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Distinct mechanisms for the impact of distraction and interruption on working memory in aging

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Abstract

Interference is known to negatively impact the ability to maintain information in working memory (WM), an effect that is exacerbated with aging. Here, we explore how distinct sources of interference, i.e., *distraction* (stimuli to-be-ignored) and *interruption* (stimuli requiring attention), differentially influence WM in younger and older adults. EEG was recorded while participants engaged in three versions of a delayed-recognition task: no interference, a distracting stimulus, and an interrupting stimulus presented during WM maintenance. Behaviorally, both types of interference negatively impacted WM accuracy in older adults significantly more than younger adults (with a larger deficit for interruptions). N170 latency measures revealed that the degree of processing both distractors and interruptors predicted WM accuracy in both populations. However, while WM impairments could be explained by excessive attention to distractors by older adults (a suppression deficit), impairment induced by interruption were not clearly mediated by age-related increases in attention to interruptors. These results suggest that distinct underlying mechanisms mediate the impact of different types of external interference on WM in normal aging.

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1. Introduction

Working memory (WM) involves the ability to store and manipulate information in mind over brief periods of time (Baddeley, 2003).¹ WM involves multiple cognitive subsystems responsible for functions such as storage, rehearsal and executive functions (Miyake and Shah, 1999). While the rehearsal of information is a fundamental aspect of WM, executive control processes are necessary for optimal performance. This includes the ability to inhibit interference from information that intervenes during the period of mem-

ory maintenance (Sakai et al., 2002). Such interference has a negative impact on WM performance, likely due to disruption of active top-down control processes required to maintain relevant information (Baddeley, 1986; Sakai, 2003; Sakai and Passingham, 2004; Sreenivasan and Jha, 2007; Yoon et al., 2006), as well as bottom-up disruption of stimulus representations in sensory cortices (Miller et al., 1996).

Here we present a framework in which interference of WM maintenance may be caused by both internal (i.e., intrusions and diversions- internally generated thoughts/images (Forster and Lavie, 2009)) and external factors (i.e., distraction and interruption (Clapp et al., 2009)) (Fig. 1); the latter of which is the focus of the current study. *Distraction* involves encountered stimuli that are irrelevant and intended to be ignored (e.g., radio playing while attempting to rehearse a phone number). This filtering of irrelevant sensory input is thought to be dependent on top-down suppression signals from the prefrontal cortex (PFC) (Chao and Knight, 1995, 1998). *Interruption* by external interference involves intervening stimuli that are purposefully attended to as an aspect of a secondary task (e.g., a phone call while holding something in mind). An

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¹ While some cognitive psychologists use the term short-term memory to refer to tasks requiring only maintenance processes and reserve the term working memory for tasks requiring maintenance plus processing (e.g., manipulation, selection, updating), in the current manuscript the term working memory refers to the brief retention of information, with and without manipulation, when it is used to guide subsequent behavior.

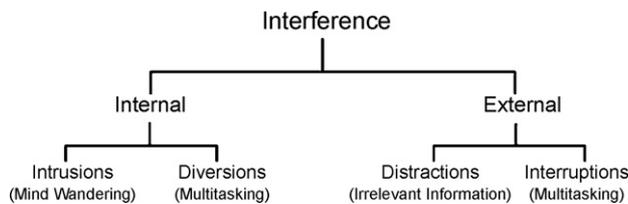


Fig. 1. Interference conceptual framework.

interruption requires a reallocation of cognitive resources, as well as processes involved in reactivating the disrupted representation afterwards, which is reliant on medial temporal lobe structures and the PFC (Sakai and Passingham, 2004; Sakai et al., 2002). For conceptual purposes, WM maintenance in the face of interruptions can be placed under the broader category of multitasking, which involves concurrently executed goal-directed operations (Salvucci and Taatgen, 2008; Salvucci et al., 2009). Recent network characterization with fMRI functional connectivity analysis revealed distinct mechanisms of influence by these two types of interference on WM maintenance (Clapp et al., 2009). Encoded information is retained throughout a maintenance period even in the presence of distraction via connectivity between the PFC and sensory cortex, while interruption results in a disruption of this connectivity, and reactivation in the post-interruption maintenance period. Given such distinct mechanisms, the impact of distraction and interruption on WM in older adults, as well as the underlying etiology of a negative influence by these two types of interference, may be different.

It has been well demonstrated that WM performance declines with age (Dobbs and Rule, 1989; Foos and Wright, 1992; Salthouse et al., 1991). However, it is believed that rote maintenance abilities are relatively spared in healthy aging (Craik and Jennings, 1992), and WM deficits are largely observed when executive processes are taxed (e.g., in the setting of interference or high memory load) (Gazzaley et al., 2007). Previous research has demonstrated that older adults have significant impairment in WM performance when they encounter interference, beyond that experienced by younger adults, (Gazzaley et al., 2008, 2005b; Reuter-Lorenz and Sylvester, 2005). Internal interference, or intrusions, have been reported to disrupt an older adults' ability to maintain information, as in studies of proactive interference (Emery et al., 2008; Lustig et al., 2001) and internally generated thoughts (Borella et al., 2007). External interference by distraction disrupts WM performance in older individuals (Hasher et al., 1999) and is attributed to a deficit in top-down suppression of irrelevant information early in the visual processing stream (Gazzaley et al., 2008, 2005b). To our knowledge, no previous studies have directly addressed the impact of interruptions on WM in an older population. However, it has been shown that older adults are more disadvantaged than younger individuals when they divide their attention (Craik and Salthouse, 2000; Crossley and Hiscock, 1992; Kramer et al., 1995; Kramer and Larish, 1996; McDowd and Craik, 1988; Park et al., 1989; Tsang and Shaner, 1998). These

differences persist even when controlled for age-related performance decrements on a single task (Crossley and Hiscock, 1992). Likewise, the ability to multitask diminishes in older adults, as assessed by driving simulations (Chaparro et al., 2005; Ponds et al., 1988), task management tests (Craik and Bialystok, 2006) and gait/posture experiments (Dumas et al., 2008; Faulkner et al., 2007).

The goal of this study was to explore the influence of these different types of external interference on WM in normal aging. To accomplish this, as well as to investigate the neural basis of any age-related behavioral effects, electroencephalography (EEG) was used to record neural activity as participants engaged in a cognitive paradigm assessing WM in the setting of distraction and interruption. Interference was introduced during the maintenance period of a simple delayed-recognition task. We performed this experiment in a group of healthy older participants and compared the data to those obtained from a population of younger adults who recently participated in the same experiment (Clapp et al., 2009). The inclusion of both types of external interference in the same experiment allows us to directly compare the consequences of age-related alterations in the suppression of irrelevant information and multitasking on WM performance. Neural analysis focused on early ERP measures associated with visual stimulus representation and attentional control

2. Methods

2.1. Participants

EEG was recorded from 24 healthy older participants (ages 61–82, mean 69.4 years) as they performed the experimental task. Participants had normal or corrected-to-normal vision, volunteered, gave consent, and were monetarily compensated to participate in the study. Participants were pre-screened, and none used any medication known to affect cognitive state. Three participant's neural and behavioral data were removed due to unacceptable noise in the EEG data.

In the experiment involving younger adults, EEG was recorded from 21 healthy younger participants (ages 18–30, mean 23.3, 14 males) as they performed the identical tasks (Clapp et al., 2009). One participant's neural and behavioral data were removed from analysis due to a failure to perform the task (no responses to probes), which was corroborated both behaviorally and neurally.

2.2. Neuropsychological testing

Participants in the older age group were screened to ensure intact executive and memory function. 11 neuropsychological tests were used, including: MMSE (Folstein et al., 1975), geriatric depression (Yesavage et al., 1982), visual-spatial function (copy of a modified Rey-Osterrieth figure), visual-episodic memory (memory for details of a modified Rey-Osterrieth figure), visual-motor sequencing (trail mak-

ing test A and B (Reitan, 1958; Tombaugh, 2004), phonemic fluency (words beginning with the letter ‘D’), semantic fluency (animals), calculation ability (arithmetic), executive functioning (Stroop interference test; Stroop, 1935), working memory and incidental recall (backward digit span and digit symbol, WAIS-R (Wechsler, 1987)). Intact function was assessed as within 1.75 standard deviations of the norm on each of the tests listed above. The neuropsychological test battery was administered on the same day as the EEG session in only 4 of the 21 participants. In all others it was administered during previous visit. Participants that performed the battery and the EEG session in the same day did not show a behavioral difference in the main task when compared to the other 17 participants.

2.3. Stimuli

The stimuli consisted of grayscale images of faces and were novel across all tasks, all runs, and all trials of the experiment. There were a variety of neutral-expression male and female faces, representing a large age range. Hair and ears were removed digitally, and a blur was applied along the contours of the face so as to remove any potential non-face-specific cues. All images were 225 pixels wide and 300 pixels tall (14 cm × 18 cm) and were presented foveally, subtending 3 degrees of visual angle.

2.4. Paradigm

This study used the same delayed-recognition paradigm utilized in Clapp et al. (2009). The paradigm consisted

of four distinct tasks presented in blocks; No Interference (NI—one-item delayed-recognition task), Distracting Stimulus (DS—participants were instructed that an interfering stimulus in the delay period was entirely irrelevant and should be ignored), Interrupting Stimulus (IS—participants were instructed to make a judgment about an interfering stimulus in the delay period) and Passive View (PV—no memory or attention requirements). An instruction slide was presented to participants before each block began, informing them of which of the four tasks they would be performing for the duration of the block (Fig. 2). Each trial began with the presentation of face picture displayed for 800 ms (Cue), followed by a delay period (6 s) and ended with the presentation of a face picture displayed for 1 s (Probe). The participants were instructed to make a match/non-match button press response to the probe as quickly as possible (right for match, left for non-match), without sacrificing accuracy. This was followed by a self-paced inter-trial interval (ITI) and instructions to remind the participants of which task they were performing. In the DS and IS tasks, the presentation of a face stimulus, displayed for 800 ms (Interference), occurred in the middle of the delay period. The interfering stimulus was jittered between 2.8 and 3.2 s after the cue. This defined a pre-interference delay period (D1—2.8–3.2 s) and post-interference delay period (D2—2.8–3.2 s),

In the DS task, participants were instructed to ignore the interfering face stimulus while maintaining the representation of the cued face in mind. In the IS task, participants were asked to judge whether the interfering face stimulus was of a male over the age of 40 years and indicate their response with a button press (both buttons pressed if it was a male over 40

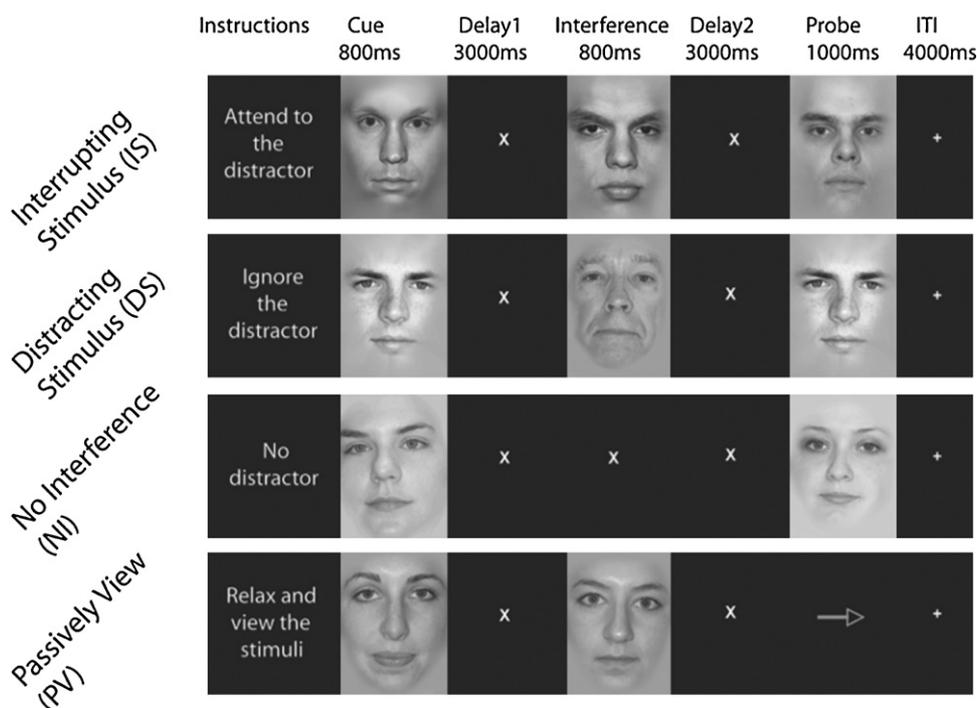


Fig. 2. Experimental paradigm. All participants performed 4 tasks, which were blocked and counterbalanced.

years, otherwise no response, i.e. for a female, or a male under 40 years). Ten percent of the trials in IS were catch trials, where the interfering face stimulus was a male over 40 years old. These trials were removed from further analysis because they were confounded by a motor response as compared to all other interfering face stimuli. An additional 4 trials (11%) were included in this task to account for these discarded trials. In the PV control task, participants were instructed not to memorize either face stimuli. At the probe, participants saw an arrow and made a button press indicating the direction it was facing (this balanced the demands for a decision-driven motor response at probe in the other tasks). Each task block was counterbalanced and repeated twice, with 40 trials in each block. These parameters were chosen in order to collect 80 trials of data for each task and keep the recording time under 1(1/2) h.

Incidental long-term memory (LTM) was assessed by a surprise post-experiment recognition test. Following the main experiment, participants participated in a post-experiment recognition test in which they viewed 350 face stimuli, which included 30 Cue faces from each task and 30 interfering faces from DS, IS and PV tasks. In addition, 140 face stimuli were used that were novel and not included in the main experiment. No cue stimuli were included that were also a match during the main experiment (i.e., no stimulus in the post-experiment test was viewed more than once in the main experiment). All stimuli (both novel stimuli and stimuli from the experiment) were randomly ordered, and the participants were asked to give a confidence judgment as to whether each image was old or new (1 = definitely new, 2 = probably new, 3 = probably old 4 = definitely old). This section of the experiment was self-paced.

2.5. Electrophysiological recordings

Electrophysiological signals were recorded at 1024 Hz through a 24-bit BioSemi ActiveTwo 64-channel Ag–AgCl active electrode EEG acquisition system (Cortech Solutions, LLC). Electrode offsets were maintained between ± 20 mV. Raw EEG data were referenced to the average off-line. All preprocessing and further analyses were completed using BrainVision Analyzer (Brain Vision, LLC). Eye movement artifacts were removed through an independent component analysis by excluding components consistent with topographies for blinks and eye movements and the electrooculogram time-series. One-second epochs were extracted from the data beginning 200 ms pre-stimulus onset and ending 800 ms post-stimulus onset. The 200 ms before stimulus onset was used to baseline-correct the epochs. Epochs were then removed if they displayed excessive peak-to-peak deflections (± 50 μ V), amplifier clipping or other artifacts. Epochs from all trials were then categorized by task, filtered (1–30 Hz), and averaged (note: .1–30 Hz filter was also used, and the data were unaffected). Only epochs from the cue and interfering stimuli were analyzed in this study.

Neural dependent measures were peak amplitudes and latencies of stimulus-locked event-related potentials (ERPs). ERP peak amplitudes and latencies were obtained from lateral occipito-temporal scalp sites over pre-selected latency ranges. Peak amplitudes/latencies were selected from electrodes of interest (EOI: see localizer section) for each individual as the largest positive/negative deflection within the following time windows for each ERP (P100—positive deflection between 80 and 140 ms, N170—negative deflection between 140 and 240 ms). Peak amplitude was calculated as the average amplitude within an 8 ms area centered around the peak amplitude deflection (± 4 ms) for each individual. Across-participant statistics were calculated using peak amplitudes and latencies obtained from each participant. Analyses involving paired *t*-tests and utilized a false-discovery rate correction for multiple comparisons (Benjamini and Hochberg, 1995).

2.6. Statistical analyses

Analyses were performed on ERPs stimulus-locked to cue and interfering faces. For ERP analyses, peak amplitude and latency of the P100 and N170 components were analyzed at the electrode of interest, as described below. An Analysis of Variance (ANOVA) for task \times age was performed on each of the neural markers of interest with Greenhouse–Geisser correction for sphericity when appropriate. Post hoc analysis consisted of both within-group, paired-sample *t*-tests (two-sided) and across-group, unpaired *t*-tests of task data, of both stimulus-based measures and modulation indices (enhancement and suppression) ($p < .05$). Post hoc analyses were corrected for multiple comparisons with a false-discovery rate (FDR) correction (Benjamini and Hochberg, 1995).

2.7. Electrode of interest

A within-experiment localization procedure to detect an electrode of interest (EOI) for each participant was performed by averaging responses to all face stimuli in the experiment (i.e., collapsing across all tasks: cue, interference and probe stimuli) (Berry et al., 2009; Clapp et al., 2009; Heinrich et al., 2005; Hoffmann et al., 1999, 2001; Rutman et al., in press). P100 and N170 EOIs were selected for each participant from a selection group of the lateral occipito-temporal electrodes (electrodes P10, PO8, P8, O2, P9, PO7, P7, and O1) as the maximal evoked response. P100 and N170 peaks were defined as the largest positive/negative (respectively) peak at the occipito-temporal electrodes within the following time windows: P100 80–140 ms, N170 140–240 ms. These time windows and the search for the EOI within the lateral occipito-temporal electrodes were guided by past studies investigating evoked responses to face stimuli (Goffaux et al., 2003; Herrmann et al., 2005)

2.8. Indices of attentional modulation

The following attentional modulation indices were used in the analyses: *Enhancement*—defined as the difference between activity measures associated with interruptors and passively viewed intervening stimuli and *Suppression*—defined as the difference between activity measures associated with passively viewed intervening stimuli and distractors. These measures were calculated such that a positive value *always* indicated greater enhancement above baseline or greater suppression below baseline. Thus, for P100 amplitude: enhancement = IS–PV, suppression = PV–DS, and for N170 latency indices: enhancement = PV–IS, suppression = DS–PV. The calculations were reversed to maintain the convention, since an earlier peak latency (lower number) is associated with enhancement and a later peak latency is associated with suppression (Gazzaley et al., 2005a).

2.9. Behavioral performance

Accuracy was calculated as the number of hits + correct rejections divided by the number of total trials within a condition. Reaction time data only includes correct responses; responses that were greater than 2.5 standard deviations from each individual's mean were removed from the analysis.

2.10. Practice effects

We analyzed the data for practice effects in the different tasks over the course of the experiment. Behavioral analyses involved comparisons of RT and accuracy between the two blocks of each task type, and neural analysis focused on comparisons of ERPs for the cue and interfering stimuli from the 40 trials in each of the two blocks. ANOVA and post hoc *t*-tests were utilized to establish the significance of practice effects.

3. Results

Results from the younger participants have been previously published (Clapp et al., 2009) and will be reported here for comparison purposes with data from the older participants.

3.1. Behavioral data

ANOVA of WM accuracy was performed with the three WM tasks (NI, DS, IS) as the within-participant factor and age (young, older) as the across-participant factor. This analysis revealed a main effect of task ($F(2,78) = 51.74, p < .001$), such that participants performed with high accuracy when no interference was present, exhibited a significant reduction in accuracy with the presence of a distractor (NI vs. DS; $p < .05$) and a further decline in performance in the setting of an interruptor (NI vs. IS, $p < .05$, IS vs. DS, $p < .05$) (Fig. 3A).

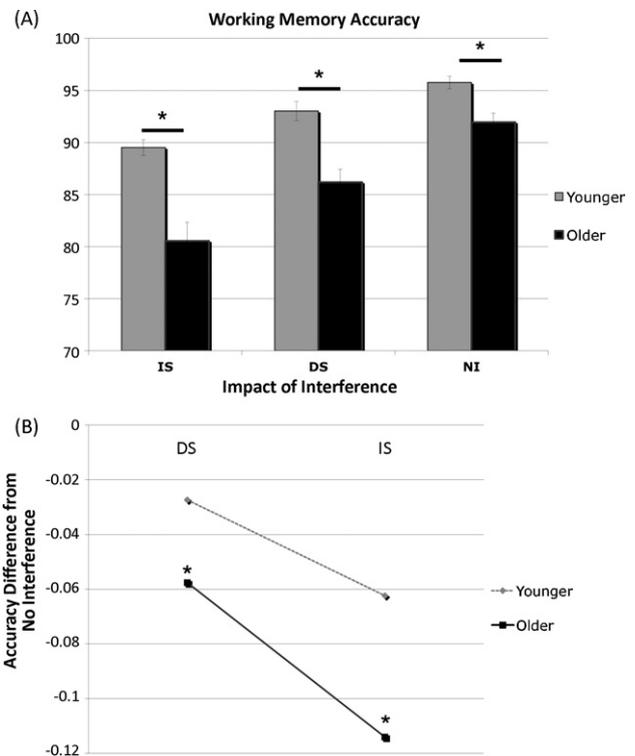


Fig. 3. Working memory accuracy and impact of interference. (A) Participants performed best in the no interference task (NI), followed by the distractor task (DS), and then the interruptor task (IS) (all comparisons are significantly different, $p < .05$). The older participants performed with a lower WM accuracy on all tasks. (B) Older participants have a greater impact on WM performance by both the distractor (DS) and the interruptor (IS), when corrected by their performance without interference ($p < .05$). Note: Asterisks represent significant differences between age groups.

Analysis also revealed a main effect of age ($F(1,39) = 25.40, p < .001$), such that older participants performed the WM tasks with lower accuracy. In addition, there was a significant task by age interaction ($F(2,78) = 4.48, p < .05$). Within-age group comparisons revealed that for both younger and older adults there was a WM accuracy decrement with the presence of a distractor and an interruptor (all comparisons; $p < .05$, see Table 1 for means and standard errors). Between-group comparisons showed that older participants performed worse than younger participants on all three WM tasks (all $p < 0.05$). Importantly, there was a disproportionately greater impact of both the distractor and interruptor on WM accuracy in the older group (NI–DS: younger vs. older, $p < .05$. NI–IS: younger vs. older, $p < .05$) (Fig. 3B). Furthermore, there was a disproportionately greater impact of the interruptor relative to the distractor in older, compared to younger participants (IS–DS: younger vs. older, $p < .05$) (Fig. 3B). All participants performed at or above 93% in the gender/age discrimination during the interruptor task.

The same ANOVA of WM reaction time, revealed a main effect of task ($F(2,78) = 23.061, p < .001$), such that participants performed with the fastest reaction times when no interference was present, exhibited a significant slowing in reaction time with the presence of a distractor, and further

Table 1
Comparisons of younger and older participants' behavioral and neural data. Standard errors are presented in parentheses.

	Younger	Older
Behavioral data		
Accuracy		
Interrupting stimulus	89% (.007)	81% (.02)
Distracting stimulus	93% (.01)	86% (.01)
No interference	96% (.006)	92% (.009)
Reaction time		
Interrupting stimulus	768 (28)	1200 (56)
No interference	675 (23)	1110 (62)
Neural data		
Encode		
P100 amplitude		
Interrupting stimulus	6.8 (0.6)	7.1 (0.6)
Distracting stimulus	6.5 (0.6)	6.7 (0.52)
No interference	6.3 (0.54)	7.2 (0.59)
Passive view	6.7 (0.58)	6.6 (0.6)
P100 latency		
Interrupting stimulus	107 (2.1)	117 (4)
Distracting stimulus	108 (2.1)	116 (3.8)
No interference	109 (2.2)	119 (3.9)
Passive view	109 (2.2)	118 (3.7)
N170 amplitude		
Interrupting stimulus	-8.7 (0.7)	-7.6 (0.83)
Distracting stimulus	-9.4 (0.96)	-8.3 (0.76)
No interference	-9.6 (1.0)	-7.6 (0.77)
Passive view	-9.9 (1.0)	-7.6 (0.94)
N170 latency		
Interrupting stimulus	173 (4.2)	189 (4.3)
Distracting stimulus	173 (4.7)	189 (3.9)
No interference	176 (4.4)	192 (4.2)
Passive view	182 (4.1)	196 (4.1)
Interference		
P100 amplitude		
Interrupting stimulus	6.9 (0.56)	6.7 (0.55)
Distracting stimulus	6.2 (0.52)	6.3 (0.49)
Passive view	6.8 (0.58)	6.3 (0.55)
P100 latency		
Interrupting stimulus	106 (2.5)	120 (3.4)
Distracting stimulus	109 (2.8)	122 (3.5)
Passive view	108 (2.6)	122 (3.3)
Passive view	-8.9 (0.73)	-8.60 (0.83)
N170 amplitude		
Interrupting stimulus	-7.7 (0.72)	-8.2 (0.67)
Distracting stimulus	-7.8 (0.71)	-7.73 (0.7)
Passive view	-8.9 (0.73)	-8.60 (0.83)
N170 latency		
Interrupting stimulus	173 (4.3)	189 (4.1)
Distracting stimulus	178 (4.5)	190 (3.7)
Passive view	176 (4.4)	193 (4.3)

slowing in the setting of an interruptor (see Table 1). Analysis also revealed a main effect of age ($F(1,39) = 62.10, p < .001$), such that older participants performed the WM tasks with slower reaction times. There was no significant task by age interaction ($F(2,78) < 1, p < .05$).

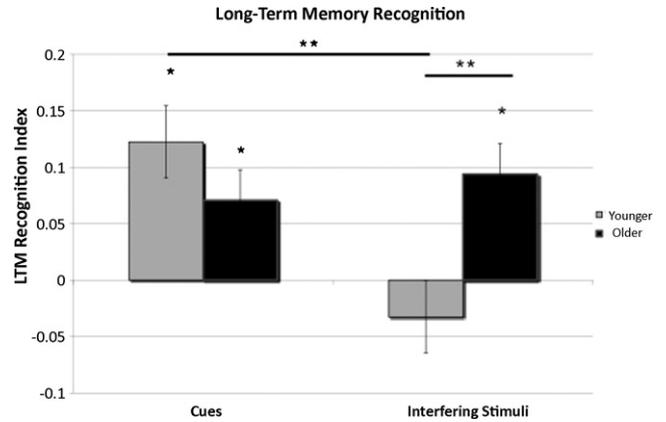


Fig. 4. Incidental long-term memory recognition. Older participants recognized interfering stimuli presented in the experiment more than younger adults and remembered them as well as the cues stimuli. Note: Single asterisks represent significant differences from 0, and double asterisks represent significant differences between ages/conditions.

Analysis of the post-experiment long-term memory recognition measures involved first correcting each participant's LTM rating for each stimulus type with their LTM rating for novel stimuli, thus equating for response bias differences. ANOVA was then performed on these LTM indices with stimulus (IS-Cue, IS-Interruptor, DS-Cue, DS-Distractor, NI-Cue, PV-Cue, PV-intervening stimulus) and age (young, older) as factors. Analysis showed a main effect of stimulus ($F(6,234) = 2.97, p < .05$), no main effect of age ($F(1,39) < 1$), but a significant stimulus by age interaction ($F(6,234) = 2.54, p < .05$). The absence of a main effect of age revealed that both age groups remembered the same amount of information over the long-term from the experiment. To explore the age by stimulus interaction further, a priori *t*-tests revealed that older participants remembered the interfering stimuli from the IS and DS tasks as well as the cue stimuli; whereas the younger participants remembered the cue stimuli significantly better than the interfering stimuli (see Table 1 and Fig. 4). Both age groups remembered the cue stimuli better than novel stimuli ($p < .05$), but only the older group remembered the interfering stimuli (from IS and DS) better than the novel stimuli ($p < .05$) (Fig. 4). Comparisons between age groups reveal that older participants remembered the interfering stimuli better over the long-term than the younger participants ($p < .01$). When the data was divided by interfering stimulus type, it revealed that older participants significantly remembered both distractors and interruptors better than the younger participants (IS-Interruptor: younger (M: -0.04, SE: 0.04) vs. older (M: -0.09, SE: 0.04), $p < .05$, DS-Distractor: younger (M: -0.03, SE: 0.045) vs. older (M: 0.088, SE: 0.03), $p = .05$) (Fig. 4). There was no significant difference between age groups for memory of the cue stimuli.

Importantly, in regards to the Passive View task, the cue and intervening stimuli presented in PV were less well remembered in the long-term compared to the cue stimuli from the WM tasks in both age groups. Furthermore, in both

age groups, PV stimuli were not remembered differently than the novel stimuli. This result suggested that minimal attention was directed to these stimuli, as instructed.

There were no significant correlations between neuropsychological measures and either neural or task performance measures.

3.2. Neural data

Two posterior ERP measures have previously been shown to be modulated by attention and associated with visual processing: The P100 (50–150 ms) (Gomez Gonzalez et al., 1994) and N170 (120–220 ms) (Gazzaley et al., 2005a; Gomez Gonzalez et al., 1994). All data presented here are for ERPs time-locked to the onset of either cue or interfering stimuli. Analyses, when appropriate, focused on the modulation indices of *enhancement* and *suppression* (described in the methods).

3.2.1. Cue stimuli

Analysis of the P100 amplitude in response to cue stimuli showed no effect of task ($F(3,117) = 1.42, p > .05$), age ($F(1,39) < 1, p > .05$) or interaction ($F(3,117) = 2.007, p > .05$). Analysis of the P100 latency showed no effect of task ($F(3,117) = 1.34, p > .05$), but a significant effect of age ($F(1,39) = 4.04, p = .05$), such that older participants had later P100 latencies than younger participants. No age by task interaction was observed ($F(3,117) < 1, p > .05$).

Analysis of the N170 amplitude revealed no effect of task ($F(3,117) = 2.172, p > .05$), age ($F(1,39) = 2.022, p > .05$) or interaction ($F(3,117) = 2.215, p > .05$). Analysis of the N170 latency showed a significant effect of task ($F(3,117) = 25.257, p < .05$), such that all WM tasks (NI, DS, IS) had earlier N170 latencies compared to the PV task, and thus significant enhancement for the encoded stimuli (all $p < .05$), and a main effect of age ($F(1,39) = 6.317, p < .05$), which revealed that older participants had later N170 latencies than younger participants (see Table 1). There was no interaction between task and age ($F(3,117) = 1.46, p > .05$).

To summarize, analyses of the cue period revealed a clear marker of attentional allocation (i.e., N170 latency), and an age-related slowing of neural processing (i.e., later P1 and N1 peaks in older adults), but none of the comparisons showed a significant age by task interaction.

3.2.2. Interfering stimuli

This analysis focused on the same ERP markers as described above, but for the intervening face stimuli presented within the delay period of the IS, DS and PV tasks.

ANOVA of the P100 amplitude showed a main effect of task ($F(2,78) = 4.61, p < .05$), such that the largest P100 was observed for the IS-Interruptor, but there was no effect of age ($F(1,39) > .05$) or interaction between age and task ($F(2,78) = 2.60, p > .05$). P100 latency showed a main effect of task ($F(2,78) = 5.129, p < .05$), such that responses to IS were faster than PV and responses to DS. A main effect

of age ($F(1,39) = 11.59, p < .05$) was also shown, once again revealing slowing of P100 latencies with age. There was no significant interaction between age and task ($F(2,78) > .05$).

N170 amplitude analysis revealed only a significant effect of task ($F(2,78) = 11.391, p < .05$), such that responses to IS were highest, followed by PV and DS. Neither the effect of age ($F(1,39) < 1$) nor the interaction between age and task were significant ($F(2,78) = 2.19, p > .05$). Analysis of N170 latency revealed a main effect of task ($F(2,78) = 19.67, p < .05$), a main effect of age ($F(1,39) = 6.41, p < .05$), and a significant task \times age interaction ($F(2,78) = 4.84, p < .05$). This measure has been revealed to reflect attention, as well as age-related changes in visual processing in previous studies (Gazzaley et al., 2008, 2005a). Post hoc *t*-tests revealed that the N170 latency for IS was earlier than for PV and DS (main effect of task), and a significantly later N170 latency was observed in older adults (main effect of age), consistent with reports in the literature of generalized slowing of processing speed with aging (Pfefferbaum et al., 1984) (see Fig. 5 and Table 1).

Analysis directed at interpreting the interaction included both within-group and between-group comparisons. For within-group comparisons, both younger and older participants displayed earlier latencies for the interruptor in the IS task than the intervening stimuli in the PV task, thus both displaying significant enhancement (young: IS-Interruptor vs. PV-intervening stimulus, $p < .05$. older: Interruptor vs. PV-intervening stimulus, $p < .05$.) (Fig. 5A–C). Earlier N170 latencies for relevant stimuli compared to passively viewed stimuli has been previously revealed in younger adults (Clapp et al., 2009; Gazzaley et al., 2005a) and is interpreted to reflect greater attention to the stimulus as mediated by more rapid synchronization of cortical areas involved in stimulus representation. Neither age group displayed significant suppression of the N170 latency for the distractors (i.e., later latency for DS than PV). Conversely, the older participants actually exhibited significant enhancement of the distractor in the DS task ($p < .05$) (i.e., earlier latency for the distractor than the passively viewed stimulus), while younger participants did not show this pattern. Between-group comparisons revealed a significant deficit in the N170 latency suppression index for distractors by older participants ($p < .01$), but no significant age-related difference in the enhancement index for the interruptors ($p = 0.658$) (Fig. 5D).

3.3. Comparisons between cue and interfering stimuli

N170 latency enhancement was compared between cue and interruptor stimuli from the IS task to determine if participants directed different degrees of attention to these two relevant stimuli. The N170 latency was utilized as the measure of comparison because it was the only early measure to reveal significant modulation for both cue and interfering stimuli. This analysis revealed that younger participants exhibited significantly greater enhancement for cues than interruptors ($p < .05$), while the older participants did not differ in their enhancement for these stimuli ($p > 0.05$). A

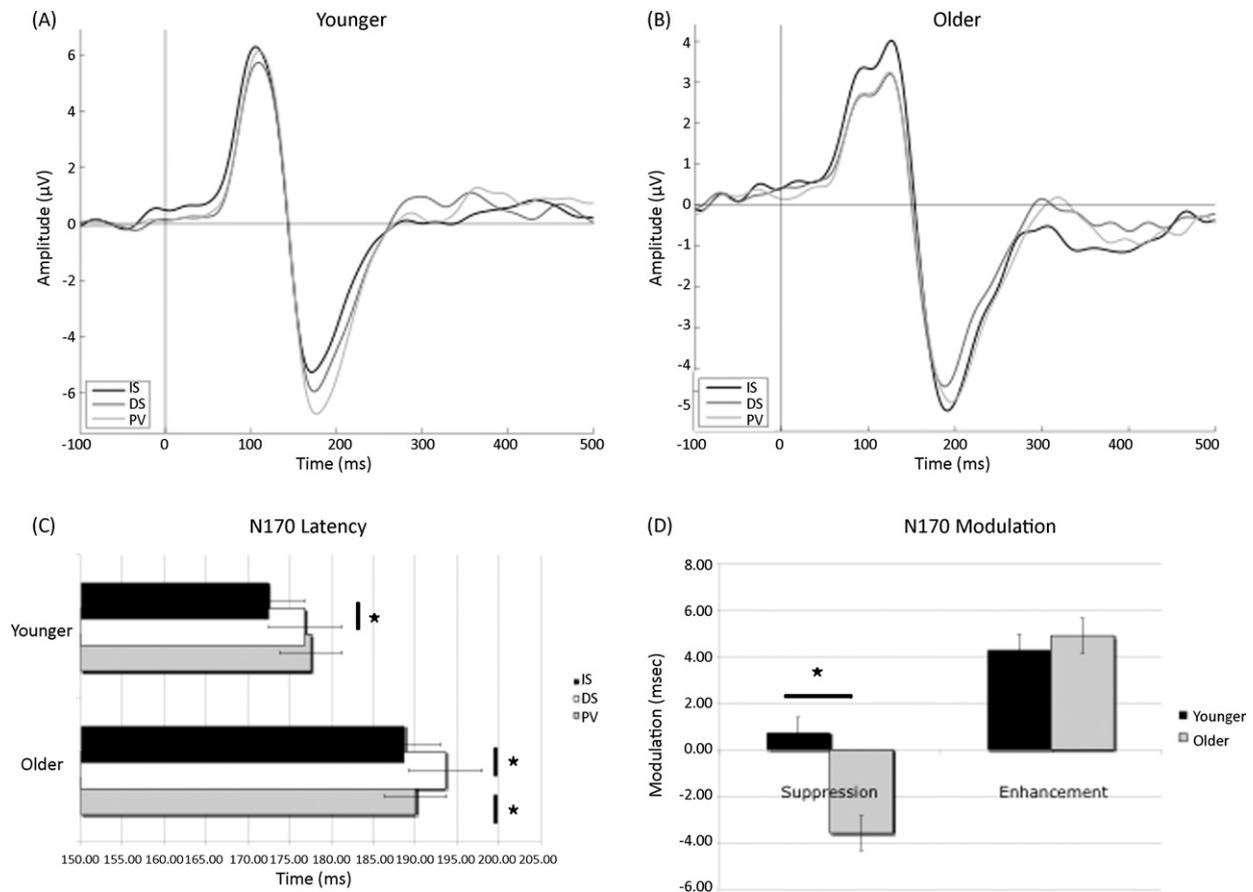


Fig. 5. Grand-averaged event-related potentials to intervening stimuli. (A) GAV ERPs from younger participants for Distractor stimuli (DS), Interruptor Stimuli (IS) and passively viewed intervening stimuli (PV). (B) ERPs from older participants. (C) N170 latency measures to intervening stimuli. Both younger and older participants significantly enhanced the interruptors (earlier peaks compared to passively viewed intervening stimuli). Unlike younger adults, older participants also showed enhancement for the distracting stimuli. (D) Comparisons of N170 latency attentional modulation indices between age groups. Older participants allocated more attention towards distractors than younger participants (suppression index), but did not differ in attention allocated towards interruptors (enhancement index).

between-group analysis reveals that younger and older participants did not differ in the amount that they enhance cue or interruptor stimuli ($p > 0.05$).

3.4. Neural-behavioral correlations

To evaluate if the magnitude of activity modulation to the cue or interfering stimuli predict WM performance, across-participant regression analyses were performed for N170 latency modulation indices (i.e., enhancement and suppression) and WM accuracy. Modulation indices were utilized because responses relative to passively viewed stimuli equate for each individual's overall ERP differences. Analyses of the interfering stimuli in older participants paralleled the results obtained from the same analysis in the younger participants (Clapp et al., 2009): (1) There was a positive correlation for both age groups between the suppression of distractors in the DS task and WM accuracy (young: $R = 0.49$, $p < 0.05$; older: $R = 0.50$, $p < 0.05$), such that those individuals who neurally suppressed distracting information the most, showed superior WM performance (Fig. 6A). (2) There was a negative corre-

lation between the amount of enhancement to interruptors in the IS task and WM accuracy (young: $R = -0.77$, $p < 0.05$; older: $R = -0.45$, $p < 0.05$), which revealed that those participants, both younger and older who enhanced the interruptor most exhibited the worst WM performance (Fig. 6B). (3) In addition, a negative correlation existed between indices of enhancement of interruptors and suppression of distractors using the N170 latency indices in both younger and older populations (young: $R = -0.7$, $p < 0.05$; older: $R = -0.55$, $p < 0.05$), revealing that those individuals who enhance the interruptor the most, also suppress distractors the least.

3.5. Practice effects

Behaviorally, performance improvement in the DS task across blocks was observed for both age groups, reflected as a decreased RT in the younger participants ($p < .05$, see Table 2 for means and standard errors), and increased WM accuracy in the older participants ($p < .05$). In the NI and IS tasks, a non-significant increase in WM accuracy was observed in both younger and older adults.

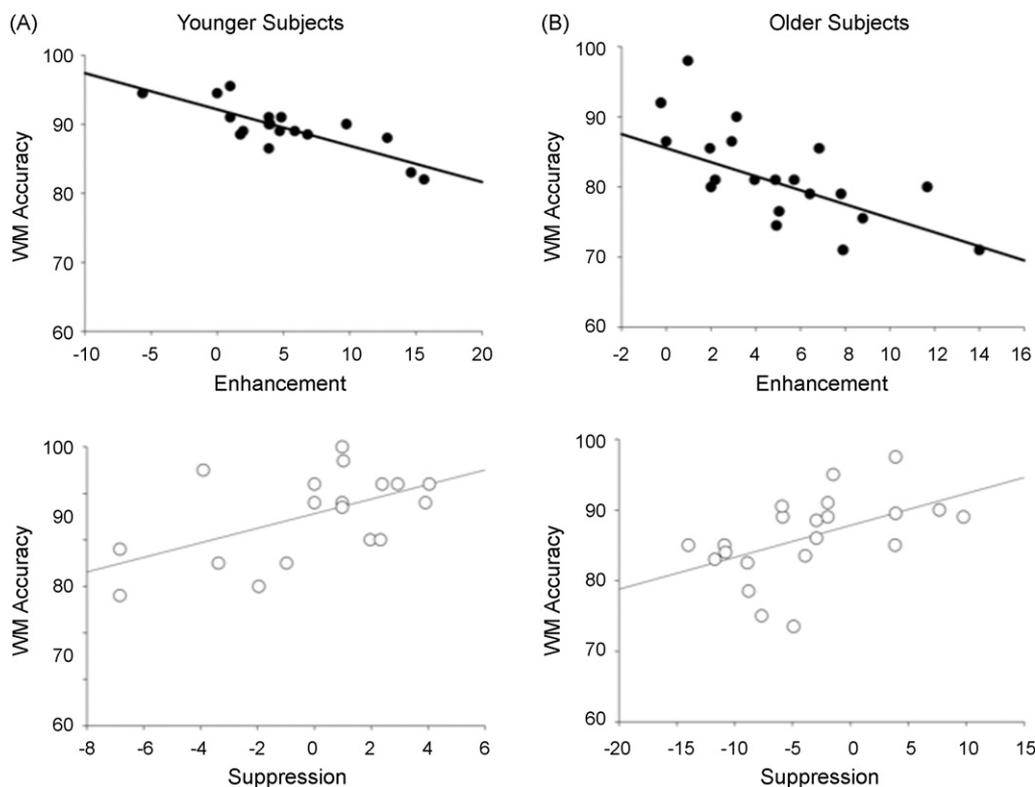


Fig. 6. Neurobehavioral correlations of the N170 latency attentional modulation indices. In both (A) younger and (B) older age groups, participants that enhance the interruptor more (upper panels) perform worse on the WM task. Likewise, participants that suppress the distractor more (upper panels) perform better on the WM task. Note: More positive value on the x-axis indicate greater enhancement above baseline or greater suppression below baseline.

Table 2
Practice effects in younger and older participants. Standard errors are presented in parentheses.

	Practice effects			
	Younger		Older	
	Block 1	Block 2	Block 1	Block 2
Behavioral findings				
Accuracy				
IS	88% (2.0)	91% (1.5) IS	79% (2.1)	81% (1.8)
DS	92% (1.5)	94% (1.6) DS	84% (1.6)	88% (1.5)
NI	95% (1.4)	96% (1.4) NI	90% (1.6)	91% (1.1)
Reaction time				
IS	824 (34)	798 (28) IS	1255 (54)	1189 (48)
DS	717 (22)	651 (22) DS	1133 (55)	1151 (54)
NI	678 (24)	650 (27) NI	1159 (57)	1089 (50)
Neural				
Encode				
IS	173 (4.3)	172 (4.1) IS	187 (3.2)	188 (4.1)
DS	178 (4.5)	180 (3.7) DS	189 (3.5)	191 (4.0)
NI	176 (4.4)	173 (3.3) NI	191 (3.0)	192 (5.1)
Interference				
IS	824 (34)	798 (28) IS	1255 (54)	1189 (48)
DS	717 (22)	651 (22) DS	1133 (55)	1151 (54)
NI	678 (24)	650 (27) NI	1159 (57)	1089 (50)

An ANOVA was used to evaluate practice effects for the neural response to cue and interfering stimuli, using task (DS, IS, NI, PV), block (first, second) and age (young, older) as factors. We again focused on the N170 latency, as it showed significant attentional modulation in both populations. For the cue stimuli there was a main effect of task ($F(3,117) = 15.15, p < .05$) and age ($F(1,39) = 11.62, p < .05$), but no effect of block ($F(1,117) < 1$), no task by age interaction ($F(3,117) < 1$), no block by task interaction ($F(3,117) = 1.03, p > .05$), and no block by task by age interaction ($F(3,117) = 1.19, p > .05$). For the interfering stimuli there was a main effect of task ($F(2,78) = 7.07, p < .05$), block ($F(1,78) = 8.17, p < .05$) and age ($F(1,39) = 5.29, p < .05$), a block by task interaction ($F(2,117) = 7.22, p > .05$), but no task by age interaction ($F(2,117) < 1$) or block by task by age interaction ($F(2,117) = 1.31, p > .05$). *t*-tests revealed that the latency of the N170 to distractors (DS task) were significantly later in the second block (younger and older, $p < .05$), but there was no across block change for the interruptors (IS task)—see Table 2 for values. Comparisons of modulation indices, showed that suppression of distractors increased in the second block (younger and older, both $p < .05$), while enhancement of interruptors remained the same across blocks. Taken together with the behavioral results, this suggests the possibility that performance improvements in the DS task may have been driven by changes in the response to distractors by both younger and older adults, as has been determined in a recent study of younger adults using the same design, but with lower level stimuli (moving flow fields of dots) (Berry et al., 2009).

4. Discussion

In the current study, behavioral and neural measures were used to compare the influence that two types of external interference, i.e., distraction and interruption, have on WM in older adults. The behavioral data revealed that both types of interference impact WM performance to a greater degree in older adults compared to younger participants studied in a previous study (Clapp et al., 2009). Furthermore, ERP data suggested that excessive attention to the interfering stimulus explains the age-related decline in WM performance, but only when the interference should be ignored (distraction). When the interference demanded attention as a secondary task (interruption), older adults do not seem to devote more attentional allocation to the interfering stimulus than younger adults, but do suffer greater impairment in WM performance. Together these findings suggest distinct mechanisms underlie the impact of different types of external interference on WM in normal aging. Additionally, both younger and older participants improved their WM performance on the Distractor task, as well as their ability to filter the distracting stimulus with practice over the experimental session, whereas practice does not influence WM performance or processing of interruptors in the Interruptor task.

4.1. Behavioral measures

Behavioral analysis revealed that healthy older adults demonstrated poorer WM accuracy than younger individuals on the single-item delayed-recognition task without interference. This finding suggests that WM processes, even for a single complex stimulus, such as a face, declines somewhat with aging. Other studies have found no difference in WM accuracy for faces over a short uninterrupted delay (Grady et al., 1998), consistent with reports that rote maintenance is spared in older adults (Craig and Jennings, 1992; Gazzaley et al., 2007). These seemingly conflicting results may be the consequence of increased task difficulty in the current study due to the use of ghosted faces (i.e. stimuli had all non-facial features removed). Additionally, this impairment in WM accuracy could be due to the fact that even in older individuals with “corrected to normal” acuity, visual deficits might be present that exacerbate memory deficits due to the decreased fidelity of stimulus representation, especially when degraded stimuli are used (Cronin-Golomb et al., 2007).

The WM deficit in older adults was exacerbated by both a distractor (irrelevant stimulus) and interruptor (stimulus requiring a judgment decision) presented during the interval of memory maintenance. This impact on WM performance was greater than that for younger adults, who also experienced negative consequences of interference (Clapp et al., 2009). These findings reveal an age-related increase in the impact external interference has on WM. Of note, the interruptor disproportionately impaired WM performance in older adults. This is consistent with previous reports that older individuals experience both a deficit in inhibiting irrelevant information (Hasher et al., 1999) and difficulty with divided attention and multitasking (Kramer and Larish, 1996). However, this is the first direct comparison of the impact that these two types of interference have on WM performance in older adults.

Older adults also exhibited significantly stronger long-term memory recognition of the distractor and interruptor stimuli when tested after the experiment, as compared to the younger adults who did not remember these stimuli. Moreover, the older adults actually remembered these distracting and interrupting stimuli in the long-term as well as they remembered the WM cue stimuli. This suggests that WM interference in aging may be caused by excessive incorporation of intervening stimuli into memory stores. Of further interest, there was no main effect of age for incidental long-term memory, revealing that both age groups complete the experiment with a comparable amount of retained information for the faces they viewed (at least within the time frame tested). This is likely the result of an increase in memory for interfering stimuli, a finding consistent with those of recent studies revealing that older participants remember more information over the long-term, even if it was irrelevant to the goals of the task (e.g., WM task) (Gazzaley et al., 2005b; Kim et al., 2007; Rowe et al., 2006). It has been

proposed that it might be an advantage for older adults to remember information even if it is irrelevant to them at the time, since this may benefit them at some later time (Kim et al., 2007). However, as seen from the context of the current study, storing information that is not required for the task at hand, may negatively impact WM performance. A recent EEG study confirms this is also true for younger adults (Zanto and Gazzaley, 2009).

4.2. Neural measures

To explore the neural basis of external interference having a more negative impact on WM performance in older adults, as well as potential mechanistic differences between types of interference, we utilized EEG and focused our analysis on early neural activity measures in visual cortex, which have been previously found to be responsive to attentional goals. The N170, an ERP component selective for face stimuli (Bentin et al., 1996) that has been localized to cortical areas in lateral visual association cortex (Gomez Gonzalez et al., 1994) has been shown to not only be a marker of attention (Clapp et al., 2009; Gazzaley et al., 2008, 2005a; Sreenivasan et al., 2009; Sreenivasan and Jha, 2007; Sreenivasan et al., 2007; Zanto et al., 2009), but also an effective measure to assess differences in attentional allocation to faces across populations (Campanella et al., 2006; Chaby et al., 2003; Gazzaley et al., 2008; McPartland et al., 2004; Nakamura et al., 2001; Tanaka and Curran, 2001; Taylor et al., 2001; Zanto et al., 2009). For example, younger adults show earlier N170 latencies for faces that were attended (i.e. enhancement relative to passive), and later latencies for faces that were ignored (i.e. suppression relative to passive) (Gazzaley et al., 2005a). Modulation of the N170 latency by attention most likely reflects the time for cortical regions to reach maximally synchronized activity during the internal representation of visual stimuli. Using these indices of enhancement and suppression, it was further shown that there was a selective deficit in the suppression of distractors in normal aging, and that this was associated with decreased WM performance (Gazzaley et al., 2008).

In the current study, measures of N170 peak latency as indicators of attentional allocation to face stimuli revealed that for both younger and older adults, the greater the magnitude of processing interfering stimuli, both distractors and interruptors, the worse the subsequent WM performance. Data revealed that more attention was directed towards interruptors than distractors, thus serving as an explanation for why WM performance was worse in the setting of interruption than distraction for both age groups. This same line of reasoning can explain why older adults exhibited poorer WM performance than younger adults in the Distraction task; i.e., they displayed significantly greater activity modulation for the distractors than the younger participants ($p=0.01$, see Fig. 5D). This result replicates previous findings and offers further support that age-related impairments in WM in the setting of distraction is a consequence of a neural suppression

deficit of irrelevant information early in the visual processing system (Gazzaley et al., 2008, 2005b).

It should be noted that younger adults did not demonstrate significant suppression of the distractor stimuli when evaluated with this paradigm (Clapp et al., 2009), as they have been shown to previously (Gazzaley et al., 2005a). This lack of suppression may stem from the design of the paradigm, specifically that it was difficult to predict the time of distractor onset and thus rapidly engage suppression mechanisms (i.e. 3 s after the cue stimuli). Furthermore, the onset of the distractor was jittered in this paradigm. Despite this, the age difference in activity modulation of the distractor was significant, such that older participants allocated more attention towards the distractor than younger adults. In fact, the older adults significantly enhanced the distractor relative to passive view. This finding replicates previous reports of age-related increases in distractor processing (Gazzaley et al., 2008, 2005b).

Of interest, we generated no neural evidence that older adults directed more attention to the interruptors than the younger adults ($p=0.658$, see Fig. 5D). However, despite seemingly equivalent attentional allocation to the interruptor, the older participants were significantly more impaired on this task compared to younger adults and were even more impacted more by interruptors than distractors. Older adults also remembered the interrupting stimuli after the experiment better than younger adults, suggesting they were processing these interfering stimuli different in some manner. Together, these findings reveal that the detrimental influence distraction and interruption have on WM performance in older adults is mediated by qualitatively different mechanisms.

It should also be emphasized that no differences were observed in ERPs to the cue stimuli across groups. Thus, age-related differences in performance in the WM tasks do not seem to be the result of alterations in how individuals encode relevant information, but rather how they interact with interfering stimuli. Furthermore, significant cross-participant correlations between the degree of enhancement of the interruptor and suppression of the distractor in both younger and older adults suggest that although the impact of these two types of interference on WM rely on different mechanisms (Clapp et al., 2009), and they impact WM in older adults via distinct mechanisms (current study), there is consistency within an individual in how they process interfering stimuli. Individual differences in interference effects have also been shown to correlate with individual differences in WM capacity (Conway et al., 2001; Kane and Engle, 2003; Vogel et al., 2005).

4.3. Mechanism of WM impairment in the presence of distraction

The etiology of the age-related suppression deficit described in the current study and previous studies has still not been completely elucidated, although given the proposed role of the PFC in top-down suppression, this region has been

implicated (Chao and Knight, 1997). It is also possible that the greater impact distraction has on WM in older adults may be due to impairments in the degree to which older adults maintain cued memoranda during the delay period. In an fMRI version of this experiment performed in younger adults (Clapp et al., 2009), it was found that in the DS task, the degree to which participants held the memoranda in mind, as measured by prefrontal cortex-visual association cortex connectivity, correlated with their suppression of the distractor, and in turn their WM accuracy on the task. One interpretation of this result is that the higher fidelity of the information being maintained in WM, the greater the resistance to distraction (although the opposite could also be true). Thus, poorer performance in the DS task by older participants may have been a consequence of diminished maintenance abilities, making them more susceptible to processing irrelevant distractions. Evidence of this emerges from the finding that older participants did not perform as well on the NI task, when no external interference was present during the delay period.

4.4. Mechanism of WM impairment in the presence of interruption (multitasking)

It has been well documented that healthy older adults perform significantly worse than younger adults when they attempt to perform two tasks concurrently (i.e., divide attention) (Craik and Salthouse, 2000; Crossley and Hiscock, 1992; Kramer et al., 1995; Park et al., 1989; Tsang and Shaner, 1998). To our knowledge, this is the first aging study to investigate the impact of an imbedded secondary task on WM performance, thus expanding our understanding of the cognitive consequences of multitasking in older adults.

It is possible that attending to an interruptor is comparable to failing to filter a distractor, as suggested by findings that the impact of distraction and interruption on WM in older adults has behavioral aspects in common (i.e., they both impair WM performance and result in long-term retention of the interfering stimuli more so than for younger adults). However, it should be noted that there are differences in the degree of impact (i.e., the interruptor disproportionately impairs WM performance in older adults), as well as an important neural difference (i.e., only attentional indices to the distractor differs with age). This suggests that the detrimental influence of interruption on WM in older adults may be mediated by a different mechanism than that of distraction. We speculate on several possible mechanisms of the interruptor age effect:

First, we directed our neural analysis at well-established modulation indices of visual attentional control, which have also revealed age by task interactions in previous studies, but it is possible that older adults may have allocated more attention towards interrupting stimuli than younger adults, and we did not identify it. However, we are convinced that the two age groups did not differ in how they represented the interrupting stimulus as reflected by early measures of stimulus representation in the visual association cortex.

Second, although the two age groups seem to attend to interrupting stimuli to the same degree from a quantitative perspective, they may differ qualitatively in how they are processing of these stimuli. For example, older adults may invoke a different network of brain regions when representing the interrupting stimuli than younger adults. Specifically, the network utilized by older individuals may involve greater recruitment of medial temporal lobe structures, which are involved in long-term memory consolidation. This would be consistent with the finding that older adults remember the interrupting stimuli better over the long-term than the younger adults, who do not remember them at all. This engagement of a different network may have a negative impact on WM performance. A functional MRI study will be conducted to address this possibility and assess if and how the involvement of a different network by older adults might undermine WM related processes.

Third, there may be an age-related difference in the ability to eliminate the representation of processed interrupting information from WM, which would then serve as an additional source of interference in making a memory decision at the time of the probe. This mechanism is consistent with the proposed concept that there is a negative impact from failed “deletion” of WM contents that are not relevant to memory goals (Hasher et al., 1999).

Fourth, we hypothesize that older individuals may differ from younger adults in their ability to reactivate the memoranda after the representation was interrupted by an interfering stimulus. Reactivation after interruption has been shown to be reliant on PFC and medial temporal lobe regions (Sakai and Passingham, 2004; Sakai et al., 2002). Related to this, it has been shown that older adults have trouble refreshing information in WM. This has been shown behaviorally (Johnson et al., 2002) and also in an fMRI study that shows reduced activation in the left prefrontal cortex area associated with refreshing (Johnson et al., 2004). Recent fMRI results from a younger population that performed the same task as the current study may also shed light on this explanation. The results revealed that in the IS task, younger adults temporarily “released” the stored memoranda as reflected by reduced prefrontal cortex-visual association cortex connectivity when the interrupting stimulus was present (Clapp et al., 2009). During the post-interference delay period, renewed PFC-visual association cortex connectivity was identified and interpreted. An fMRI study will investigate age-related changes in functional connectivity associated with reactivation of interrupted memoranda and its relationship to subsequent WM performance.

4.5. Practice effects

Practice effects across the two blocks were also investigated and suggested that individuals of both age groups improve their ability to filter distractions to the benefit of their WM performance (i.e. increased neural suppression

of distractor stimuli and increased WM performance). In a variety of cognitive tasks, practice has been shown to lead to improved performance in younger adults, reflected as decreased RT and improved accuracy (Poldrack, 2000). Additionally, previous research has reported WM practice effects across a single experimental session (Berry et al., 2009; Koch et al., 2006; Landau et al., 2007; Landau et al., 2004). In fact, studies have revealed increases in attentional suppression of task-irrelevant motion stimuli with practice in younger adults (Berry et al., 2009; Vidnyanszky and Sohn, 2005), as well as inhibition of prepotent responses (Clare Kelly et al., 2006).

There were no clear practice effects on the IS task either behaviorally or neurally over the course of the experiment. Past research has shown conflicting results about whether older adults can acquire the ability to perform two cognitive operations in parallel. Some have shown that this does not occur (Gothe et al., 2007), whereas others have shown that older adults can improve their dual task skills (Bherer et al., 2008). However, these studies use extensive training, whereas in the current study no training was administered.

Single-session practice effects were also investigated in a previous study performed with younger adults using the same paradigm, but low-level stimuli (moving flow fields of dots) (Berry et al., 2009). WM measures of recognition accuracy and RT improved significantly over the course the experimental session for tasks that included interfering stimuli (IS and DS), but not for the same task without interference (NI). In the current study, significant practice effects were only observed in the distractor condition (DS). It must be noted, however, that a non-significant increase in WM accuracy was observed in both younger and older adults in the IS task, thus potentially with more practice this would have been significant. These results support previous findings of retained plasticity in the older brain (Bherer et al., 2006), at least in the context of their ability to filter irrelevant information.

5. Conclusion

This study contributes to our growing appreciation of the complex interaction between interference and WM in normal aging by exploring differential effects of distraction and interruption within the same experiment. Results revealed that in both cases, external interference leads to diminishment in WM performance, with the decline being accounted for by excessive attentional allocation to distracting stimuli, and a distinct mechanism for the impact of interruption on WM performance. Investigation with functional neuroimaging will be pursued to further elucidate the mechanisms of these distinct influences on WM performance with aging.

Conflict of interest

There are no conflicts of interest.

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References

- Baddeley, A., 1986. Working Memory. Oxford University Press, Oxford.
- Baddeley, A., 2003. Working memory: looking back and looking forward. *Nat. Rev. Neurosci.* 4 (10), 829–839.
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate—a practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B: Methodological* 57, 289–300.
- Bentin, S., Allison, T., Puce, A., Perez, E., McCarthy, G., 1996. Electrophysiological studies of face perception in humans. *J. Cogn. Neurosci.* 8 (6), 551–565.
- Berry, A.S., Zanto, T.P., Rutman, A.M., Clapp, W.C., Gazzaley, A., 2009. Practice-related improvement in working memory is modulated by changes in processing external interference. *J. NeuroPhysiol.* 102 (3), 1779–1789.
- Bherer, L., Kramer, A.F., Peterson, M.S., Colcombe, S., Erickson, K., Becic, E., 2006. Testing the limits of cognitive plasticity in older adults: application to attentional control. *Acta Psychol. (Amst.)* 123 (3), 261–278.
- Bherer, L., Kramer, A.F., Peterson, M.S., Colcombe, S., Erickson, K., Becic, E., 2008. Transfer effects in task-set cost and dual-task cost after dual-task training in older and younger adults: further evidence for cognitive plasticity in attentional control in late adulthood. *Exp. Aging Res.* 34 (3), 188–219.
- Borella, E., Carretti, B., Cornoldi, C., De Beni, R., 2007. Working memory, control of interference and everyday experience of thought interference: when age makes the difference. *Aging Clin. Exp. Res.* 19 (3), 200–206.
- Campanella, S., Montedoro, C., Strel, E., Verbanck, P., Rosier, V., 2006. Early visual components (P100, N170) are disrupted in chronic schizophrenic patients: an event-related potentials study. *Neurophysiol. Clin.* 36 (2), 71–78.
- Chaby, L., George, N., Renault, B., Fiori, N., 2003. Age-related changes in brain responses to personally known faces: an event-related potential (ERP) study in humans. *Neurosci. Lett.* 349 (2), 125–129.
- Chao, L.L., Knight, R.T., 1995. Human prefrontal lesions increase distractibility to irrelevant sensory inputs. *Neuroreport* 6 (12), 1605–1610.
- Chao, L.L., Knight, R.T., 1997. Prefrontal deficits in attention and inhibitory control with aging. *Cereb. Cortex* 7 (1), 63–69.
- Chao, L.L., Knight, R.T., 1998. Contribution of human prefrontal cortex to delay performance. *J. Cogn. Neurosci.* 10 (2), 167–177.
- Chaparro, A., Wood, J.M., Carberry, T., 2005. Effects of age and auditory and visual dual tasks on closed-road driving performance. *Optom. Vis. Sci.* 82 (8), 747–754.
- Clapp, W.C., Rubens, M.T., Gazzaley, A., 2009. Mechanisms of working memory disruption by external interference. *Cereb. Cortex*.
- Clare Kelly, A.M., Hester, R., Foxe, J.J., Shpaner, M., Garavan, H., 2006. Flexible cognitive control: effects of individual differences and brief practice on a complex cognitive task. *Neuroimage* 31 (2), 866–886.
- Conway, A.R., Cowan, N., Bunting, M.F., 2001. The cocktail party phenomenon revisited: the importance of working memory capacity. *Psychon. Bull. Rev.* 8 (2), 331–335.
- Craik, F.I., Bialystok, E., 2006. Planning and task management in older adults: cooking breakfast. *Mem. Cognit.* 34 (6), 1236–1249.
- Craik, F.I., Jennings, J.M., 1992. Human memory. In: Craik, F.I., Salthouse, T.A. (Eds.), *Handbook of Aging and Cognition*. Erlbaum, Hillsdale, NJ.
- Craik, F.I., Salthouse, T.A., 2000. *Handbook of Aging and Cognition II*. Erlbaum, Mahwah, NJ.

- Cronin-Golomb, A., Gilmore, G.C., Neargarder, S., Morrison, S.R., Laudate, T.M., 2007. Enhanced stimulus strength improves visual cognition in aging and Alzheimer's disease. *Cortex* 43 (7), 952–966.
- Crossley, M., Hiscock, M., 1992. Age-related differences in concurrent-task performance of normal adults: evidence for a decline in processing resources. *Psychol. Aging* 7 (4), 499–506.
- Dobbs, A.R., Rule, B.G., 1989. Adult age differences in working memory. *Psychol. Aging* 4 (4), 500–503.
- Doumas, M., Smolders, C., Krampe, R.T., 2008. Task prioritization in aging: effects of sensory information on concurrent posture and memory performance. *Exp. Brain Res.*
- Emery, L., Hale, S., Myerson, J., 2008. Age differences in proactive interference, working memory, and abstract reasoning. *Psychol. Aging* 23 (3), 634–645.
- Faulkner, K.A., Redfern, M.S., Cauley, J.A., Landsittel, D.P., Studenski, S.A., Rosano, C., Simonsick, E.M., Harris, T.B., Shorr, R.I., Ayonayon, H.N., Newman, A.B., 2007. Multitasking: association between poorer performance and a history of recurrent falls. *J. Am. Geriatr. Soc.* 55 (4), 570–576.
- Folstein, M.F., Folstein, S.E., McHugh, P.R., 1975. "Mini-mental state". A practical method for grading the cognitive state of patients for the clinician. *J. Psychiatr. Res.* 12 (3), 189–198.
- Foos, P.W., Wright, L., 1992. Adult age differences in the storage of information in working memory. *Exp. Aging Res.* 18 (1–2), 51–57.
- Forster, S., Lavie, N., 2009. Harnessing the wandering mind: the role of perceptual load. *Cognition* 111 (3), 345–355.
- Gazzaley, A., Clapp, W., Kelley, J., McEvoy, K., Knight, R.T., D'Esposito, M., 2008. Age-related top-down suppression deficit in the early stages of cortical visual memory processing. *Proc. Natl. Acad. Sci. U.S.A.* 105 (35), 13122–13126.
- Gazzaley, A., Cooney, J.W., McEvoy, K., Knight, R.T., D'Esposito, M., 2005a. Top-down enhancement and suppression of the magnitude and speed of neural activity. *J. Cogn. Neurosci.* 17 (3), 507–517.
- Gazzaley, A., Cooney, J.W., Rissman, J., D'Esposito, M., 2005b. Top-down suppression deficit underlies working memory impairment in normal aging. *Nat. Neurosci.* 8 (10), 1298–1300.
- Gazzaley, A., Sheridan, M.A., Cooney, J.W., D'Esposito, M., 2007. Age-related deficits in component processes of working memory. *Neuropsychology* 21 (5), 532–539.
- Goffaux, V., Jemel, B., Jacques, C., Rossion, B., Schyns, P., 2003. ERP evidence for task modulations on face perceptual processing at different spatial scales. *Cogn. Sci.* 27 (2), 313–325.
- Gomez Gonzalez, C.M., Clark, V.P., Fan, S., Luck, S.J., Hillyard, S.A., 1994. Sources of attention-sensitive visual event-related potentials. *Brain Topogr.* 7 (1), 41–51.
- Gothe, K., Oberauer, K., Kliegl, R., 2007. Age differences in dual-task performance after practice. *Psychol. Aging* 22 (3), 596–606.
- Grady, C.L., McIntosh, A.R., Bookstein, F., Horwitz, B., 1998. Age-related changes in regional cerebral blood flow during working memory for faces. *Neuroimage* 8 (4), 409–425.
- Hasher, L., Zacks, R.T., May, C.P., 1999. Inhibitory control, circadian arousal, and age. In: Gopher, D., Koriat, A. (Eds.), *Attention and Performance*, vol. XVII. MIT Press, Cambridge, MA, pp. 653–675.
- Heinrich, S.P., Renkl, A.E., Bach, M., 2005. Pattern specificity of human visual motion processing. *Vision Res.* 45 (16), 2137–2143.
- Herrmann, M., Ehlis, A., Ellgring, H., Fallgatter, A., 2005. Early stages (P100) of face perception in humans as measured with event-related potentials (ERPs). *J. Neural. Transm.* 112 (8), 1073–1081.
- Hoffmann, M., Dorn, T.J., Bach, M., 1999. Time course of motion adaptation: motion-onset visual evoked potentials and subjective estimates. *Vision Res.* 39 (3), 437–444.
- Hoffmann, M.B., Unsold, A.S., Bach, M., 2001. Directional tuning of human motion adaptation as reflected by the motion VEP. *Vision Res.* 41 (17), 2187–2194.
- Johnson, M.K., Mitchell, K.J., Raye, C.L., Greene, E.J., 2004. An age-related deficit in prefrontal cortical function associated with refreshing information. *Psychol. Sci.* 15 (2), 127–132.
- Johnson, M.K., Reeder, J.A., Raye, C.L., Mitchell, K.J., 2002. Second thoughts versus second looks: an age-related deficit in reflectively refreshing just-activated information. *Psychol. Sci.* 13 (1), 64–67.
- Kane, M.J., Engle, R.W., 2003. Working-memory capacity and the control of attention: the contributions of goal neglect, response competition, and task set to Stroop interference. *J. Exp. Psychol. Gen.* 132 (1), 47–70.
- Kim, S., Hasher, L., Zacks, R.T., 2007. Aging and a benefit of distractibility. *Psychon. Bull. Rev.* 14 (2), 301–305.
- Koch, K., Wagner, G., von Connsbruch, K., Nenadic, I., Schultz, C., Ehle, C., Reichenbach, J., Sauer, H., Schlosser, R., 2006. Temporal changes in neural activation during practice of information retrieval from short-term memory: an fMRI study. *Brain Res.* 1107 (1), 140–150.
- Kramer, A.F., Larish, J.F., Strayer, D.L., 1995. Training for attentional control in dual task settings: a comparison of young and old adults. *J. Exp. Psychol. Appl.*, 50–76.
- Kramer, A.F., Larish, J.L., 1996. Aging and dual-task performance. In: Rogers, W.A., Fisk, A.D., Walker, N. (Eds.), *Aging and Skilled Performance*. Lawrence Erlbaum Associates, pp. 83–110.
- Landau, S.M., Garavan, H., Schumacher, E.H., D'Esposito, M., 2007. Regional specificity and practice: dynamic changes in object and spatial working memory. *Brain Res.* 1180, 78–89.
- Landau, S.M., Schumacher, E.H., Garavan, H., Druzgal, T.J., D'Esposito, M., 2004. A functional MRI study of the influence of practice on component processes of working memory. *Neuroimage* 22 (1), 211–221.
- Lustig, C., May, C.P., Hasher, L., 2001. Working memory span and the role of proactive interference. *J. Exp. Psychol. Gen.* 130 (2), 199–207.
- McDowd, J.M., Craik, F.I., 1988. Effects of aging and task difficulty on divided attention performance. *J. Exp. Psychol. Hum. Percept. Perform.* 14 (2), 267–280.
- McPartland, J., Dawson, G., Webb, S.J., Panagiotides, H., Carver, L.J., 2004. Event-related brain potentials reveal anomalies in temporal processing of faces in autism spectrum disorder. *J. Child Psychol. Psychiatry* 45 (7), 1235–1245.
- Miller, E.K., Erickson, C.A., Desimone, R., 1996. Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *J. Neurosci.* 16 (16), 5154–5167.
- Miyake, A., Shah, P., 1999. *Models of Working Memory: Mechanisms of Active Maintenance and Executive Control*. Cambridge University Press, New York.
- Nakamura, A., Yamada, T., Abe, Y., Nakamura, K., Sato, N., Horibe, K., Kato, T., Kachi, T., Ito, K., 2001. Age-related changes in brain neuro-magnetic responses to face perception in humans. *Neurosci. Lett.* 312 (1), 13–16.
- Park, D.C., Smith, A.D., Dudley, W.N., Lafronza, V.N., 1989. Effects of age and a divided attention task presented during encoding and retrieval on memory. *J. Exp. Psychol. Learn. Mem. Cogn.* 15 (6), 1185–1191.
- Pfefferbaum, A., Ford, J.M., Wenegrat, B.G., Roth, W.T., Kopell, B.S., 1984. Clinical application of the P3 component of event-related potentials. I. Normal aging. *Electroencephalogr. Clin. Neurophysiol.* 59 (2), 85–103.
- Poldrack, R.A., 2000. Imaging brain plasticity: conceptual and methodological issues—a theoretical review. *Neuroimage* 12 (1), 1–13.
- Ponds, R.W., Brouwer, W.H., van Wolfelaar, P.C., 1988. Age differences in divided attention in a simulated driving task. *J. Gerontol.* 43 (6), P151–P156.
- Reitan, R., 1958. Validity of the trail making test as an indicator of organic brain damage. *Perceptual Motor Skills* 8, 271–276.
- Reuter-Lorenz, P., Sylvester, C.-Y.C., 2005. The cognitive neuroscience of working memory and aging. In: Cabeza, R., Nyberg, L., Park, D. (Eds.), *Cognitive Neuroscience of Aging*. University Press, Oxford.
- Rowe, G., Valderrama, S., Hasher, L., Lenartowicz, A., 2006. Attentional disregulation: a benefit for implicit memory. *Psychol. Aging* 21 (4), 826–830.
- Rutman, A.M., Clapp, W.C., Chadick, J.Z., Gazzaley, A., in press. Early top-down control of visual processing predicts working memory performance. *J. Cogn. Neurosci.*
- Sakai, K., 2003. Reactivation of memory: role of medial temporal lobe and prefrontal cortex. *Rev. Neurosci.* 14 (3), 241–252.

- Sakai, K., Passingham, R.E., 2004. Prefrontal selection and medial temporal lobe reactivation in retrieval of short-term verbal information. *Cereb. Cortex* 14 (8), 914–921.
- Sakai, K., Rowe, J.B., Passingham, R.E., 2002. Active maintenance in prefrontal area 46 creates distractor-resistant memory. *Nat. Neurosci.* 5 (5), 479–484.
- Salthouse, T.A., Babcock, R.L., Shaw, R.J., 1991. Effects of adult age on structural and operational capacities in working memory. *Psychol. Aging* 6 (1), 118–127.
- Salvucci, D.D., Taatgen, N.A., 2008. Threaded cognition: an integrated theory of concurrent multitasking. *Psychol. Rev.* 115 (1), 101–130.
- Salvucci, D.D., Taatgen, N.A., Borst, J.P., 2009. Toward a Unified Theory of the Multitasking Continuum: From Concurrent Performance to Task Switching, Interruption, and Resumption Paper Presented at the Conference on Human Factors in Computing Systems, Boston, MA.
- Sreenivasan, K.K., Goldstein, J.M., Lustig, A.G., Rivas, L.R., Jha, A.P., 2009. Attention to faces modulates early face processing during low but not high face discriminability. *Atten. Percept. Psychophys.* 71 (4), 837–846.
- Sreenivasan, K.K., Jha, A.P., 2007. Selective attention supports working memory maintenance by modulating perceptual processing of distractors. *J. Cogn. Neurosci.* 19 (1), 32–41.
- Sreenivasan, K.K., Katz, J., Jha, A.P., 2007. Temporal characteristics of top-down modulations during working memory maintenance: an event-related potential study of the N170 component. *J. Cogn. Neurosci.* 19 (11), 1836–1844.
- Stroop, J.R., 1935. Studies of interference in serial verbal reactions. *J. Exp. Psychol.* 18, 643–662.
- Tanaka, J.W., Curran, T., 2001. A neural basis for expert object recognition. *Psychol. Sci.* 12 (1), 43–47.
- Taylor, M.J., Edmonds, G.E., McCarthy, G., Allison, T., 2001. Eyes first! Eye processing develops before face processing in children. *Neuroreport* 12 (8), 1671–1676.
- Tombaugh, T.N., 2004. Trail Making Test A and B: normative data stratified by age and education. *Arch. Clin. Neuropsychol.* 19 (2), 203–214.
- Tsang, P.S., Shaner, T.L., 1998. Age, attention, expertise, and time-sharing performance. *Psychol. Aging* 13 (2), 323–347.
- Vidnyanszky, Z., Sohn, W., 2005. Learning to suppress task-irrelevant visual stimuli with attention. *Vision Res.* 45 (6), 677–685.
- Vogel, E.K., McCollough, A.W., Machizawa, M.G., 2005. Neural measures reveal individual differences in controlling access to working memory. *Nature* 438 (7067), 500–503.
- Wechsler, D., 1987. Wechsler Memory Scale—Revised Manual. The Psychological Corporation, San Antonio, TX.
- Yesavage, J.A., Brink, T.L., Rose, T.L., Lum, O., Huang, V., Adey, M., Leirer, V.O., 1982. Development and validation of a geriatric depression screening scale: a preliminary report. *J. Psychiatr. Res.* 17 (1), 37–49.
- Yoon, J.H., Curtis, C.E., D’Esposito, M., 2006. Differential effects of distraction during working memory on delay-period activity in the prefrontal cortex and the visual association cortex. *Neuroimage* 29 (4), 1117–1126.
- Zanto, T.P., Gazzaley, A., 2009. Neural suppression of irrelevant information underlies optimal working memory performance. *J. Neurosci.* 29 (10), 3059–3066.
- Zanto, T.P., Hennigan, K., Ostberg, M., Clapp, W.C., Gazzaley, A., 2009. Predictive knowledge of stimulus relevance does not influence top-down suppression of irrelevant information in older adults. *Cortex*.