the three- and five-item sets, in-set probes were equally likely for each serial position. Participants were given either two or three blocks per set size. The determination of whether two or three blocks would be necessary to achieve a favorable signal-to-noise ratio was made by visual inspection of the ERPs from the first two blocks.

Electrophysiological Recordings

Participants 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 k Ω , and reference electrodes were in a linked mastoid configuration. Eye movements were monitored using electrodes placed above and below the left eye. The EEG and EOG were digitally amplified with a bandpass of DC–100 Hz (digitization rate = 500 Hz). Electrophysiological (EEG, EOG) and behavioral data were collected continuously. An eyeblink correction algorithm was used to correct for artifacts (Gratton, Coles, & Donchin, 1983). Individual sweeps were then sorted and averaged according to stimulus type (in-set or out-of-set). Epochs lasted from 998 ms before probe onset to 1,000 ms after probe presentation. Incorrect trials were not included in the ERP averages. Sweeps were visually inspected for artifacts before being accepted into the average.

Data Analysis

Behavioral measures included reaction time, relative to the onset of probe stimuli, and accuracy. Accuracy was the percent of correct responses among all trials with a response. ERPs were digitally filtered using two filter settings, depending on the component of interest. In this report, only ERPs to probes will be presented. For the auditory N100 and P200 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 amplitudes were defined relative to a 100-ms prestimulus baseline period. The N100 was defined as the maximum negative peak between 80 and 180 ms and the P200 was defined as the maximum positive peak between 150 and 250 ms. The LPW was quantified by window measures of the mean amplitude from 200 to 398 and 400 to 598 ms. To simplify the statistical analysis, the components were measured from the sites having the largest amplitude for each component (Cz site for N100 and P200, Pz site for the LPW). Previous studies using auditory stimuli for memory set items and probes show that probe N100 amplitudes measured at Cz and LPW amplitudes measured at Pz are inversely related to set size.

The peak of the LPW corresponds to the “P300” wave of previous reports using the Sternberg working memory task (e.g., Adam & Collins, 1978; Ford, Roth, Mohs, Hopkins, & Kopell, 1979; Kramer & Strayer, 1988; Marsh, 1975; Pratt, Michalewski, Barrett, & Starr, 1989). The neutral term “LPW” was used rather than “P300” because the neurobiological relationship between the long-lasting positive shift of the LPW in this task and the P300 commonly studied in other tasks, such as the target detection or “oddball” task, is uncertain.

Statistical Analysis

Data were analyzed using repeated-measures analysis of variance (ANOVA). The Greenhouse–Geisser correction was applied to control type I error when appropriate; adjusted p values were reported. P values $< .05$ were considered significant and effect sizes were expressed using partial eta squared (η^2 ; Tabachnick & Fidell, 1996). Behavioral analysis included the factors of set size (one-, three-, five-item memory sets), and probe type (in-set vs. out-of-set). Analysis of event-related potential amplitudes and latencies included the factors of set size and time window (200–398, 400–598 ms) for the LPW analysis.

Results

Behavior

Reaction time as a function of set size is shown in Figure 1. A 2 (probe type) $\times$ 3 (set size) ANOVA showed significant main effects of set size, $F_{(2,32)} = 31.9$, $p < .001$, $\eta^2 = .67$, $\epsilon = .98$, and probe type, $F_{(1,16)} = 7.5$, $p < .02$, $\eta^2 = .32$. Reaction times increased with greater memory load, and reaction times to in-set probes were shorter than out-of-set probes. The mean slope of the set size $\times$ reaction time function was 68.6 ± 8.6 ms/item. The probe type $\times$ set size interaction failed to attain significance ($p < .06$). There were no significant differences in accuracy across set size, with 98.1, 98.3, and 97.7% correct responses for one-, three-, and five-item set sizes, respectively.

Event-Related Potentials

Grand average potentials from midline sites are shown in Figure 2. Auditory probes elicited an N100-P200 complex having a maximum amplitude at Cz, followed by a sustained LPW that was largest at the Pz site. A series of negative (N200) and positive (P300) components following the P200 were also present, and were coincident with the beginning of the LPW. The apparent sustained positivity beginning ~ 800 ms is due to setting the prestimulus baseline at the end of a negative potential that developed between the last memory set item and the probe.

N100. The N100 and P200 after bandpass filtering are shown in Figure 3(a, b) for in-set and out-of-set probes, respectively. Amplitude and latency of the N100 at the Cz site were analyzed using 2 (probe type) $\times$ 3 (set size) ANOVA tests. For N100 amplitude there were no significant effects for set size ($p > .10$) or probe type, and the set size $\times$ probe type interaction was also not significant. In the grand average N100, amplitude was larger for one item versus three and five items for out-of-set probes, but separate analysis of out-of-set probes did not show a significant effect of set size ($p > .06$). There were also no significant effects for N100 latency.

Figure 1. Reaction time as a function of memory load. There was a significant effect of set size on reaction time, with approximately linear increases in reaction time among set sizes. Reaction times to in-set probes were significantly shorter than out-of-set probes, especially for the one-item set size.

Figure 2. Event-related potentials to in-set (left column) and out-of-set (right column) probes as a function of set size (one vs. five items). Components of interest include the N100 and P200, which peaked at ~ 100 and 200 ms, respectively, and had maximal amplitudes at the Cz site. The late positive wave (LPW) began ~ 200 ms and lasted until at least 600 ms in all conditions, and was largest at Pz. Probe onset is indicated by vertical lines. Midline scalp sites are shown (anterior to posterior order: Fz, Cz, Pz, Oz). Potentials were filtered from DC–16 Hz.

P200. Amplitude and latency of the P200 were at the Cz site analyzed using a 2 (probe type) $\times$ 3 (set size) ANOVA. There were no significant effects of probe type, set size, or probe type $\times$ set size on P200 amplitude. For P200 latency, there was a significant effect for probe type, $F_{(1,16)} = 4.6$, $p < .05$, $\eta^2 = .22$, with slightly longer latencies for out-of-set probes (215.6 ± 5.0 ms) versus in-set probes (211.1 ± 3.9 ms). There were no significant effects for set size, and the set size $\times$ probe type interaction was also not significant.

Lpw. The LPW was widely distributed across central and posterior scalp sites, with a maximal amplitude at the Pz site (see Figure 2). For simplicity, analysis was restricted to the Pz site (Figure 3c, d; for detailed topographic analysis see Golob and Starr, in press). Amplitude of the LPW was analyzed using a 2 (probe type) $\times$ 3 (set size) $\times$ 2 (window: 200–398, 400–598 ms) ANOVA at the Pz site. There was a significant main effect of set size, $F_{(2,32)} = 14.6$, $p < .001$, $\eta^2 = .48$, $\epsilon = .87$, with the largest amplitude for the one-item set (10.7 ± 1.1 μ V), intermediate for three items (7.4 ± 1.0 μ V), and smallest for five items (5.8 ± 1.3 μ V). Significant main effects were also observed for

Figure 3. Event-related potentials to probes at Cz and Pz sites. (a, b): Bandpass filtered (1–16 Hz) potentials at the Cz site to illustrate the N100 and P200 components as a function of set size. There was no significant effect of set size on either N100 or P200 amplitude. N100 amplitude for out-of-set probes in the one-item set size was somewhat larger than three or five items, but this difference did not attain significance. (c, d): Low-pass filtered (DC–16 Hz) potentials at the Pz site to illustrate LPW amplitude as a function of set size. There was a significant effect of set size, with the largest amplitudes for the one-item set, intermediate for three items, and smallest amplitude for the five-item set size. Measurement windows used to quantify LPW amplitude (200–398 and 400–598 ms) are shown by the shaded bars in (c).

probe type, $F_{(1,16)} = 41.2$, $p < .01$, $\eta^2 = .47$, with larger amplitudes for in-set probes, and window, $F_{(1,16)} = 12.3$, $p < .01$, $\eta^2 = .44$; (200–398 < 400–598 ms). There were also significant probe type $\times$ window, $F_{(1,16)} = 7.0$, $p < .02$, $\eta^2 = .30$, and probe type $\times$ set size, $F_{(2,32)} = 4.2$, $p < .04$, $\eta^2 = .21$, $\epsilon = .83$, interactions. The significant interactions indicated that the difference in LPW amplitude according to probe type (in-set > out-of-set) was larger for the first time window. Differences between probe types were not equivalent among set sizes, with the largest mean difference for the one-item set size (4 μV , in set > out-of-set) and smaller mean differences in the three- (1.2 μV) and five-item (0.2 μV) set sizes (see Figure 3c, d).

The correlation between reaction time differences (five-item – one-item) and LPW amplitude differences (Pz site: one-item – five-item) was significant for in-set (400–598 ms time window: $r = .53$, $p < .05$) and out-of-set (200–398 ms time window: $r = .48$, $p < .05$; 400–598 ms: $r = .52$, $p < .03$) probes.¹ When one outlier subject having a large difference in reaction time for in-set probes (2.4 SD , reaction time five-item – one-item = 674 ms) was excluded from the analysis, correlations at Pz (200–398 ms: $r = .68$, $p < .01$; 400–598 ms: $r = .60$, $p < .02$) and Cz (200–398 ms: $r = .82$, $p < .001$; 400–598 ms: $r = .70$, $p < .001$) increased substantially.

¹The correlational analysis of changes in reaction time versus changes in LPW amplitude was suggested by an anonymous reviewer.

Figure 4. Plots of event-related potential amplitudes as a function of set size (one, three, five items) and probe type (in-set, out-of-set). (a): Probe N100 amplitude as a function of set size and probe type. There were no significant effects of set size on N100 amplitude when memory set items were presented in the visual modality. (b): N100 amplitudes from a previous study having auditory stimuli at both encoding and retrieval for comparison with panel A (data from Golob & Starr, 2000). For both in-set and out-of-set probes, N100 amplitudes exhibited approximately linear reductions with increased set size in young subjects. Smaller overall N100 amplitudes in the auditory–auditory paradigm, as compared with the current study (visual–auditory), were due to the recent presentation of auditory stimuli on the memory set, which attenuates probe N100 amplitudes (i.e., a refractory effect). (c): Mean LPW amplitudes during the 200–398-ms time window. LPW amplitude differed significantly among set sizes, with the largest differences for one versus three and five items. (d): Mean LPW amplitudes during the 400–598-ms time window. Significant differences in LPW amplitude among set sizes were observed for both in-set and out-of-set probes. At this time window, LPW amplitudes had an approximately linear association with set size.

In summary, N100 amplitude to probes did not vary with memory load, but the subsequent LPW did show amplitude reductions with increasing memory load. N100 and LPW amplitudes are plotted in Figure 4. Note that during the initial LPW time window (200–398 ms) amplitudes for one-item probes, especially in-set probes, were larger than three- and five-item probes, which were approximately equal. During the second time window (400–598 ms), monotonic reductions in LPW amplitude were observed with increasing memory load.

Discussion

The main findings were that in a crossmodal working memory task (visual encoding, auditory retrieval), N100 amplitudes in response to auditory probe stimuli did not significantly differ as a function of memory load. In contrast, the subsequent LPW component did exhibit amplitude reductions as a function of memory load. These findings bear on the functional neuroanatomy, time course, and extraction of cue information during working memory retrieval.

Time Course and Functional Neuroanatomy during Retrieval

Sensory cortical areas have been proposed to participate in memory retrieval (e.g., Damasio, 1989). Previous event-related potential studies in young subjects that used auditory stimuli for both the memory set and probe reported linear reductions in N100 amplitude with increasing memory load (Conley et al., 1999; Golob & Starr, 2000). Control studies in young (Conley et al., 1999; Golob & Starr, in press) and elderly subjects (Golob & Starr, 2000) show that N100 amplitude is not significantly different across memory loads when subjects hear the same stimulus sequences but are instructed to passively listen to "memory set" items and judge whether the subsequent probe was an even or odd number. Thus, the control studies that do not require the encoding or retrieval of item information indicate that the inverse relationship between N100 amplitude and memory load observed using exclusively auditory stimuli is not attributable to N100 refractory effects.

The modulation of N100 amplitude as a function of memory load suggests that the auditory cortex may participate in working memory retrieval because the neural generators of the N100 have been localized to secondary auditory cortex and adjacent areas (Arezzo, Pickoff, & Vaughan, 1975; Godey, Schwartz, de Graaf, Chauvel, & Liegeois-Chauvel, 2001; Knight, Scabini, Woods, & Clayworth, 1988; Liegeois-Chauvel, Musolino, Badier, Marquis, & Chauvel, 1994; Pantev et al., 1995; Picton et al., 1999; Zouridakis, Simos, & Papanicolaou, 1998). N100 amplitude is also modulated by phonological variables that could be useful for probe classification (i.e., in-set vs. out-of-set), such as differences between voice onset times (Dorman, 1974; Molfese, 1978) and specific consonants (Gage, Poeppel, Roberts, & Hickok, 1998; Lawson & Gaillard, 1981; Molfese, 1984). Imaging studies in humans suggest that certain areas of sensory cortex activated during encoding are reactivated during memory retrieval (Nyberg et al., 2000; Persson & Nyberg, 2000; Wheeler et al., 2000). Animal studies also show that neurons in auditory (Gottlieb, Vaadia, & Abeles, 1989; Sakurai, 1994), somatosensory (Zhou & Fuster, 1996), and extrastriate cortex (Nakamura & Colby, 2000) can differentially respond during the encoding, storage, and retrieval phases of working memory. Auditory association cortex in monkey is also necessary for retention of auditory information in working memory (Colombo et al., 1990).

Collectively, the above findings suggest that auditory cortical areas may contribute to a network supporting working memory for auditory information. The current results qualify this interpretation, however, by suggesting that the extent of auditory cortex participation in retrieval may be a function of the correspondence between the modalities of material presented during encoding and retrieval. The findings that auditory N100 amplitude during retrieval changes with memory load when auditory, but not visual, stimuli were presented for memorization is consistent with the encoding specificity principle, which states that the effectiveness of a retrieval cue depends, in part, on its similarity to the material during encoding (Tulving, 1983; Tulving & Thomson, 1973). We also note that in the present study participants performed at high levels of accuracy at all set sizes, indicating that changes in N100 amplitude with memory load is not a necessary process for accurate retrieval using auditory cues. Instead, the changes in N100 amplitude when auditory stimuli are present at encoding and retrieval may indicate one possible source of information supporting memory retrieval.

Verbal working memory studies using PET or fMRI show that posterior parietal lobe activation increases as a function of memory load (Braver et al., 1997; Rypma, Prabhakaran, Desmond, Glover, & Gabrieli, 1999; Smith & Jonides, 1997), with similar areas of activation for auditory or visual stimuli (Schumacher et al., 1996). A linkage between temporo-parietal cortex, working memory ability, and the LPW is suggested by the finding that subjects with impaired working memory following lesions involving temporal-parietal regions have attenuated LPW amplitudes (Starr & Barrett, 1987). Taken together, these findings are consistent with the possibility that the LPW is generated, in part, by posterior parietal lobe activity. However, the proposal that parietal regions are involved in the generation of the LPW is speculative because the association between LPW amplitude and activations in parietal regions in neuroimaging studies has not been evaluated, and convergent evidence using ERP source analysis techniques or human intracranial recordings during this task is currently unavailable.

Cognitive Processes and ERP Results

The absence of memory load effects on N100 amplitude suggest that top-down processes associated with the identities of the items in the memory set were not involved as factors modulating N100 amplitude in this task. With respect to attention, previous studies indicate amplitude modulations of the N100 and a concurrent slow wave in dichotic listening tasks (Hillyard, Hink, Schwent, & Picton, 1973; Näätänen & Picton, 1987). N100 amplitude to targets also varies as a function of prior cue information in attentional cueing tasks (Golob, Pratt, & Starr, 2002; Hugdahl & Nordby, 1994). Assuming that similar attentional processes are engaged at retrieval regardless of auditory or visual encoding, the finding that N100 amplitude did not change across memory loads in the crossmodal task suggests that the modulation of N100 amplitude in previous studies using only auditory stimuli is not associated with modality-independent attentional factors. However, dichotic listening and cued attention tasks have many differences from the present working memory task, such as experimental procedures, the elicited ERP components, and the analysis of the ERPs using difference waveforms. Thus, a systematic assessment would be required before drawing any firm conclusions regarding the possible association between attention and ERPs in the current task.

The LPW may be modulated by the presence of semantic information conveyed by the probe because modulation of LPW amplitude by memory load was due to the meaning of the probe digit, and could not have been based on whether the probe stimulus physically matched, or failed to match, a stimulus presented in the memory set. A previous study using a two-item memory set reported no significant effects of memory set modality (visual or auditory) on P300 amplitude or latency to acoustic probes (Pratt, Erez, & Geva, 1997). The results from Pratt et al. are consistent with the notion that LPW amplitude in the current verbal working memory task is associated with the number of items in working memory that are represented by modality-independent semantic information.

The N400 is an ERP lasting from ~250 to 500 ms that is sensitive to variables involving the context of semantic information or the organization of semantic memory (Kutas & Federmeier, 2000; Kutas & Hillyard, 1980). These variables were held constant across set sizes, and thus changes in N400

amplitude are not likely to account for the inverse association between LPW amplitude and set size. Additional research would be required to determine how similar the N400 and LPW are in terms of their neural and cognitive properties.

In direct access or parallel retrieval models memory accessibility is, in part, a function of the memory trace strength, which is assumed to be proportional to accuracy and reaction time (Murdock, 1985; Norman & Wickelgren, 1969; Ratcliff, 1978; Wickelgren & Norman, 1966). The well-known linear increase in reaction time as a function of set size in the Sternberg task may, therefore, be related to reductions in mean trace strength with increased memory load. One possibility is that the LPW is also associated with memory trace strength. This possibility is consistent with the results of Finnigan, Humphreys, Dennis, and Geffen (2002), who proposed that the amplitude of a slow wave at parietal sites lasting from ~300 to 500 ms after cues in an episodic recognition task is modulated by memory trace strength. It is also important to note that changes in ERP amplitudes as a function of memory load may reflect a third variable that covaries with memory load, such as serial position. Trace strength and parallel retrieval models can account for serial position effects by including parameter values that covary with serial position (Murdock, 1971; Ratcliff, 1978). Previous studies using exclusively auditory stimuli have shown that N100 and LPW/P300 amplitudes vary as a function of serial position (Chao

& Knight, 1996; Golob & Starr, in press). Alternatively, ERP amplitude changes associated with memory load may relate to factors reflecting cue-based processes at retrieval rather than trace strength, as in long-term memory tasks. LPW amplitude reductions may also relate to negativity associated with memory load observed in a selective search task that is a combination of selective attention and memory search task (Wijers, Mulder, Okita, & Mulder, 1989) or in a semantic category memory search task (Mecklinger, Kramer, & Strayer, 1992).

In summary, probe recognition may be conceptualized as a constructive process that extracts information from the probe stimulus, with the stimulus evaluation process compiling successively more information having increasingly abstract properties; information that is eventually used to decide whether the probe was or was not a member of the memory set (e.g., Miller, 1988; Ratcliff, 1978). Neuroanatomical considerations demand that auditory probe information is first processed in auditory cortical areas before processing can take place in higher order association regions. The results showing that in a cross-modal working memory task, LPW amplitude, but not N100 amplitude, is inversely associated with memory load are consistent with a stimulus evaluation process that initially depends on the physical properties of the probe and is then followed by further processing related to more abstract semantic properties.

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