Published in final edited form as:

Psychophysiology. 2013 December ; 50(12): 1263–1274. doi:10.1111/psyp.12140.

Cortical potentials in an auditory oddball task reflect individual differences in working memory capacity

Kate A. Yurgil^{1,2,3} and Edward J. Golob^{3,4}

¹VA Center of Excellence for Stress and Mental Health, San Diego, CA 92161

²VA San Diego Healthcare System, San Diego, CA 92161

³Department of Psychology, Tulane University, New Orleans, LA 70118

⁴Program in Neuroscience, Tulane University, New Orleans, LA 70118

Abstract

This study determined whether auditory cortical responses associated with mechanisms of attention vary with individual differences in working memory capacity (WMC) and perceptual load. The operation span test defined subjects with low vs. high WMC, who then discriminated target/nontarget tones while EEG was recorded. Infrequent white noise distracters were presented at midline or $\pm 90^\circ$ locations, and perceptual load was manipulated by varying nontarget frequency. Amplitude of the N100 to distracters was negatively correlated with WMC. Relative to targets, only high WMC subjects showed attenuated N100 amplitudes to nontargets. In the higher WMC group, increased perceptual load was associated with decreased P3a amplitudes to distracters and longer-lasting negative slow wave to nontargets. Results show that auditory cortical processing is associated with multiple facets of attention control related to WMC and possibly higher-level cognition.

In everyday life attention and short-term memory (STM) are highly interactive. For example, recently attended items are usually retained in STM, and top-down goals in STM are one way to select what is to be attended. The ballet of interactions among attention and STM is termed “working memory” and reflects the ability to store and process information in an accessible state over brief periods of time (Baddeley & Hitch, 1974; Cowan, 1999). Selective attention controls how information is stored and processed in working memory. Conversely, information in working memory may guide attentional resources towards goal-related items in the environment (Desimone, 1996; Desimone & Duncan, 1995; Duncan, 1998).

Top-down attention and working memory capacity

The interplay of attention and STM is often assessed using complex span tasks such as reading span (Daneman & Carpenter, 1980) and operation span (Turner & Engle, 1989). These tasks engage both storage and processing functions of working memory by

interleaving presentation of items to be remembered with a secondary task. Overall performance is used to estimate the amount of information that can be handled effectively by working memory, termed “working memory capacity, WMC” (Engle, Kane, Tuholski, Miyake, & Shah, 1999; Unsworth & Engle, 2007). Complex span scores strongly predict individual differences in higher-level cognition such as fluid and crystallized intelligence (Engle et al., 1999), reading comprehension (Daneman & Carpenter, 1980), age-related declines in cognitive functions (Verhaeghen, Marcoen, & Goossens, 1993) and everyday phenomena such as mind-wandering (Kane et al., 2007) and “choking” under pressure (Beilock & Carr, 2005). Thus, complex span tasks appear to tap into basic cognitive functions that have broad importance.

When examining interactions between attention and WMC, previous studies found that individuals with high WMC are less distractible compared to low WMC during cognitive tasks, such as proactive interference in short-term memory (Kane & Engle, 2000), dichotic listening (Colflesh & Conway, 2007; Conway, Cowan, & Bunting, 2001), Stroop (Kane & Engle, 2003), and anti-saccade tasks (Kane, Bleckley, Conway, & Engle, 2001; Unsworth, Schrock, & Engle, 2004). Individuals with high WMC may store pertinent information and suppress stimuli incongruent with top-down goals better than those with low WMC (Engle & Kane, 2003; Reynolds & Desimone, 1999). Note that with the exception of proactive interference, the above studies show that individual differences in WMC are manifest during tasks of attention control. Researchers have speculated that attention control is the main reason that complex span tasks successfully predict performance in a wide range of more complex tasks (Engle, 2002; McCabe, Roediger, McDaniel, Balota, & Hambrick, 2010).

Bottom-up attention and perceptual load

Attention control can be challenged by varying the perceptual demands of a task. If attentional selection operates at multiple points in time that depend on task load, such as the degree of perceptual demand (Lavie, Hirst, De Fockert, & Viding, 2004), it would follow that higher perceptual loads encourage early selection while lower perceptual loads permit later selection. Attention control may be modulated by bottom-up manipulations of perceptual load and the presence of irrelevant stimuli, or distracters (Lavie, 1995; Lavie et al., 2004). When perceptual demands are low, distracters may capture attention that is easily divided among incoming stimuli (Lavie et al., 2004). As perceptual demands increase, attention may be allocated more towards fulfilling top-down goals, and be less sensitive to distracter interference (Duncan, 1980; Johnsen & Briggs, 1973; Kerr, 1973; Navon, 1989). Note that the similarity between stimulus properties of goal-relevant stimuli and distracters is critical (Folk, Remington, & Johnston, 1992), and the ability of distracters to attract attention is also contingent upon top-down control (Folk et al., 1992; Folk, Remington, & Wright, 1994). Thus, any associations between WMC and attention control may vary with perceptual load demands.

Attention and event-related potentials

Given that the interplay of attention and memory processes is a key determinant of WMC, we examined event-related potentials associated with attention control and short-term

memory as a function of individual differences in WMC. Event-related potentials (ERPs) supply covert measures of stimulus processing and have been used to study individual differences in cognitive function, including differences associated with intelligence (Brumback-Peltz, Gratton, & Fabiani, 2012), normal aging (Goodin, Squires, Henderson, & Starr, 1978), mild cognitive impairment (Golob, Irimajiri, & Starr, 2007), Alzheimer's disease (Polich, 1991), and schizophrenia (Jeon & Polich, 2003). Prior studies that examined ERPs associated with attention showed that compared to lower WMC, higher WMC was associated with larger auditory N100 and smaller P300 amplitudes to target tones as well as larger visual ERPs during a visual flanker task (Brumback, Low, Gratton, & Fabiani, 2004, 2005). Furthermore, potentials during memory retrieval of recollected stimuli were correlated with WMC scores (Elward & Wilding, 2010). ERPs elicited by sentences containing implausible noun-verb relations (Nakano, Saron, & Swaab, 2010) or contextually unanticipated nouns (Otten & Van Berkum, 2009) also differed between individuals with higher vs. lower WMC, suggesting that WMC may influence the ability to process information that violates top-down expectations. The present study used an auditory oddball target detection task and focused on ERPs associated with obligatory stimulus processing (N100, P200), controlled attention (P3b, slow wave), and distraction (P3a). These potentials occur within ~500 ms after stimulus presentation and provide detailed measures of processes occurring between stimulus input and, when present, response output. Next we give a brief overview of how these ERP measures relate to attention control and memory.

The N100 and P200 peaks are auditory cortical responses that reflect bottom-up information such as stimulus features (Crowley & Colrain, 2004; Vaughan, Arezzo, & Picton, 1988), as well as top-down influences such as selective attention (Golob, Johnson, & Starr, 2002; Hillyard, Hink, Schwent, & Picton, 1973) and short-term memory load (Conley, Michalewski, & Starr, 1999; Golob & Starr, 2000). For example, attention to infrequent targets presented amidst frequent standard stimuli typically enhances N100 amplitude and decreases P200 amplitude (Crowley & Colrain, 2004). The modulation of auditory sensory potentials by attention and memory-related variables provides a rationale for exploring their relations to WMC, which has already received some support (Brumback et al., 2004, 2005).

Paradigms like the 3-stimulus oddball task are typically used to elicit the P300. The 3-stimulus oddball requires subjects to respond mentally or physically to an infrequent target presented amidst frequently occurring standard stimuli and infrequently occurring distracters. All stimuli elicit the obligatory auditory ERPs (P50, N100, and P200), whereas infrequent targets and distracters also elicit the P300. A large body of work supports the context updating model (Donchin, 1981; Donchin & Coles, 1988), which views the P300 as a reflection of the confluence of top-down factors (e.g., task goals, attentive control, and experience retained by short-term memory) relative to the bottom-up, sensory properties of the current stimulus. The top-down factors together form a model of the subject's recent experience, and the P300 is elicited when a stimulus, to some degree, violates the current model. Generally, P300 amplitude increases with stimulus rarity (Duncan-Johnson & Donchin, 1977, 1982; Johnson & Donchin, 1982; Squires, Squires, & Hillyard, 1975) and is sensitive to changes in working memory (Donchin, Kramer, & Wickens, 1986) and attentional resource allocation (Polich, 2007).

The P300 has two distinguishable subcomponents, each associated with unique scalp topography and attentional mechanism (Johnson, 1986; Polich, 2003). An infrequent, distracter stimulus not requiring a response elicits an earlier “P3a” peak which typically is largest over frontal/central regions (Friedman, Cycowicz, & Gaeta, 2001). The P3a has been associated with involuntary orientation (Escera, Alho, Schröger, & Winkler, 2000) and response inhibition (Azizian, Freitas, Watson, & Squires, 2006; Falkenstein, Hoormann, Christ, & Hohnsbein, 2000; Polich, 2012) for infrequent, novel and repetitive stimuli that are not relevant to the subject’s task (Spencer, Dien, Donchin, 2001). In comparison, infrequent targets elicit a later, more parietally distributed peak often called the “P3b” (Courchesne, Hillyard, & Galambos, 1975; Squires, Squires, & Hillyard, 1975). Amplitude of P3b is thought to reflect attentional resource allocation with respect to top-down goals stored in short-term memory (Donchin & Coles, 1988; Polich, 1996). Lastly, negative slow potentials that occur between ~100–400 ms are often observed in tasks demanding attentional resource allocation (Alho, Woods, Algazi, & Näätänen, 1992; Hillyard et al., 1973; Näätänen, 1991) and may reflect sustained attention to task-relevant information.

Present study

Using ERP and behavioral measures, we assessed attention control as a function of WMC. Selected ERPs were used to assess responses to stimuli associated with stimulus classification with respect to top-down goals (targets, nontargets) as well as bottom-up responses to distracter stimuli. The goal of this study was to determine whether neural responses associated with top-down control and bottom-up orienting underlie broad group differences in WMC. First, we assessed whether high WMC contributes to enhanced early stimulus discrimination (targets vs. nontargets) and/or reduced distracter processing (N100, P200). Second, we assessed for group differences in late resource allocation to task-relevant (target-P3b) and irrelevant (distracter-P3a) stimuli. Third, we tested for group differences in sustained processing of stimuli relevant to task goals stored in STM (nontarget slow wave).

Methods

Subjects

Thirty subjects ages 18 to 25 years were recruited from Tulane University and screened for normal hearing thresholds (0.5–8.0 hKz) using a Maico audiometer (Eden Prairie, MN). Mean age was 20.55 ($SD = 2.23$) years, and 16 were male. All subjects sat in front of a computer monitor in a sound attenuating, electrically shielded booth and completed two tasks: a computer-automated operation span task (OSPAN; Unsworth, Heitz, Schrock, & Engle, 2005) to assess working memory capacity and a 3-stimulus auditory oddball paradigm to assess attention control. EEG was recorded during performance of the oddball task.

Stimuli and procedures

Operation span task—Subjects were presented a mathematical operation (e.g., $(4*2) + 1 = ?$) followed by a numerical solution. Subjects selected “TRUE” if the numerical solution was correct or “FALSE” if it was not. After solving the operation, a letter (e.g., “T”) was

presented for 800 ms, followed by more alternating math operations and letters until the completion of a trial. A matrix of 12 possible letters was presented and subjects selected letters from the preceding trial in serial order. Subjects may select the word “BLANK” as a placeholder for a forgotten letter, or “CLEAR” to erase all selected letters. Upon completing recall, subjects selected “EXIT” and performance feedback was provided for 2,000 ms.

Subjects completed 75 trials (3–7 letters per trial). To account for individual differences in math computation and to prevent rehearsal, the available computation time was limited to each subject’s average solving time during a preceding practice session. Trials in which the subject did not complete the operation in the available time were counted as error. Subjects were instructed to maintain performance accuracy of at least 85% and were alerted whenever their performance dropped below that threshold.

Outcome measures were the sum of perfectly recalled sets (OSPAN score), total letters recalled, and math operation errors in speed and accuracy. A median-split defined low vs. high WMC. Although previous behavioral studies generated WMC groups based on upper and lower quartiles (see Conway et al., 2005), a median-split enabled us to use the full range of OSPAN scores for correlations and analyses.

Auditory oddball task—A modified 3-stimulus (target, nontarget, distracter) oddball paradigm (Combs & Polich, 2006) was administered under low and high perceptual load. Auditory stimuli were created using Adobe Audition 1.5 and rendered in 3-dimensional space along the horizontal azimuth using SLABscape (NASA). Infrequent pure tone targets (1,000 Hz, probability = .12) and frequent nontargets (probability = .76) were presented at 0° along the horizontal azimuth. Perceptual load was manipulated by varying nontarget frequency (low load = 500 Hz, high load = 950 Hz). White noise stimuli were also occasionally presented (100–10,000 Hz, probability = .12) to assess ERP responses to task-irrelevant distracters. The distracters were presented from one of three locations (probability = .04 per location): midline (0°) to match the location of nontargets and targets, or at far left or right locations ($\pm 90^\circ$). Stimuli were delivered at a fixed 2.0 s inter-stimulus interval (~60dB nHL, 200 ms duration). A total of eight stimulus blocks were presented (200 stimuli/block, 4 blocks/perceptual load condition), with presentation order of task conditions counterbalanced across subjects.

Subjects wore etymotic insert earphones and were given brief instructions for discriminating auditory stimuli under low and high perceptual load. In both conditions subjects were instructed to respond to targets by pressing a button with their dominant thumb. Button presses were classified as correct responses to targets (hits), target omissions (misses), or responses to nontargets or distracters (false alarms).

EEG recording and analysis

EEG recording was conducted inside a sound attenuating, electrically shielded booth during the auditory oddball task. EEG was digitized at 500 Hz (DC-100 Hz bandpass). Before testing, subjects were fitted for a 64-electrode cap containing Ag/AgCl electrodes with a reference electrode placed between CZ and CPZ. Four additional electrodes were placed

above and below the left eye, and lateral to the corners of each eye to track eye movement. Electrode impedances were < 10 kohms.

Raw EEG data were corrected for DC drifts and eye blink artifacts using Neuroscan software (Compumedics-Neuroscan, Charlotte, NC), and epochs were –500 to 1000 ms relative to stimulus onset. Potentials were digitally re-referenced in a linked mastoid configuration. ERPs were averaged as a function of WMC (low, high), stimulus-type (nontarget, target, distracter) and perceptual load (low, high). Distracter sounds were sub-averaged based on spatial location (–90, 0, +90°). In previous work we showed variations in P3a amplitude across attended locations (Golob & Holmes, 2011), however we found no notable differences in ERPs elicited by left vs. right distracters, nor when comparing peripheral ($\pm 90^\circ$) vs. midline distracters (0°). Thus, ERPs elicited from all distracter locations were averaged together. All distracter and nontarget single-trials not rejected because of artifact (< 10% of trials) or false hit responses were included in the respective ERP averages. Only correctly identified target trials were included in the target ERP average, which yielded a mean of 91.6 out of 96 possible trials across perceptual load conditions with no differences between WMC groups, $F(1, 27) = .55, p = .467$.

Event-related potentials were baselined from –100 to 0 ms and bandpass filtered (0.1–16 Hz, 12 dB down). Measures from midline electrodes were selected for quantitative analysis on the basis of previous studies showing maximal amplitudes at midline sites (Starr & Golob, 2006). The N100 was defined as the largest negative deflection between 80 and 180 ms, P200 as the first positive deflection following the N100 that occurred between 120 and 150 ms. If no P200 was found in that time window, the P200 was identified as the first positive peak following the N100 as long as it peaked before 300 ms. The P300 peaks were defined as largest positive peak to distracters (P3a) or targets (P3b) that followed the P200 and occurred between 250 and 500 ms. Note that there were clear P300 peaks within the defined latency range in both load conditions. Two window measures were used to capture mean amplitude of a negative slow wave from 200–298 ms (early slow wave) and 300–398 ms (late slow wave). These early and late slow wave measurements allowed for more precise characterization of slow wave activity that may change over time as a function of WMC and/or perceptual load.

Statistical Analysis

Behavioral measures on auditory oddball task included reaction time to targets, false alarms and target omissions, and were tested using Mixed Model ANOVA tests with factors of WMC (low, high) and perceptual load (low, high). Analysis of ERP measures used Mixed Model ANOVAs with factors of WMC (low, high), perceptual load (low, high), and stimulus type (nontarget, target). The specific factors in each ANOVA models are given in the Results section. Significance level was set at .05 for all analyses. Greenhouse-Geisser corrections were applied when appropriate as well as post hoc testing used paired *t* tests with Bonferroni correction for multiple comparisons.

Results

Behavior

One subject did not complete the auditory oddball task and was excluded from analyses. Performance data on operation span and auditory oddball tasks are shown in Table 1. OSPAN scores ranged from 19 to 75 correctly identified sets ($M = 52.4$). It was possible for subjects to have identical OSPAN scores. Subjects who scored less than the median (OSPAN = 55) were classified as low WMC ($n = 13$, $M = 39.38$, range = 19–52), and those who scored greater than or equal to the median were classified as high WMC ($n = 16$, $M = 62.94$, range = 55–75). OSPAN scores were positively correlated with total letters recalled, $r(27) = .96$, $p < .001$, and a negatively correlated with total math errors, $r(27) = -.51$, $p = .004$. As expected, total letters recalled and total math errors were negatively correlated, $r(27) = -.55$, $p = .002$, indicating a linear relationship between storage and processing abilities as measured by complex span tasks (Waters & Caplan, 1996).

Target reaction times were significantly longer under high perceptual load, $F(1, 27) = 29.68$, $p < .001$, as did target omissions, $F(1, 27) = 7.12$, $p = .013$, indicating that the manipulation of perceptual load was effective. There were no significant effects of WMC on behavior during the auditory task, thus any WMC differences in ERPs were not secondary to performance differences between groups.

Event-related potentials

Nontargets and targets: N100, P200 and P3b—Waveforms to target, nontarget and distracter stimuli are shown in Figure 1, and results from ANOVA outcomes for each ERP assessed are shown in Table 2. Amplitudes and latencies of the N100 and P200 were analyzed separately using 2 (WMC) $\times 2$ (stimulus type: nontargets, targets) $\times 2$ (load) ANOVA tests. Frontocentral topographies have been demonstrated for both peaks (Picton, Hillyard, Krausz & Galambos, 1974; Vaughan, Ritter & Simson, 1980), thus measures were taken from electrode sites that displayed maximum N100 (Fz) and P200 (Cz) amplitudes.

Average N100 amplitude to nontargets and targets are shown in Figure 2. There were significant interactions between stimulus type and WMC, $F(1, 27) = 7.60$, $p = .010$, and between stimulus type and perceptual load, $F(1, 27) = 8.56$, $p = .007$. Follow-up Bonferroni t tests with adjusted alpha levels of .0125 per test (.05/4) indicated smaller N100 amplitudes to nontargets vs. targets for high WMC, $F(1, 15) = 22.56$, $p < .001$, but not for low WMC, $F(1, 12) = 2.38$, $p = .149$. In addition, nontargets elicited smaller N100 amplitudes compared to targets under low load, $F(1, 28) = 19.46$, $p < .001$, but not under high load, $F(1, 28) = 4.39$, $p = .045$. There were main effects of stimulus and perceptual load with reduced N100 amplitudes to nontargets vs. targets, $F(1, 27) = 20.61$, $p < .001$, and larger amplitude under low vs. high perceptual load, $F(1, 27) = 30.55$, $p < .001$. There were no significant correlations between WMC and N100 amplitudes to nontargets or targets. Latency of N100 was longer for high WMC compared to low WMC, $F(1, 27) = 5.58$, $p = .026$, and for nontargets vs. targets, although stimulus differences varied with load, $F(1, 27) = 15.48$, $p < .001$. Bonferroni t tests with adjusted alpha of .025 per test (.05/2) showed latency

differences between nontargets vs. targets were highly significant under low load, $F(1, 28) = 19.74, p < .001$, and marginally significant under high load, $F(1, 28) = 5.64, p = .025$.

There were no effects of WMC on nontarget and target P200, however there were effects of load and stimulus type, with larger amplitudes under low vs. high perceptual load, $F(1, 27) = 6.19, p = .019$, and to nontargets vs. targets, $F(1, 27) = 10.17, p = .004$ (Figure 3). P200 latency showed a significant interaction between load and stimulus type, $F(1, 27) = 9.52, p = .005$. Bonferroni t tests with adjusted alpha of .025 per test (.05/2) revealed significantly longer latencies to nontargets vs. targets under low load, $F(1, 28) = 26.43, p < .001$, but not high load, $F(1, 28) = 3.57, p = .069$. There was also a main effect of stimulus with longer P200 latencies for nontargets vs. targets, $F(1, 27) = 16.53, p < .001$.

Target P3b was analyzed using a 2 (WMC) $\times$ 2 (load) ANOVA test. Measures were taken at Pz, as target P300 amplitude increased from frontal to parietal midline sites (Johnson, 1993). High perceptual load elicited longer P3b latencies, $F(1, 27) = 16.94, p < .001$, and smaller P3b amplitudes, $F(1, 27) = 28.01, p < .001$. Load effects on P3b amplitude seemed to be driven by load differences in high WMC, although the interaction between WMC and load was not significant, $F(1, 27) = 3.42, p = .076$.

Distracters: N100, P200, and P3a—Distracter N100 measures taken at Fz were analyzed using 2 (WMC) $\times$ 2 (load) ANOVA tests. Low WMC was associated with significantly larger distracter N100 amplitudes compared to high WMC, $F(1, 27) = 8.46, p = .007$ (Figure 2). There was also a significant effect of load due to smaller N100 amplitudes, $F(1, 27) = 10.10, p = .004$, and longer latencies, $F(1, 27) = 14.10, p < .001$, in the high load condition. Correlation analyses with Bonferroni adjusted alpha levels of .025 per test (.05/2) showed a negative relationship between OSPAN scores and N100 amplitude that approached significance under low load, $r(27) = .40, p = .033$, but was significant under high load, $r(27) = .54, p = .003$, with smaller N100 amplitudes associated with larger OSPAN scores. Post-hoc polynomial regressions suggested a linear trend between N100 amplitude and OSPAN that was significant under low load, $R^2 = .16, F(1, 27) = 5.05, p = .033$, and high load, $R^2 = .29, F(1, 27) = 11.04, p = .003$. Whereas, curvilinear trend was less significant (low load: $R^2 = .17, F(1, 26) = 2.70, p = .086$; high load: $R^2 = .32, F(1, 26) = 5.96, p = .007$).

Separate 2 (WMC) $\times$ 2 (load) ANOVA tests were used to analyze distracter P200 and P3a measures taken at Cz, which elicited maximum peak amplitudes (Azizian et al., 2006; Falkenstein, Hoormann, & Hohnsbein, 1999; Vaughn, Ritter & Simson, 1980). There were no significant effects of WMC or load on distracter P200 amplitude, although there was a trend for longer latencies for low WMC, $F(1, 27) = 3.77, p = .063$, (Figure 3). There was a significant effect of load on P3a amplitude, $F(1, 27) = 12.87, p = .001$, that varied with WMC, $F(1, 27) = 5.25, p = .030$ (Figure 4). Bonferroni t tests with adjusted alpha levels of .025 per test (.05/2) revealed reduced P3a amplitude from low to high load for high WMC, $F(1, 15) = 15.37, p < .001$, but not for low WMC, $F(1, 12) = 1.12, p = .312$.

Negative slow wave—Comparisons of nontarget slow wave are shown in Figure 5. At fronto-central sites in the high load condition, nontarget slow wave was more negative from

about 200–400 ms relative to the low load condition (Figure 5A). Amplitudes during this time period were quantified by two time windows (200–298 ms and 300–398). A 2 (WMC) $\times 2$ (load) $\times 2$ (time) analysis at the Cz site showed significant interactions between WMC group and load, $F(1, 27) = 4.38, p = .046$, and between load and time, $F(1, 27) = 55.81, p < .001$. Bonferroni t tests with adjusted alpha levels of .0125 per test (.05/4) showed that load differences (low – high load) were significant for both WMC groups but were greater for high WMC, mean difference = 1.17, $F(1, 15) = 32.89, p < .001$, than for low WMC, mean difference = .61, $F(1, 12) = 14.43, p = .005$ (Figure 5B,C). High load elicited more negative slow wave amplitude from 200 to 300 ms, $F(1, 28) = 129.29, p < .001$, but not from 300 to 400 ms, $F(1, 28) = 2.15, p = .154$. There were main effects of load and time, with more amplitudes under high load, $F(1, 27) = 43.77, p < .001$, and during the second time window from 300 to 400 ms, $F(1, 27) = 34.23, p < .001$.

Discussion

This study tested whether auditory cortical responses associated with attention control varied with WMC and perceptual load. Differences between WMC groups were evident for the relatively early N100 as well as later P300 and slow wave. Compared to low WMC, high WMC displayed reduced N100 amplitude to nontargets vs. targets, and higher OSPAN scores predicted smaller N100 amplitude to distracters. Increases in perceptual load corresponded with reduced distracter-P3a amplitude and more prolonged negative slow wave for high WMC only. Aside from these group differences, increases in perceptual load generally reduced ERP amplitudes. Overall, the findings show that WMC is associated with individual differences in effective filtering of task-relevant information during relatively early (N100, P200) and later (P3a, slow wave) auditory stimulus discrimination, and that increasing perceptual demands affects both controlled and automatic attentional processes.

Effects of working memory capacity

Early N100 and P200—Relative to low WMC, high WMC was associated with reduced N100 amplitude to nontargets vs. targets and longer N100 latencies. These results are consistent with previous findings of larger amplitudes to visual targets and increased auditory N100 amplitude to target tones for high WMC (Brumback et al., 2004, 2005). It has been well-established that selective attention to sounds presented rapidly is associated with increases in the N100 and related auditory potentials that last ~400–500 ms (Hillyard et al., 1973; Näätänen & Picton, 1987). In addition to the involvement of primary and secondary auditory cortex, association regions including inferior parietal and inferior frontal cortex also show selective attention effects during this time period (Ross, Hillyard, & Picton, 2010). Thus relatively early sensory processing evident by the N100 may be only one aspect of a cortical network involved in attention control, a network that is engaged for at least several hundred ms after stimulus onset.

Early responses to distracters were similar, with reduced N100 amplitude in adults with high WMC. Furthermore, distracter N100 amplitude was negatively related to individual OSPAN scores. Given the role of the N100 in controlled attention, heightened responses to distracters suggest that adults with low WMC may be more inclined to attend to salient but

irrelevant information. These results are consistent with recent findings of higher WMC associated with smaller auditory brainstem responses to distracters under certain conditions (Sörqvist, Stenfelt, & Rönnerberg, 2012) as well as behavioral findings showing greater distracter interference for low WMC and better top-down control for high WMC (Reynolds & Desimone, 1999; Unsworth & Engle, 2007).

Later P300 and slow wave—WMC differences were also evident during later distracter processing. High perceptual load reduced distracter P3a amplitude, but only for subjects with high WMC. The P3a, which is associated with attentional orienting to infrequent, distracting stimuli (Friedman, Cycowicz, & Gaeta, 2001), typically has a fronto-central distribution (Knight, 1990; Polich & Criado, 2006) and may reflect frontal lobe involvement during inhibitory processing (Barceló, Suwazono, & Knight, 2000; Knight, 1997; Spencer, Dien, & Donchin, 2001). In general, the more distracting the stimulus, the larger the P3a amplitude (Muller-Gass, 2002), thus reduced P3a in high WMC may reflect less distractibility when top-down attention is allocated to task-relevant items. Current results differ from previous findings that show enhanced P3a with task difficulty (Combs & Polich, 2006) or no amplitude change (Frank, Yee, & Polich, 2012). Differences between these and the current findings may be due to task differences across studies.

Group differences in sustained processing were assessed by measuring negative slow wave to nontargets. Slow wave amplitude was more negative for high vs. low WMC particularly under high perceptual load. Increased negative slow wave amplitude has been associated previously with selective attention (Alho et al., 1992; Hillyard et al., 1973; Näätänen, 1991) and memory load (Ruchkin, Johnson, Canoune, & Ritter, 1990). Thus effects of nontarget processing may be somewhat longer-lasting for high WMC, especially when perceptual demands are high.

Storage vs. processing—Other studies have examined ERPs in relation to performance on visual change detection tasks that require brief retention (400ms) of information, also termed “working memory capacity”. Subjects with high short-term memory capacity displayed enhanced amplitudes to targets vs. distracters (Fukuda & Vogel, 2009, 2011) and greater increase in target amplitude with increasing set size (Vogel & Machizawa, 2004). Performance on storage tasks like the change detection task only modestly predicts higher-level cognition, unlike performance on complex span tasks like OSPAN which require both storage and processing functions (Conway, Jarrold, Kane, Miyake, & Towse, 2007; Daneman & Carpenter, 1980). Furthermore, latent variables derived from complex span tasks are strongly associated with broad aspects of higher cognition such as intelligence and reading comprehension, while variance in short-term storage is indirectly linked to higher cognition via its association with the complex span factor (Engle et al., 1999; Shelton, Elliott, Matthews, Hill, & Gouvier, 2010). Recent studies on visual working memory capacity have a similar pattern, with notable associations between storage plus processing ability and higher-level cognition (Cowan et al., 2005; Johnson et al., 2013; Shipstead, Redick, & Engle, 2012).

The present results showing that N100 amplitude in an auditory oddball task is associated with complex span WMC suggests a relation between the N100, attention, control and

processing rather than storage. However, there may be important similarities in attention control between some storage and complex span tasks (Cowan et al., 2005; Shipstead et al., 2012). Previous work has shown that in a short-term storage task auditory N100 amplitudes during retrieval are modulated by memory load (Conley et al., 1999; Golob & Starr, 2004). Thus, additional work is needed to delineate more precisely which cognitive processes involved in complex span performance are best related to sensory ERP measures.

Taken together, attenuated N100 amplitudes to nontargets and distracters, reduced P3a, and longer-lasting nontarget slow wave in adults with high WMC may indicate more effective filtering of task-relevant information, relative to low WMC. In addition to “proactive” attentional selection as in the current study, WMC may also be associated with “reactive” control in action monitoring (Braver, 2012). The error negativity (ERN), which is elicited on trials in which subjects commit an error (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991), has been shown to be larger in subjects with high vs. low WMC (Miller, Watson, & Strayer, 2012). Enhanced ERN is thought to reflect anterior cingulate cortex activity (Cohen, Botvinick, & Carter, 2000; Watson, Lambert, Miller, & Strayer, 2011), and is also implicated in attention control (Mesulam, 1990; Posner & Rothbart, 1998). These ERP findings suggest that WMC may be associated with several points of cognitive control during task performance, including early sensory responses, attentional modulation of sensory processing, and subsequent action monitoring. The influence of top-down factors such as WMC on sensory responses highlights recent movements in cognitive hearing science towards examining automatic processes and high-level cognitive functions conjunctively rather than in isolation (Arlinger, Lunner, Lyxell, & Pichora-Fuller, 2009).

Effects of perceptual load

Perceptual load influenced all measured ERPs, with larger amplitudes in the low vs. high load condition. There were also latency differences for some ERPs, with longer target latencies in the high load condition (P3b) and longer distracter latencies in the low load condition (N100). These load effects were sometimes modulated by stimulus-type. When perceptual load was low, targets elicited larger N100 amplitudes and shorter N100 and P200 latencies compared to nontargets, thus high perceptual load attenuated any stimulus effects. Furthermore, dissociating targets from physically similar nontargets depletes attentional resources (Lavie & Cox, 1997; Lavie et al., 2004), an effect that may be independent of individual WMC. Similar reductions in N100 and P200 amplitudes are seen in other tasks, such as smaller amplitudes during dichotic vs. passive listening (Yurgil & Golob, 2010).

Increased load also affected target and distracter processing. High perceptual load has been associated previously with reduced P3a (Harmony et al., 2000; Muller-Gass & Schröger, 2007) and P3b (Comerchero & Polich, 1999; Gaál, Csuhaj, & Molnár, 2007), which may reflect engagement of top-down attention control (Johnson, 1986). High perceptual load also elicited longer reaction times and more target omissions, which is in accordance with previous findings (Comerchero & Polich, 1999).

As with previous work (Combs & Polich, 2006), perceptual load varied with nontarget frequency. Auditory cortical regions retain the topographic organization established in the cochlea (Woolsey & Walzl, 1942), which can be detected with source localization

techniques based on scalp EEG and magnetoencephalographic data (Verkindt, Bertrand, Perrin, Echallier, & Pernier, 1995; Zouridakis, Simos, & Papanicolaou, 1998). In general higher frequencies are associated with somewhat smaller N100 amplitudes and small shifts to a more frontal topography (Näätänen & Picton, 1987; Verkindt et al., 1995). Thus some of the difference in N100 and P200 amplitudes in low vs. high load may relate to differences in the nontarget frequencies. Load effects on targets are not subject to the same uncertainty because target frequency was fixed across load conditions. Therefore, smaller P300 amplitudes and longer latencies under high load likely reflect cognitive processes implicated in stimulus discrimination.

Conclusion

In summary, the present findings suggest that WMC contributes to individual differences in ERPs associated with attention during an auditory oddball task. Neural activity in adults with high WMC reflected less distractibility, better early top-down control, and more sustained processing of task-relevant items relative to low WMC.

Acknowledgments

The authors would like to thank Dr. Emily Elliott, Louisiana State University, for her expertise on working memory, and Debra Karhson, Laura Manning, Jeremy Nelson and Carrie Pauker, Tulane University, for their assistance on this project. This work was supported the National Science Foundation, BCS-0844961.

References

- Alho K, Woods DL, Algazi A, Näätänen R. Intermodal selective attention. II. Effects of attentional load on processing of auditory and visual stimuli in central space. *Electroencephalography and Clinical Neurophysiology*. 1992; 82:356–368. [http://dx.doi.org/10.1016/0013-4694\(92\)90005-3](http://dx.doi.org/10.1016/0013-4694(92)90005-3). [PubMed: 1374704]
- Arlinger S, Lunner T, Lyxell B, Pichora-Fuller MK. The emergence of cognitive hearing science. *Scandinavian Journal of Psychology*. 2009; 50:371–384. <http://dx.doi.org/10.1111/j.1467-9450.2009.00753.x>. [PubMed: 19778385]
- Azizian A, Freitas AL, Watson TD, Squires NK. Electrophysiological correlates of categorization: P300 amplitude as index of target similarity. *Biological Psychology*. 2006; 71:278–288. <http://doi.org/10.1016/j.biopsycho.2005.05.002>. [PubMed: 16043279]
- Baddeley, A.; Hitch, G. Working memory. In: Bower, GH., editor. *The psychology of learning and motivation: Advances in research and theory*. Vol. 8. New York, NY: Academic Press; 1974. p. 47-87. Retrieved from <http://www.citeulike.org/group/890/article/633449>
- Barceló F, Suwazono S, Knight RT. Prefrontal modulation of visual processing in humans. *Nature Neuroscience*. 2000; 3:399–403. <http://dx.doi.org/10.1038/73975>.
- Beilock SL, Carr TH. When high-powered people fail: Working memory and “choking under pressure” in math. *Psychological Science*. 2005; 16:101–105. <http://dx.doi.org/10.1111/j.0956-7976.2005.00789.x>. [PubMed: 15686575]
- Braver TS. The variable nature of cognitive control: A dual mechanisms framework. *Trends in Cognitive Sciences*. 2012; 16:106–113. <http://dx.doi.org/10.1016/j.tics.2011.12.010>. [PubMed: 22245618]
- Brumback CR, Low KA, Gratton G, Fabiani M. Sensory ERPs predict differences in working memory span and fluid intelligence. *Neuroreport*. 2004; 15:373–376. <http://dx.doi.org/10.1097/00001756-200402090-00032>. [PubMed: 15076771]
- Brumback CR, Low KA, Gratton G, Fabiani M. Putting things into perspective: Individual differences in working-memory span and the integration of information. *Experimental Psychology*. 2005; 52:21–30. <http://dx.doi.org/10.1027/1618-3169.52.1.21>. [PubMed: 15779527]

- Cohen JD, Botvinick M, Carter CS. Anterior cingulate and prefrontal cortex: Who's in control? *Nature Neuroscience*. 2000; 3:421–423. <http://dx.doi.org/10.1038/74783>.
- Colflesh GJH, Conway ARA. Individual differences in working memory capacity and divided attention in dichotic listening. *Psychonomic Bulletin & Review*. 2007; 14:699–703. <http://dx.doi.org/10.3758/BF03196824>. [PubMed: 17972736]
- Combs LA, Polich J. P3a from auditory white noise stimuli. *Clinical Neurophysiology*. 2006; 117:1106–1112. <http://dx.doi.org/10.1016/j.clinph.2006.01.023>. [PubMed: 16564203]
- Comerchero MD, Polich J. P3a and P3b from typical auditory and visual stimuli. *Clinical Neurophysiology*. 1999; 110:24–30. [http://dx.doi.org/10.1016/S0168-5597\(98\)00033-1](http://dx.doi.org/10.1016/S0168-5597(98)00033-1). [PubMed: 10348317]
- Conley EM, Michalewski HJ, Starr A. The N100 auditory cortical evoked potential indexes scanning of auditory short-term memory. *Clinical Neurophysiology*. 1999; 110:2086–2093. [http://dx.doi.org/10.1016/S1388-2457\(99\)00183-2](http://dx.doi.org/10.1016/S1388-2457(99)00183-2). [PubMed: 10616113]
- Conway ARA, Cowan N, Bunting MF. The cocktail party phenomenon revisited: The importance of working memory capacity. *Psychonomic Bulletin & Review*. 2001; 8:331–335. <http://dx.doi.org/10.3758/BF03196169>. [PubMed: 11495122]
- Conway, ARA.; Jarrold, C.; Kane, MJ.; Miyake, A.; Towse, JN. Variation in working memory: An introduction. In: Conway, ARA.; Jarrold, C.; Kane, MJ.; Miyake, A.; Towse, JN., editors. *Variation in working memory*. New York, NY: Oxford University Press; 2007. p. 3-20.
- Conway ARA, Kane MJ, Bunting MF, Hambrick DZ, Wilhelm O, Engle RW. Working memory span tasks: A methodological review and user's guide. *Psychonomic Bulletin & Review*. 2005; 12:769–786. <http://dx.doi.org/10.3758/BF03196772>. [PubMed: 16523997]
- Courchesne E, Hillyard SA, Galambos R. Stimulus novelty, task relevance and the visual evoked potential in man. *Electroencephalography and Clinical Neurophysiology*. 1975; 39:131–43. [http://dx.doi.org/10.1016/0013-4694\(75\)90003-6](http://dx.doi.org/10.1016/0013-4694(75)90003-6). [PubMed: 50210]
- Cowan, N. An embedded-processes model of working memory. In: Miyake, A.; Shah, P., editors. *Models of working memory: Mechanisms of active maintenance and executive control*. New York, NY: Cambridge University Press; 1999. p. 62-101. <http://dx.doi.org/10.1017/CBO9781139174909.006>
- Cowan N, Elliott EM, Saults JS, Morey CC, Mattox S, Hismjatullina A, Conway ARA. On the capacity of attention: Its estimation and its role in working memory and cognitive aptitudes. *Cognitive Psychology*. 2005; 51:42–100. <http://dx.doi.org/10.1016/j.cogpsych.2004.12.001>. [PubMed: 16039935]
- Crowley KE, Colrain IM. A review of the evidence for P2 being an independent component process: Age, sleep and modality. *Clinical Neurophysiology*. 2004; 115:732–744. <http://dx.doi.org/10.1016/j.clinph.2003.11.021>. [PubMed: 15003751]
- Daneman M, Carpenter PA. Individual differences in working memory and reading. *Journal of Verbal Learning and Verbal Behavior*. 1980; 19:450–466. [http://dx.doi.org/10.1016/S0022-5371\(80\)90312-6](http://dx.doi.org/10.1016/S0022-5371(80)90312-6).
- Desimone R. Neural mechanisms for visual memory and their role in attention. *Proceedings of the National Academy of Sciences of the United States of America*. 1996; 93:13494–1349. <http://dx.doi.org/10.1073/pnas.93.24.13494>. [PubMed: 8942962]
- Desimone R, Duncan J. Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*. 1995; 18:193–222. <http://dx.doi.org/10.1146/annurev.ne.18.030195.001205>.
- Donchin E. Surprise!... Surprise? *Psychophysiology*. 1981; 18:493–513. <http://dx.doi.org/10.1111/j.1469-8986.1981.tb01815.x>. [PubMed: 7280146]
- Donchin E, Coles MGH. Is the P300 component a manifestation of context updating? *Brain Behavioral Science*. 1988; 11:357–374. <http://dx.doi.org/10.1017/S0140525X00058027>.
- Donchin, E.; Kramer, AF.; Wickens, CD. Applications of event related brain potentials to problems in engineering psychology. In: Coles, MGH.; Donchin, E.; Porges, SW., editors. *Psychophysiology: Systems, processes, and applications*. New York, NY: Guilford; 1986. p. 702-718.
- Duncan J. The locus of interference in the perception of simultaneous stimuli. *Psychological Review*. 1980; 87:272–300. <http://dx.doi.org/10.1037/0033-295X.87.3.272>. [PubMed: 7384344]

- Duncan J. Converging levels of analysis in the cognitive neuroscience of visual attention. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*. 1998; 353:1307–1317. <http://dx.doi.org/10.1098/rstb.1998.0285>.
- Duncan-Johnson CC, Donchin E. On quantifying surprise: The variation in event-related potentials with subjective probability. *Psychophysiology*. 1977; 14:456–467. <http://dx.doi.org/10.1111/j.1469-8986.1977.tb01312.x>. [PubMed: 905483]
- Duncan-Johnson CC, Donchin E. The P300 component of the event-related brain potential as an index of information processing. *Biological Psychology*. 1982; 14:1–52. [http://dx.doi.org/10.1016/0301-0511\(82\)90016-3](http://dx.doi.org/10.1016/0301-0511(82)90016-3). [PubMed: 6809064]
- Elward RL, Wilding EL. Working memory capacity is related to variations in the magnitude of an electrophysiological marker of recollection. *Brain Research*. 2010; 1342:55–62. <http://dx.doi.org/10.1016/j.brainres.2010.04.040>. [PubMed: 20423706]
- Engle RW. Working memory capacity as executive attention. *Current Directions in Psychological Science*. 2002; 11:19–23. <http://dx.doi.org/10.1111/1467-8721.00160>.
- Engle RW, Kane MJ. Executive attention, working memory capacity, and a two-factor theory of cognitive control. *Psychology of Learning and Motivation*. 2003; 44:145–199. [http://dx.doi.org/10.1016/S0079-7421\(03\)44005-X](http://dx.doi.org/10.1016/S0079-7421(03)44005-X).
- Engle, RW.; Kane, MJ.; Tuholski, SW.; Miyake, A.; Shah, P. Individual differences in working memory capacity and what they tell us about controlled attention, general fluid intelligence, and functions of the prefrontal cortex. In: Miyake, A.; Shah, P., editors. *Models of working memory: Mechanisms of active maintenance and executive control*. New York, NY: Cambridge University Press; 1999. p. 102-134. <http://dx.doi.org/10.1017/CBO9781139174909.007>
- Escera C, Alho K, Schröger E, Winkler I. Involuntary attention and distractibility as evaluated with event-related brain potentials. *Audiology and Neuro-Otology*. 2000; 5:151–166. <http://dx.doi.org/10.1159/000013877>. [PubMed: 10859410]
- Falkenstein M, Hohnsbein J, Hoormann J, Blanke L. Effects of crossmodal divided attention on late ERP components. II. Error processing in choice reaction tasks. *Electroencephalography and Clinical Neurophysiology*. 1991; 78:447–455. [http://dx.doi.org/10.1016/0013-4694\(91\)90062-9](http://dx.doi.org/10.1016/0013-4694(91)90062-9). [PubMed: 1712280]
- Falkenstein M, Hoormann J, Christ S, Hohnsbein J. ERP components on reaction errors and their functional significance. A tutorial *Biological Psychology*. 2000; 51:87–107. [http://dx.doi.org/10.1016/S0301-0511\(99\)00031-9](http://dx.doi.org/10.1016/S0301-0511(99)00031-9).
- Falkenstein M, Hoormann J, Hohnsbein J. ERP components in Go/Nogo tasks and their relation to inhibition. *Acta Psychologica*. 1999; 101:267–291. [http://doi:10.1016/S0001-6918\(99\)00008-6](http://doi:10.1016/S0001-6918(99)00008-6). [PubMed: 10344188]
- Folk CL, Remington RW, Johnston JC. Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology*. 1992; 18:1033–1044. <http://dx.doi.org/10.1037/0096-1523.18.4.1030>.
- Folk CL, Remington RW, Wright JH. The structure of attentional control: Contingent attentional capture by apparent motion, abrupt onset, and color. *Journal of Experimental Psychology Human Perception and Performance*. 1994; 20:317–329. <http://dx.doi.org/10.1037/0096-1523.20.2.317>. [PubMed: 8189195]
- Friedman D, Cycowicz YM, Gaeta H. The novelty P3: An event-related brain potential (ERP) sign of the brain's evaluation of novelty. *Neuroscience and Biobehavioral Reviews*. 2001; 25:355–373. [http://dx.doi.org/10.1016/S0149-7634\(01\)00019-7](http://dx.doi.org/10.1016/S0149-7634(01)00019-7). [PubMed: 11445140]
- Fukuda K, Vogel EK. Human variation in overriding attentional capture. *Journal of Neuroscience*. 2009; 29:8726–8733. <http://dx.doi.org/10.1523/JNEUROSCI.2145-09.2009>. [PubMed: 19587279]
- Fukuda K, Vogel EK. Individual differences in recovery time from attentional capture. *Psychological Science*. 2011; 22:361–368. <http://dx.doi.org/10.1177/0956797611398493>. [PubMed: 21310945]
- Frank DW, Yee RB, Polich J. P3a from white noise. *International Journal of Psychophysiology*. 2012; 85:236–241. <http://dx.doi.org/10.1016/j.ijpsycho.2012.04.005>. [PubMed: 22542460]
- Gaál ZA, Csuhaj R, Molnár M. Age-dependent changes of auditory evoked potentials – effect of task difficulty. *Biological Psychology*. 2007; 76:196–208. <http://dx.doi.org/10.1016/j.biopsycho.2007.07.009>. [PubMed: 17767993]

- Golob EJ, Holmes JL. Cortical mechanisms of auditory spatial attention in a target detection task. *Brain Research*. 2011; 1384:128–139. [http://dx.doi.org/10.1016/S1388-2457\(01\)00713-1](http://dx.doi.org/10.1016/S1388-2457(01)00713-1). [PubMed: 21295017]
- Golob EJ, Irimajiri R, Starr A. Auditory cortical activity in amnesic mild cognitive impairment: Relationship to subtype and conversion to dementia. *Brain*. 2007; 130:740–752. <http://dx.doi.org/10.1093/brain/awl375>. [PubMed: 17293359]
- Golob EJ, Johnson JK, Starr A. Auditory event-related potentials during target detection are abnormal in mild cognitive impairment. *Clinical Neurophysiology*. 2002; 113:151–161. [http://dx.doi.org/10.1016/S1388-2457\(01\)00713-1](http://dx.doi.org/10.1016/S1388-2457(01)00713-1). [PubMed: 11801437]
- Golob EJ, Starr A. Age-related qualitative differences in auditory cortical responses during short-term memory. *Clinical Neurophysiology*. 2000; 111:2234–2244. [http://dx.doi.org/10.1016/S1388-2457\(00\)00468-5](http://dx.doi.org/10.1016/S1388-2457(00)00468-5). [PubMed: 11090777]
- Goodin DS, Squires KC, Henderson BH, Starr A. Age-related variations in evoked potentials to auditory stimuli in normal human subjects. *Electroencephalography and Clinical Neurophysiology*. 1978; 44:447–458. [http://dx.doi.org/10.1016/0013-4694\(78\)90029-9](http://dx.doi.org/10.1016/0013-4694(78)90029-9). [PubMed: 76553]
- Harmony T, Bernal J, Fernández T, Silva-Pereyra J, Fernández-Bouzas A, Marosi E, Reyes A. Primary task demands modulate P3a amplitude. *Cognitive Brain Research*. 2000; 9:53–60. [http://dx.doi.org/10.1016/S0926-6410\(99\)00044-0](http://dx.doi.org/10.1016/S0926-6410(99)00044-0). [PubMed: 10666557]
- Hillyard SA, Hink RF, Schwent VL, Picton TW. Electrical signs of selective attention in the human brain. *Science*. 1973; 182:177–180. <http://dx.doi.org/10.1126/science.182.4108.177>. [PubMed: 4730062]
- Jeon YW, Polich J. Meta-analysis of P300 schizophrenia studies: Patients, paradigms and practical implications. *Psychophysiology*. 2003; 40:684–701. <http://dx.doi.org/10.1111/1469-8986.00070>. [PubMed: 14696723]
- Johnsen AM, Briggs GE. On the locus of display load effects in choice reactions. *Experimental Psychology*. 1973; 99:266–271. <http://dx.doi.org/10.1037/h0034632>.
- Johnson MK, McMahon RP, Robinson BM, Harvey AN, Hahn B, Leonard CJ, Gold JM. The relationship between working memory capacity and broad measures of cognitive ability in healthy adults and people with schizophrenia. *Neuropsychology*. 2013; 27:220–229. <http://dx.doi.org/10.1037/a0032060>. [PubMed: 23527650]
- Johnson R. A triarchic model of P300 amplitude. *Psychophysiology*. 1986; 23:367–384. <http://dx.doi.org/10.1111/j.1469-8986.1986.tb00649.x>. [PubMed: 3774922]
- Johnson R. On the neural generators of the P300 component of the event-related potential. *Psychophysiology*. 1993; 30:90–97. <http://dx.doi.org/10.1111/j.1469-8986.1993.tb03208.x>. [PubMed: 8416066]
- Johnson R, Donchin E. Sequential expectancies and decision-making in a changing environment: An electrophysiological approach. *Psychophysiology*. 1982; 19:183–200. <http://dx.doi.org/10.1111/j.1469-8986.1982.tb02545.x>. [PubMed: 7071298]
- Kane MJ, Bleckley MK, Conway ARA, Engle RW. A controlled-attention view of working-memory capacity. *Journal of Experimental Psychology: General*. 2001; 130:169–183. <http://dx.doi.org/10.1037/0096-3445.130.2.169>. [PubMed: 11409097]
- Kane MJ, Brown LH, McVay JC, Silvia PJ, Myin-Germeys I, Kwapił TR. For whom the mind wanders, and when: An experience-sampling study of working memory and executive control in daily life. *Psychological Science*. 2007; 18:614–621. <http://dx.doi.org/10.1111/j.1467-9280.2007.01948.x>. [PubMed: 17614870]
- Kane MJ, Engle RW. Working-memory capacity, proactive interference, and divided attention: Limits on long-term memory retrieval. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2000; 26:336–358. <http://dx.doi.org/10.1037/0278-7393.26.2.336>.
- Kane MJ, Engle RW. Working-memory capacity and the control of attention: The contributions of goal neglect, response competition, and task set to Stroop interference. *Journal of Experimental Psychology: General*. 2003; 132:47–70. <http://dx.doi.org/10.1037/0278-7393.26.2.336>. [PubMed: 12656297]

- Kerr B. Processing demands during mental operations. *Memory & Cognition*. 1973; 1:401–412. <http://dx.doi.org/10.3758/BF03208899>. [PubMed: 24214632]
- Knight, RT. Neural mechanisms of event-related potentials: Evidence from human lesion studies. In: Rohrbaugh, J.; Parasuraman, R.; Johnson, R., editors. *Event-related brain potentials: Basic issues and applications*. New York, NY: Oxford University Press; 1990. p. 3-18.
- Knight RT. Distributed cortical network for visual attention. *Journal of Cognitive Neuroscience*. 1997; 9:75–91. <http://dx.doi.org/10.1162/jocn.1997.9.1.75>. [PubMed: 23968181]
- Lavie N. Perceptual load as a necessary condition for selective attention. *Journal of Experimental Psychology. Human Perception and Performance*. 1995; 21:451–468. <http://dx.doi.org/10.1037/0096-1523.21.3.451>. [PubMed: 7790827]
- Lavie N, Cox S. On the efficiency of visual selective attention: Efficient visual search leads to inefficient distractor rejection. *Psychological Science*. 1997; 8:395–398. <http://dx.doi.org/10.1111/j.1467-9280.1997.tb00432.x>.
- Lavie N, Hirst A, De Fockert JW, Viding E. Load theory of selective attention and cognitive control. *Journal of Experimental Psychology: General*. 2004; 133:339–354. <http://dx.doi.org/10.1037/0096-3445.133.3.339>. [PubMed: 15355143]
- McCabe DP, Roediger HL, McDaniel MA, Balota DA, Hambrick DZ. The relationship between working memory capacity and executive functioning: Evidence for a common executive attention construct. *Neuropsychology*. 2010; 24:222–243. <http://dx.doi.org/10.1037/a0017619>. [PubMed: 20230116]
- Mesulam MM. Large-scale neurocognitive networks and distributed processing for attention, language, and memory. *Annals of Neurology*. 1990; 28:597–613. <http://dx.doi.org/10.1002/ana.410280502>. [PubMed: 2260847]
- Miller AE, Watson JM, Strayer DL. Individual differences in working memory capacity predict action monitoring and the error-related negativity. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2012; 38:757–763. <http://dx.doi.org/10.1037/a0026595>.
- Muller-Gass A. Event-related potential measures of the inhibition of information processing: I. Selective attention in the waking state. *International Journal of Psychophysiology*. 2002; 46:177–195. [http://dx.doi.org/10.1016/S0167-8760\(02\)00111-3](http://dx.doi.org/10.1016/S0167-8760(02)00111-3). [PubMed: 12445947]
- Muller-Gass A, Schröger E. Perceptual and cognitive task difficulty has differential effects on auditory distraction. *Brain Research*. 2007; 1136:169–177. <http://dx.doi.org/10.1016/j.brainres.2006.12.020>. [PubMed: 17223092]
- Näätänen R. Mismatch negativity outside strong attentional focus: A commentary on Woldorff et al. 1991. *Psychophysiology*. 1991; 28:478–484. <http://dx.doi.org/10.1111/j.1469-8986.1991.tb00735.x>. [PubMed: 1745727]
- Näätänen R, Picton T. The N1 wave of the human electric and magnetic response to sound: A review and analysis of the component structure. *Psychophysiology*. 1987; 24:375–425. <http://dx.doi.org/10.1111/j.1469-8986.1987.tb00311.x>. [PubMed: 3615753]
- Nakano H, Saron C, Swaab TY. Speech and span: Working memory capacity impacts the use of animacy but not of world knowledge during spoken sentence comprehension. *Journal of Cognitive Neuroscience*. 2010; 22:2886–2898. <http://dx.doi.org/10.1162/jocn.2009.21400>. [PubMed: 19929760]
- Navon D. The locus of attentional selection: Is it early, late, or neither? *European Journal of Cognitive Psychology*. 1989; 1:47–68. <http://dx.doi.org/10.1080/09541448908403071>.
- Otten M, Van Berkum JJ. Does working memory capacity affect the ability to predict upcoming words in discourse? *Brain Research*. 2009; 1291:92–101. <http://dx.doi.org/10.1016/j.brainres.2009.07.042>. [PubMed: 19631622]
- Picton TW, Hillyard SA, Krausz HI, Galambos R. Human auditory evoked potentials. I: Evaluation of components. *Electroencephalography and Clinical Neurophysiology*. 1974; 36:179–190. [http://doi.org/10.1016/0013-4694\(74\)90155-2](http://doi.org/10.1016/0013-4694(74)90155-2). [PubMed: 4129630]
- Polich, J. P300 in the evaluation of aging and dementia. In: Brunia, CHM.; Mulder, G.; Verbaten, MN., editors. *Event-related brain potential research (EEG Suppl)*. Amsterdam: Elsevier; 1991. p. 304-323.

- Polich J. Meta-analysis of P300 normative aging studies. *Psychophysiology*. 1996; 33:334–353. <http://dx.doi.org/10.1111/j.1469-8986.1996.tb01058.x>. [PubMed: 8753933]
- Polich, J. Theoretical overview of P3a and P3b. In: Polich, J., editor. *Detection of change: Event-related potential and fMRI findings*. Boston, MA: Kluwer Academic Publishers; 2003. p. 83-98. http://dx.doi.org/10.1007/978-1-4615-0294-4_5
- Polich J. Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*. 2007; 118:2128–2148. <http://dx.doi.org/10.1016/j.clinph.2007.04.019>. [PubMed: 17573239]
- Polich, J. Neuropsychology of P300. In: Luck, SJ.; Kappenman, ES., editors. *Handbook of event-related potential components*. New York, NY: Oxford University Press; 2012. p. 159-188. Retrieved from <http://futureofeeg.wdfiles.com/local--files/start/JP2.pdf>
- Polich J, Criado JR. Neuropsychology and neuropharmacology of P3a and P3b. *International Journal of Psychophysiology*. 2006; 60:172–185. <http://dx.doi.org/10.1016/j.ijpsycho.2005.12.012>. [PubMed: 16510201]
- Posner MI, Rothbart MK. Attention, self-regulation and consciousness. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*. 1998; 353:1915–1927. <http://dx.doi.org/10.1098/rstb.1998.0344>.
- Reynolds JH, Desimone R. The role of neural mechanisms of attention in solving the binding problem. *Neuron*. 1999; 24:19–29. [http://dx.doi.org/10.1016/S0896-6273\(00\)80819-3](http://dx.doi.org/10.1016/S0896-6273(00)80819-3). [PubMed: 10677024]
- Ross B, Hillyard SA, Picton TW. Temporal dynamics of selective attention during dichotic listening. *Cerebral Cortex*. 2010; 20:1360–1371. <http://dx.doi.org/10.1093/cercor/bhp201>. [PubMed: 19789185]
- Ruchkin DS, Johnson R, Canoune H, Ritter W. Short-term memory storage and retention: An event-related brain potential study. *Electroencephalography and Clinical Neurophysiology*. 1990; 76:419–439. [http://dx.doi.org/10.1016/0013-4694\(90\)90096-3](http://dx.doi.org/10.1016/0013-4694(90)90096-3). [PubMed: 1699736]
- Shelton JT, Elliott EM, Matthews RA, Hill BD, Gouvier WD. The relationship of working memory, secondary memory, and general fluid intelligence: Working memory is special. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2010; 36:813–820. <http://dx.doi.org/10.1037/a0019046>.
- Shipstead Z, Redick TS, Engle RW. Is working memory training effective? *Psychological Bulletin*. 2012; 138:628–654. <http://dx.doi.org/10.1037/a0027473>. [PubMed: 22409508]
- Sörqvist P, Stenfelt S, Rönnerberg J. Working memory capacity and visual-verbal cognitive load modulate auditory-sensory gating in the brainstem: Toward a unified view of attention. *Journal of Cognitive Neuroscience*. 2012; 24:2147–2154. http://dx.doi.org/10.1162/jocn_a_00275. [PubMed: 22849400]
- Spencer KM, Dien J, Donchin E. Spatiotemporal analysis of the late ERP responses to deviant stimuli. *Psychophysiology*. 2001; 38:343–358. <http://dx.doi.org/10.1111/1469-8986.3820343>. [PubMed: 11347879]
- Squires NK, Squires KC, Hillyard SA. Two varieties of long-latency positive waves evoked by unpredictable auditory stimuli in man. *Electroencephalography and Clinical Neurophysiology*. 1975; 38:387–401. [http://dx.doi.org/10.1016/0013-4694\(75\)90263-1](http://dx.doi.org/10.1016/0013-4694(75)90263-1). [PubMed: 46819]
- Starr, A.; Golob, EJ. Cognitive factors modulating auditory cortical potentials. In: Burkard, R.; Don, M.; Eggermont, JJ., editors. *Auditory evoked potentials: Basic principles and clinical application*. Philadelphia, PN: Lippincott Williams & Wilkins; 2006. p. 508-525.
- Turner ML, Engle RW. Is working memory capacity task dependent? *Journal of Memory and Language*. 1989; 28:127–154. [http://dx.doi.org/10.1016/0749-596X\(89\)90040-5](http://dx.doi.org/10.1016/0749-596X(89)90040-5).
- Unsworth N, Engle RW. The nature of individual differences in working memory capacity: Active maintenance in primary memory and controlled search from secondary memory. *Psychological Review*. 2007; 114:104–132. <http://dx.doi.org/10.1037/0033-295X.114.1.104>. [PubMed: 17227183]
- Unsworth N, Heitz RP, Schrock JC, Engle RW. An automated version of the operation span task. *Behavior Research Methods*. 2005; 37:498–505. <http://dx.doi.org/10.3758/BF03192720>. [PubMed: 16405146]

- Unsworth N, Schrock JC, Engle RW. Working memory capacity and the antisaccade task: Individual differences in voluntary saccade control. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2004; 30:1302–1321. <http://dx.doi.org/10.1037/0278-7393.30.6.1302>.
- Vaughan, HG.; Arezzo, JC.; Picton, TW. The neural basis of event-related potentials. In: Picton, TW., editor. *Human event-related potentials*. Amsterdam: Elsevier; 1988. p. 45-96.
- Vaughan HG, Ritter W, Simson R. Topographic analysis of auditory event-related potentials. *Progress in Brain Research*. 1980; 54:279–285. [http://doi:10.1016/S0079-6123\(08\)61635-0](http://doi:10.1016/S0079-6123(08)61635-0). [PubMed: 7220926]
- Verhaeghen P, Marcoen A, Goossens L. Facts and fiction about memory aging: A quantitative integration of research findings. *Journal of Gerontology*. 1993; 48:157–171. <http://dx.doi.org/10.1093/geronj/48.4.P157>.
- Verkint C, Bertrand O, Perrin F, Echallier JF, Pernier J. Tonotopic organization of the human auditory cortex: N100 topography and multiple dipole model analysis. *Electroencephalography and Clinical Neurophysiology: Evoked Potentials Section*. 1995; 96:143–156. [http://dx.doi.org/10.1016/0168-5597\(94\)00242-7](http://dx.doi.org/10.1016/0168-5597(94)00242-7).
- Vogel EK, Machizawa MG. Neural activity predicts individual differences in visual working memory capacity. *Nature*. 2004; 428:748–751. <http://dx.doi.org/10.1038/nature02447>. [PubMed: 15085132]
- Waters GS, Caplan D. The measurement of verbal working memory capacity and its relation to reading comprehension. *The Quarterly Journal of Experimental Psychology*. 1996; 49:51–79. <http://dx.doi.org/10.1080/027249896392801>. [PubMed: 8920099]
- Watson, JM.; Lambert, AE.; Miller, AE.; Strayer, DL. The magical letters P, F, C, and sometimes U: The rise and fall of executive attention with the development of prefrontal cortex. In: Fingerman, K.; Berg, C.; Smith, J.; Antonucci, T., editors. *Handbook of lifespan psychology*. New York, NY: Springer; 2011. p. 407-436.
- Woolsey CN, Walzl EM. Topical projection of nerve fibres from local regions of the cochlea to the cerebral cortex of the cat. *Johns Hopkins Hospital Bulletin*. 1942; 71:315–344.
- Yurgil KA, Golob EJ. Neural activity before and after conscious perception in dichotic listening. *Neuropsychologia*. 2010; 48:2952–2958. <http://dx.doi.org/10.1016/j.neuropsychologia.2010.06.004>. [PubMed: 20542046]
- Zouridakis G, Simos PG, Papanicolaou AC. Multiple bilaterally asymmetric cortical sources account for the auditory N1m component. *Brain Topography*. 1998; 10:183–189. <http://dx.doi.org/10.1023/A:1022246825461>. [PubMed: 9562539]

Figure 1. ERP waveforms to target, nontarget and distracter stimuli under low and high perceptual load across midline electrode sites.

Figure 2.

N100 amplitude elicited by nontargets, targets, and distracters measured at electrode site Fz. On the left, amplitude to nontargets vs. targets differed between WMC groups ($p = .010$) and between perceptual load conditions ($p = .007$). On the right, amplitude to distracters was larger under low vs. high load ($p = .004$) and for low vs. high WMC ($p = .007$). Distracter N100 amplitude decreased as OSPAN score increased under low ($R^2 = .16$, $p = .033$) and high load ($R^2 = .29$, $p = .003$). Significance: * $p < .05$; ** $p < .01$; *** $p < .001$.

Figure 3.

P200 amplitude and latency elicited by nontargets, targets, and distracters measured at electrode site Cz. On the left, task-related P200 amplitude was larger under low vs. high load ($p = .019$) and to nontargets vs. targets ($p = .004$); P200 latency to nontargets vs. targets differed between perceptual load conditions ($p = .005$). On the right, there was a trend for longer latencies to distracters for low vs. high WMC ($p = .063$). Significance: * $p < .05$; ** $p < .01$; *** $p < .001$.

Figure 4.

P300 amplitude to targets (P3b) measured at Pz and to distracters (P3a) measured at Cz. On the left, target P3b amplitude was larger under low vs. high load ($p < .001$). On the right, distracter P3a amplitude was modulated by an interaction between load and WMC ($p = .030$). Significance * $p < .05$; ** $p < .01$; *** $p < .001$.

Figure 5.

Topographic distributions of amplitude differences (high – low load) in nontarget slow wave (A). Load difference across sites was greatest from 200–298ms, and slow wave amplitude at Cz was significantly more negative for high vs. low WMC under high load ($p < .05$) (B,C). Significance: * $p < .05$; ** $p < .01$; *** $p < .001$.

Table 1
Behavioral performance on OSPAN and auditory oddball tasks for low vs. high WMC

	Low WMC <i>n</i> = 13		High WMC <i>n</i> = 16		Total <i>n</i> = 29	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Operation Span ^a						
OSPAN Score	39.38	12.15	62.94	7.58	52.38	15.37
Total Letters	59.00	7.12	70.06	3.91	65.10	7.84
Math Errors %						
Speed	2.05	1.93	1.33	1.76	1.66	1.84
Accuracy	7.38	5.29	6.08	3.23	6.67	4.25
Auditory Oddball ^b						
Target RT (ms)						
Low load	421.07	65.57	421.65	70.87	421.39	67.33
High load	476.83	70.66	471.42	71.02	473.85	69.64
False Alarms %						
Low load	0.36	0.28	0.45	0.29	0.41	0.28
High load	0.35	0.25	0.36	0.21	0.36	0.23
Omissions %						
Low load	2.32	5.11	2.28	3.51	2.30	4.22
High load	8.65	9.77	5.40	10.01	6.86	9.86

^a Subjects with scores below the median OSPAN score (55) were classified as low WMC; those with scores at or above the median were classified as high WMC. OSPAN was positively correlated with total letters recalled, $r(27) = .96$, $p < .001$ and negatively correlated with total math errors, $r(27) = -.51$, $p = .004$. Total letters recalled and total math errors were negatively correlated, $r(27) = -.55$, $p = .002$.

^b High perceptual load in the auditory target detection task increased target reaction time ($p < .001$) and target omission errors ($p = .013$).

Table 2

F ratios from ANOVA results across ERP analyses

	N100 (Fz)		P200 (Cz)		P300		Slow Wave (Cz)	
	Target/Nontarget	Distracter	Target/Nontarget	Distracter	Distracter-P3a (Cz)	Target-P3b (Pz)	Nontarget	
Load	30.55***	10.10**	6.19*	1.29	12.87**	28.01***	43.77***	
Stimulus	20.61***	—	10.17**	—	—	—	—	
WMC	1.59	8.46**	1.51	2.07	0.00	1.01	3.70	
Load × Stimulus	8.56**	—	0.92	—	—	—	—	
Load × WMC	0.01	2.05	0.01	0.10	5.25*	3.42	4.38*	
Stimulus × WMC	7.60**	—	0.00	—	—	—	—	
Load × Stimulus × WMC	0.00	0.05	—	—	—	—	—	
Time	—	—	—	—	—	—	34.23***	
Load × Time	—	—	—	—	—	—	55.81***	
Time × WMC	—	—	—	—	—	—	0.13	
Load × Time × WMC	—	—	—	—	—	—	2.43	

All F ratios above were calculated using 1 (effect) and 27 (error) degrees of freedom. Post-hoc analyses for significant effects are discussed in text.

Significance:

* $p < .05$;

** $p < .01$;

*** $p < .00$