THE GERONTOLOGICAL SOCIETY OF AMERICA®

Journals of Gerontology: Psychological Sciences
cite as: *J Gerontol B Psychol Sci Soc Sci*, 2016, Vol. 00, No. 00, 1–10
doi:10.1093/geronb/gbw029
Advance Access publication March 14, 2016

OXFORD

Original Research Report

Inhibitory Selection Mechanisms in Clinically Healthy Older and Younger Adults

Teal S. Eich,[1] Beatriz M. M. Gonçalves,[1,2] Derek E. Nee,[3] Qolamreza Razlighi,[1] John Jonides,[4] and Yaakov Stern[1]

[1]Cognitive Neuroscience Division, Department of Neurology and the Taub Institute, Columbia University Medical Center, New York. [2]Faculdade de Medicina da Bahia, Federal University of Bahia, Salvador, Brazil. [3]Helen Wills Neuroscience Institute, University of California, Berkeley. [4]Department of Psychology, University of Michigan, Ann Arbor.

Correspondence should be addressed to Teal S. Eich, PhD, Cognitive Neuroscience Division, Department of Neurology and the Taub Institute, Columbia University Medical Center, 630 West 168th Street, P & S Box 16, NY 10032. E-mail: tse4@columbia.edu.

Received October 29, 2015; Accepted February 24, 2016

Decision Editor: Nicole Anderson, PhD

Abstract

Objective: Declines in working memory are a ubiquitous finding within the cognitive-aging literature. A unitary inhibitory selection mechanism that serves to guide attention toward task-relevant information and resolve interference from task-irrelevant information has been proposed to underlie such deficits. However, inhibition can occur at multiple time points in the memory-processing stream. Here, we tested whether the time point at which inhibition occurs in the memory-processing stream affects age-related memory decline.

Method: Clinically healthy younger (n = 23) and older (n = 22) adults performed two similar item-recognition working memory tasks. In one task, participants received an instruction cue telling them which words to attend to followed by a memory set, promoting perceptual inhibition at the time of encoding. In the other task, participants received the instruction cue after they received the memory set, fostering inhibition of items already in memory.

Results: We found that older and younger adults differed in their ability to inhibit items both during encoding and when items had to be inhibited in memory but that these age differences were exaggerated when irrelevant information had to be inhibited from memory. These results provide insights into the mechanisms that support cognitive changes to memory processes in healthy aging.

Key Words: Attention—Encoding—Inhibition—Memory—Suppression

Working memory, a complex construct that enables the short-term retention of information in order to guide goal-directed behavior (Baddeley, Logie, Bressi, Della Sala, & Spinnler, 1986; Jonides et al., 2008), supports a variety of cognitive abilities, including learning, reasoning, and verbal comprehension (Kane & Engle, 2002). Age-related declines in working memory span—the amount of information that can be stored and processed simultaneously—have frequently been reported (Charness, 1987; Gick, Craik, & Morris, 1988; Salthouse, 1988). According to one meta-analysis, the average older adult (M age = 70.2 years) lies at the 21st percentile of the distribution of working memory span scores among all adults (Verhaeghen, Marcoen, & Goossens, 1993). Given this, many have argued that reductions in memory capacity are directly responsible for general age-related deficits in cognition (Rabinowitz, Ackerman, Craik, & Hinchley, 1982; Salthouse, 1988).

Central to the efficient functioning of memory, however, is the ability to guide attention toward task-relevant information and resolve interference from task-irrelevant information. A case in point: most tasks that assess working memory span include multiple sets of trials, with recall required on each trial only for items from the most recent set of items. Failures to inhibit items from a previous list may cause proactive interference, where previously learned information interferes with learning and retrieval on a subsequent list (Anderson & Neely, 1996). According to the Inhibitory Deficit Theory (Hasher, Lustig, & Zacks, 2007; Hasher & Zacks, 1988), inhibitory failures represent a central mechanism that underlie commonly seen age-related memory deficits (Kester, Benjamin, Castel, & Craik, 2002). Inhibition under this theory is a single process that prevents irrelevant information from entering working memory, rids memory of irrelevant information, and stops habitual responses from being made (Hasher, Zacks, & May, 1999). Inhibitory failures, rather than a reduction in memory capacity itself, may therefore play a critical and causal role in typically seen age-related memorial deficits. Indeed, a recent study by Sylvain-Roy, Lungu, and Belleville (2015) that compared performance in older adults on three attentional control functions that underlie working memory (shifting, inhibition, and updating) found age-related impairments only in inhibitory processes after controlling for processing speed.

Inhibition can occur at multiple time points in the memory-processing stream, including during encoding or once information has entered memory. Inhibitory impairments during either or both of these time points have been posited to lead to memory failures (Healey, Hasher, & Campbell, 2013). Studies assessing negative priming have suggested that older adults have difficulty inhibiting information at the time of encoding (Hasher, Stoltzfus, Zacks, & Rypma, 1991; Kane, Hasher, Stoltzfus, Zacks, & Connelly, 1994). Other lines of research have shown that older adults fail to inhibit conceptual aspects of distracting information at the time of encoding (Kim, Hasher, & Zacks, 2007). Further, perceptual aspects of distracting information have been shown to reduce memory performance for older relative to younger adults (Kemper, McDowd, Metcalf, & Liu, 2008; Lustig & Hasher, 2001; Lustig, Hasher, & Tonev, 2006; Rozek, Kemper, & McDowd, 2012). Finally, results from studies using brain imaging have shown that older adults, unlike younger adults, do not inhibit task-irrelevant information during visual working memory encoding. These failures correlate with impaired memory (Gazzaley, Cooney, Rissman, & D'Esposito, 2005). Combined, these results suggest that older adults are impaired in the ability to inhibit distracting irrelevant information at the time of encoding.

Age invariance in encoding distractors has also been reported, however. Using electroencephalogram, older adults were shown to exhibit a selective deficit in inhibiting task-irrelevant information during visual working memory encoding, but only in the very early stages of visual processing (Gazzaley et al., 2008). Jost, Bryck, Vogel, and Mayr (2011) corroborated these findings showing that age-related differences in inhibiting distracting information during encoding were predominantly expressed between 350 and 550 ms after the start of encoding. Wnuczko, Pratt, Hasher, and Walker (2012) also reported that inhibition of distracting visual information presented in the early stages of visual processing was intact in both older and younger adults. These results suggest that the inhibition of irrelevant information in older adults is generally intact, albeit slowed.

With regard to inhibition of information already in memory, Sego, Golding, and Gottlob (2006) and Zellner and Bauml (2006) found that older adults performed equivalently to younger adults in a directed forgetting paradigm. In both of these studies, older and younger adults were able to recall the appropriate "remember" words, and recall of the "forget" words was poor, suggesting age equivalency in the ability to appropriately inhibit information from memory. However, several other studies have shown the opposite. Dulaney, Marks, and Link (2004) and Zacks, Radvansky, and Hasher (1996) found that older adults recalled fewer "remember" words and made more (erroneous) intrusions from the "forget" list. Anderson, Reinholz, Kuhl, and Mayr, (2011), using two variants of the think/no-think paradigm, demonstrated that older adults had compromised inhibitory abilities, which resulted in deficits in intentional suppression at the time of retrieval. More recently, Healey and colleagues (2013) showed that older adults, unlike younger adults, did not suppress competitors during interference resolution, demonstrating an age-related deficit specifically for inhibition of items already in memory.

Although numerous studies have examined different aspects of, and conditions under which inhibitory processes affect memory in older adults (Campbell, Hasher, & Thomas, 2010; Hasher & Zacks, 1988; Hulicka, 1967; Ikier & Hasher, 2006; Ikier, Yang, & Hasher, 2008; Kane, 2002; Logan & Balota, 2003; Radvansky, Zacks, & Hasher, 2005; Winocur & Moscovitch, 1983), it has been challenging to determine whether age-related inhibitory deficits result from declines in a unitary inhibitory system that is independent of when inhibition takes place, or whether instead there are qualitatively different kinds of inhibitory control processes, only some of which are affected by age. Many tasks that aim to assess the impact of inhibition in memory confound these different levels of processing (Cohen et al., 1997; Jonides & Nee, 2005; Milham, Banich, & Barad, 2003; Milham et al., 2001; Monchi, Petrides, Petre, Worsley, & Dagher, 2001) or test inhibition at only one point in the memory-processing stream. For example, directed forgetting paradigms test inhibition of items that are already in memory, whereas negative priming paradigms test inhibition at the time of encoding. Furthermore, the majority of tasks assessing inhibitory processes rely upon inhibition after-effects (e.g., testing performance on a target that served as a distractor in a previous trial), rather than direct tests of memory for items that should have been inhibited (Anderson et al., 2011).

To help shed light on the nature of inhibitory declines and their association to memory performance in older adults, we tested older and younger adults on a pair of tasks called Ignore and Suppress. These tasks are variants of the Sternberg Item-Recognition task (1969), in which a memory set containing a few items is presented, followed by a brief delay, and then a probe to which the participant responds positively if it matches an item in the memory set, and negatively otherwise. In both Ignore and Suppress, the items in the memory set are four English words presented in two different colors (red and blue). The difference between the two tasks rests in the placement of the instruction cue relative to the memory set. In Ignore, just before the memory set is presented, the participant is instructed to attend to items of a particular color (e.g., the blue ones) and to consider only these items when responding to the probe. In Suppress, the participant is instructed to remember items of a particular color after the memory set is presented and to consider only these items when responding to the probe. The critical index of inhibitory abilities (the Inhibition Index) is calculated as the difference in performance between two different types of probes, each of which requires a negative response: (a) Lure probes, which are items that appeared in the memory set but should have been either ignored or suppressed (RING in Figure 1) and (b) Control probes, which never appeared in the memory set (HEAT in Figure 1). Although the instructions in our tasks are to attend to and remember words of a specific color, we refer to the conditions as “Ignore” and “Suppress” to both represent the cognitive processes that are presumably involved in following these instructions, and to mirror previous literature using these tasks (Ahmari, Eich, Cebenoyan, Smith, & Blair Simpson, 2014; Eich, Nee, Insel, Malapani, & Smith, 2014; Joormann, Nee, Berman, Jonides, & Gotlib, 2010; Nee & Jonides, 2008, 2009; Smith, Eich, Cebenoyan, & Malapani, 2011).

Past research with these tasks allows for different predictions to be made about the magnitude of Inhibition Index in Ignore and Suppress. The Ignore task, according to functional MRI evidence provided by Nee and Jonides (2008), is equivalent in nature to a negative priming task. In a typical negative priming paradigm, participants are presented with items and told to attend to certain items (targets) and ignore the other items (distractors). On critical trials, a target that had served as a distractor on a previous trial is tested. Tipper (2001) showed that younger adults are slower to respond and less accurate on these critical trials (analogous to Lure probes in our task), relative to when they are tested on a target item that had not previously been a distractor (analogous to Control probes in our task). These reductions to performance arise because the target, which had previously been inhibited in order to shield processing from interference, now needs to be actively released from inhibition, a process that takes time and incurs errors. Older adults failed to exhibit these typical negative priming effects, and performed “better” than younger adults on these critical trials, presumably because they did not inhibit the distractors to begin with (and thus did not need to release them from inhibition when they became targets on later trials; Hasher et al., 1991; Kane et al., 1994).

In the Suppress task, the instruction cue telling participants which two words to remember comes only after the memory set has already been presented. The participant therefore cannot use perceptual inhibition to eliminate half of the words, as they do not yet know which words will be relevant and which will be irrelevant. Instead, in this task, memorial inhibition is needed to filter out the

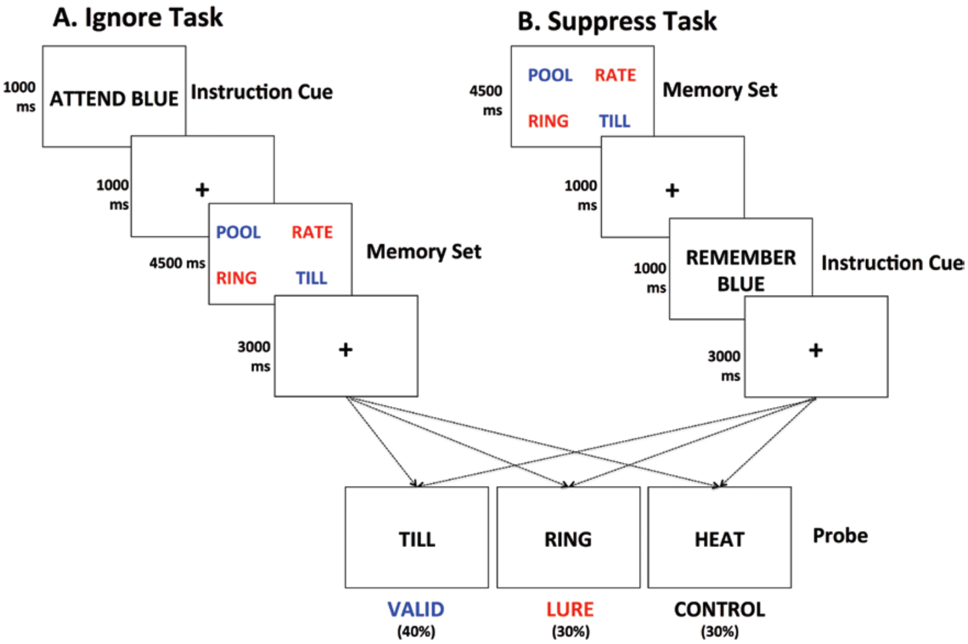

Figure 1. Schematic of the (**A**) Ignore task and (**B**) Suppress task. On each trial, participants received one type of probe. Valid probes required an affirmative response, whereas Lure and Control probes required a negative response.

two irrelevant words, allowing the two relevant words to be selected and rehearsed in working memory. Nee and Jonides (2008, 2009) reported the left ventrolateral prefrontal cortex (VLPFC) was uniquely recruited in the Suppress task but not in the Ignore task. This area has previously been shown to be involved in the resolution of proactive interference. Jonides and colleagues (2000), for example, assessed with positron emission tomography the neural function of older and younger adults using a recent-negatives paradigm, in which the critical trials were Lure probes on a current trial that had served as Valid (but untested) probes on a previous trial. For these probes, participants must adjudicate between the familiarity of the probe (which creates a prepotent positive response) and the current task demands (which require a negative response). They found that older adults showed reduced VLPFC activations and increased interference effects relative to younger adults, suggesting that this area is "functionally involved in mediating resolution among conflicting representations in working memory" (p. 188). In the Suppress task, then, if a participant is unable to use inhibitory control processes to suppress the irrelevant information (RING and RATE in Figure 1B), Lure probes will appear familiar, and participants will be more likely to respond positively on the basis of familiarity, increasing the difference score between the two types of negative probes (Monsell, 1978; Smith & Jonides, 1998).

These past results imply that the inhibition of perceptual information at the time of encoding and the inhibition of information already in memory, tapped by the Ignore and Suppress tasks, are qualitatively different cognitive processes, subserved by different neural mechanisms. When the instruction cue occurs before the memory set—in the Ignore task—inhibition occurs on perceptual representations prior to entry into memory. When the instruction cue is given after the memory set—in the Suppress task—inhibition occurs on information already in memory. The combination of these two tasks in one experimental paradigm allows us to make the following predictions: if older adults have compromised perceptual inhibitory abilities, the results will mirror those of negative priming tasks, and older adults will exhibit a Lure–Control Inhibition Index that is smaller (Lure = Control and will be closer to zero) than younger adults in the Ignore task. On the other hand, if inhibition of information in memory is impaired in older adults, they will exhibit a larger Lure–Control Inhibition Index (Lure > Control) than younger adults in the Suppress task.

Method

Procedure

Experimental tasks were presented using E-Prime software (Psychology Software Tools, Inc., Pittsburgh, PA). In the Ignore task (Figure 1A), participants were first presented with an instruction cue telling them to ATTEND to either the red or blue words. One second later, a four-word memory set was presented, followed by a test probe. Participants were instructed to respond positively to the probe if it matched either of the words that they were told to attend to (POOL and TILL in Figure 1A) and to respond negatively otherwise. Responses were made by pressing either the 0 key (labeled "NO") to indicate a negative response or the 1 key (labeled "YES") to indicate a positive response. Forty percent of the probes were "Valid," in which the test word was congruent with the instruction color (TILL in Figure 1A); 30% of the probes were "Lures," where the test word was of the color that should have been ignored or suppressed, and hence required a negative response (RING in Figure 1A), and the remaining 30% of the probes were "Controls," or words that were not present in the memory set (HEAT in Figure 1A). The Suppress task (Figure 1B) was similar to the Ignore task, except that participants were first presented with the four-word memory set, and then after a short delay, they received the instruction cue telling them to REMEMBER either the red or blue words. The rest of the trial events—including the three types of probes—were identical to the Ignore task, except that the interval between the instruction cue and the probe was shorter in order to keep the overall length of each trial equivalent across the two tasks.

Every participant received four blocks each of the Ignore and Suppress tasks, with 25 trials per block, including, on average, 10 Valid trials, 7.5 Control trials, and 7.5 Lure trials. Participants completed at least two practice blocks (one each of Ignore and Suppress) with feedback before beginning the experiment. Ignore and Suppress task blocks were alternated, with the order of the blocks counterbalanced across participants. All words were drawn from a set of 80 four-letter nouns. Feedback was not given on experimental trials.

Participants

Forty-five English-speaking participants [23 young (M age = 31.39 years, SD = 5.34, range 24–39, 14 women and 9 men) and 22 old (M age = 67.59 years, SD = 4.11, range 61–76, 10 women and 12 men)] were recruited to the study through random mail market surveys, posted flyers, and Internet advertisements. This sample size is adequate to detect simple and interaction effects using repeated measures analysis of variance (ANOVA) with a power of more than 90% ($1 - \beta = .91$) according to calculations done in G*Power (V3.1) (Faul, Erdfelder, Lang, & Buchner, 2007), assuming an α-level error probability of .05 and a medium effect size f of .25 (Cohen, 1969). Older adults were screened for dementia using the Mattis Dementia Rating Scale (Mattis, 1988). Education level did not differ between older and younger adults ($t(42) = -.59$, $p > .5$; education level was unavailable for one younger adult). After the procedure was fully explained, written informed consent was obtained for all participants.

The research was approved by the Columbia University Institutional Review Board.

Statistical Analysis

Statistical analyses were performed using SPSS 22 (SPSS, Chicago, Illinois). The data of major interest were the participant's mean reaction times (RTs) for correct trials, scaled RT for correct trials (the average RT for each condition divided by the average RT across conditions, within participants), and accuracy rates (% correct). For each participant, trials on which RTs were 2 *SD*s from their individual mean in each condition were excluded (an average of 8.9 trials for younger and 8.1 trials for older adults, ($t(43) = 1.34$, NS). We examined the cross-sectional relationship of Task (Ignore, Suppress), Trial Type (Valid, Control, Lure), and Age (Old, Young) using general linear models. Nominally significant p values were defined as $p \leq .05$.

Results

An ANOVA on RT with Age as a between-participant factor and Task and Trial Type as within-participant factors revealed significant main effects for all three factors: RT was slower in Suppress relative to Ignore ($F(1, 43) = 32.75$, $p < .001$, $\eta_p^2 = .43$), for Old relative to Young ($F(1, 43) = 12.82$, $p = .001$, $\eta_p^2 = .23$), and for Trial Type ($F(2, 86) = 54.28$, $p < .001$, $\eta_p^2 = .56$). Pairwise comparisons confirmed that Lure trials had longer latencies than both Control (M difference = 117.71, $p < .001$, 95% confidence interval (CI) [98.38, 137.04]) and Valid trials (M difference = 94.70, $p < .001$, 95% CI [66.20, 123.21]) but that Control and Valid trials did not differ from each other (M difference = −23.01, $p = .06$, 95% CI [−46.75, 0.74]). The model also revealed significant two-way interactions between Task and Age ($F(1, 43) = 10.84$, $p = .002$, $\eta_p^2 = .20$) and Task and Trial Type ($F(2, 86) = 66.42$, $p < .001$, $\eta_p^2 = .61$). The interaction of Trial Type and Age was not significant ($F(2, 86) = 1.99$, $p = .14$). However, critically, the two-way interactions were moderated by a significant three-way interaction between Age, Task, and Trial Type ($F(2, 86) = 11.28$, $p < .001$, $\eta_p^2 = .21$). These results indicate that the contrast between Trial Type was greater for older adults than for younger adults, but only in the Suppress task.

We next investigated the main index of selection processes, the Inhibition Index, operationalized as the difference scores between the two kinds of negative probes (Lure, Control). An ANOVA of the Inhibition Index across Task and Age revealed a main effect of Task ($F(1, 43) = 112.83$, $p < .001$, $\eta_p^2 = .72$) and a main effect of Age $F(1, 43) = 5.74$, $p = .02$, $\eta_p^2 = .12$). These main effects were qualified by a significant interaction of these two factors ($F(1, 43) = 24.57$, $p = .001$, $\eta_p^2 = .36$). Post hoc t tests revealed that in the Ignore task, older adults had a lower Inhibition Index than did younger adults ($t(43) = 2.05$, $p = .05$, 95% CI [0.56, 77.47]). On the other hand, in the Suppress task, the Inhibition Index difference score was significantly greater for older adults relative to younger adults ($t(43) = -4.23$, $p = .012$, 95% CI [−193.29, −68.42]). These results are illustrated in Figure 2.

As older adults exhibited longer latencies relative to younger adults, there is a possibility of scaled effects on the RT differences. To attempt to remove this effect, we transformed the RT data by dividing the mean RT for each condition by the average RT, within participants, creating scaled-proportional RT values. We then performed the comparable analyses using these values. An ANOVA on scaled RT with Age, Task, and Trial Type revealed that scaled RT was slower in the Suppress relative to the Ignore condition ($F(1, 43) = 35.69$, $p < .001$, $\eta_p^2 = .45$) and for Trial Type ($F(2, 86) = 67.25$, $p < .001$, $\eta_p^2 = .61$). Pairwise comparisons confirmed that Lure trials had longer latencies than both Control trials (M difference = 0.13, $p < .001$, 95% CI [0.11, .15]) and Valid trials (M difference = 0.10, $p < .001$,

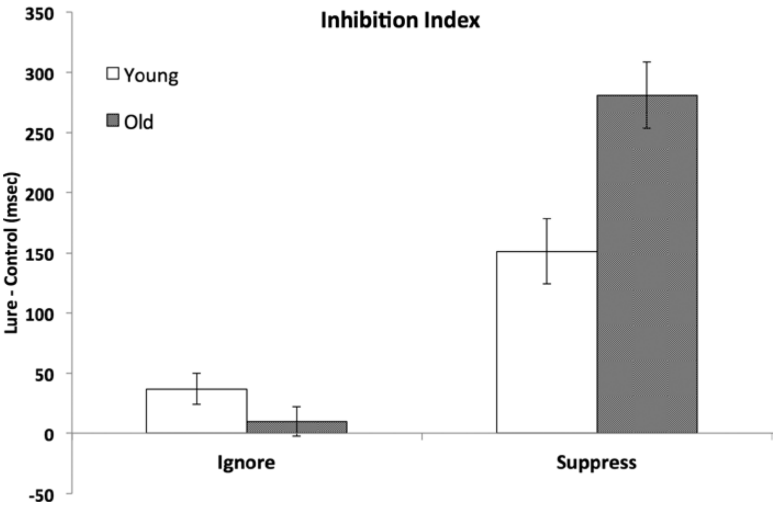

Figure 2. The Inhibition Index (performance on Lure trials–Control trials) as a function of Age (Younger vs Older adults) and Task (Ignore vs Suppress). Error bars indicate standard error of the mean.

95% CI [0.08, 0.13]), and Valid trials had longer latencies than Control trials (M difference = –0.03, $p = .03$, 95% CI –0.05, –0.002]). The difference in scaled RT between old and young was not significant ($F(1, 43) < 1$). The model also revealed significant two-way interactions between Task and Age ($F(1, 43) = 9.74$, $p = .003$, $\eta_p^2 = .19$) and Task and Trial Type ($F(2, 86) = 74.63$, $p < .001$, $\eta_p^2 = .63$). The interaction of Trial Type and Age was not significant ($F(2, 86) < 1$). However, critically, like with the raw RT data, the two-way interactions were moderated by a significant three-way interaction between Age, Task, and Trial Type ($F(2, 86) = 4.47$, $p = .01$, $\eta_p^2 = .09$).

The ANOVA on the scaled-RT Inhibition Index revealed a main effect of Task ($F(1, 43) = 124.86$, $p < .001$, $\eta_p^2 = .74$). The main effect of Age was not significant $F(1, 43) < 1$). However, like before, we found a significant interaction between these two factors ($F(1, 43) = 10.99$, $p = .002$, $\eta_p^2 = .21$). Post hoc t tests revealed once again that in the Ignore task, older adults had significantly lower scaled differenced scores than did younger adults ($t(43) = 2.29$, $p = .03$, 95% CI [0.01, 0.08]), but in the Suppress task, older adults had significantly greater scaled difference scores ($t(43) = -2.37$, $p = .02$, 95% CI [–0.13, –0.01]).

To test for the dissociability of the mechanisms supporting performance in the Ignore and Suppress tasks, we also correlated performance on the two measures of inhibition, both collapsing across Age as well in each Age group separately. The correlation between the Ignore Inhibition Index and the Suppress Inhibition Index was not significant for either the younger ($r = .24$, $n = 23$, $p = .28$) or the older adults ($r = .076$, $n = 22$, $p = .74$) alone, or across the entire sample ($r = -.06$, $n = 45$, $p = .69$).

Finally, we investigated accuracy rates. We found a significant main effect of Task ($F(1, 43) = 22.08$, $p < .001$, $\eta_p^2 = .34$) such that performance was greater in the Ignore task relative to the Suppress task, and for Trial Type ($F(2, 86) = 5.73$, $p = .005$, $\eta_p^2 = .12$) such that accuracy was highest on Control trials and lowest for Lure trials. Pairwise comparisons confirmed that Lure trials had lower accuracy rates than both Control trials (M difference = –.04, $p = .004$, 95% CI [–0.65, –0.01]) and Valid trials (M difference = –0.03, $p = .02$, 95% CI [–0.05, –0.003]). However, accuracy rates for Valid and Control trials did not significantly differ (M difference = 0.01, $p = .22$). We also found a significant interaction between Task and Trial Type ($F(2, 86) = 3.69$, $p = .03$, $\eta_p^2 = .08$). However, neither the main effect of Age nor any of the Age interactions were significant (all Fs < 1). The main effect of Task in an ANOVA of the Inhibition Index for accuracy was not significant ($F(1, 43) = 3.79$, $p = .06$, $\eta_p^2 = .08$), nor was the main effect of Age or the Task by Age interaction (Fs < 1).

Overall RT, scaled RT, and accuracy data are presented in Table 1. Across the experiment, younger participants averaged fewer than 6% errors (94.2% accuracy), and older adults averaged fewer than 7% errors (93.6% accuracy). These high accuracy rates potentially reflect a ceiling effect, and thus the RT analyses may provide better measures of performance across the different tasks and trials as a function of age. Taken together, these results suggest that, compared with younger adults, clinically healthy nondemented older adults show inhibitory impairments both for perceptual information and for memorial information, but this impairment was exaggerated in the Suppress task relative to the Ignore task.

Discussion

Inhibitory deficits have been proposed to mechanistically underlie working memory reductions in older adults. In the current study, we tested younger and older adults on the Ignore and Suppress tasks, which allow the contributions of inhibition at different time points in the memory-processing stream to be simultaneously, but separately, examined and teased apart (in support of the dissociability of these two tasks, we found that performance measures of inhibition in the Ignore and Suppress tasks were not correlated, either across the entire sample, or in each Age group

Table 1. Overall Reaction Time (RT), Scaled RT, and Accuracy Data

		Ignore [Mean (*SD*)]		Suppress [Mean (*SD*)]	
	Trial type	Young	Old	Young	Old
RT (ms)	Control	748.56 (254.13)	943.37 (189.15)	767.21 (284.55)	1,004.47 (142.72)
	Lure	794.96 (281.12)	950.56 (178.02)	910.49 (309.82)	1,278.61 (240.81)
	Valid	781.26 (238.36)	970.89 (170.86)	769.33 (273.15)	1,034.35 (168.27)
	Lure–Control	46.21 (63.55)	7.19 (64.35)	143.29 (67.01)	274.15 (131.78)
Scaled RT	Control	0.95 (0.09)	0.92 (0.08)	0.96 (0.06)	0.98 (0.06)
	Lure	0.99 (0.06)	0.92 (0.08)	1.15 (0.11)	1.24 (0.10)
	Valid	0.99 (0.09)	0.95 (0.08)	0.97 (0.06)	1.01 (0.09)
	Lure–Control	0.05 (0.07)	0.99 (0.02)	0.19 (0.09)	0.26 (0.11)
Accuracy (proportion correct)	Control	0.997 (0.06)	0.97 (0.05)	0.94 (0.13)	0.94 (0.15)
	Lure	0.95 (0.09)	0.96 (0.05)	0.89 (0.15)	0.86 (0.15)
	Valid	0.96 (0.08)	0.95 (0.06)	0.94 (0.08)	0.92 (0.10)
	Lure–Control	–0.02 (0.05)	–0.02 (0.05)	–0.04 (0.12)	–0.07 (0.17)

alone.). Of significant interest was the finding of an interaction between the Ignore and Suppress task Inhibition Indexes and Age, which revealed that age differences in inhibitory processes were especially large in the Suppress task. Older adults in the Suppress task responded significantly slower to Lure probes relative to Control probes, and this difference was significantly larger for older adults relative to younger adults. These results both corroborate results from Inhibitory Deficit Theory proposed by Hasher and Zacks (1988), indicating that older adults show deficits in inhibition, and extend them, showing that multiple forms of dissociable inhibitory abilities are compromised.

One might argue that the age-related effects presented here could be explained by a pure difficulty argument. If we operationalize difficulty by RT, as is often done in tasks assessing cognitive control processes, in the Suppress task, older adults show longer latencies and an increased Lure–Control difference score. However, it is critical to note that the crossover two-way interaction rules out a purely difficulty-based interpretation of our results. In the Ignore task, Lure trials were also more difficult than Control trials, as they have larger RTs. Yet older adults show a narrowing of the gap between these two types of negative trials. Because in most tasks of cognitive control, worse performance is typically positively related to a greater effect, here, pure difficultly can be de-correlated from the putative index of the inhibitory control process. That is, it isn't the case that older adults are just slower; for the Ignore Inhibition Index, they are actually relatively faster than younger adults. The scaled RT analyses show the same pattern of results, further driving this point.

It is also possible that the age-related deficit in the Suppress task reflects noninhibitory mechanisms. Older adults show declines in source memory, including impairments in memory for contextual features of events such as color and location (Chalfonte & Johnson, 1996). In the Suppress task, the participant must bind item information (stimuli color) with task demands (which stimuli should be remembered and suppressed). The difference between Lure and Control items could reflect a failure of relational encoding, rather than a failure in inhibitory processes. However, if this were the case, one would expect to find the analogous difference between Valid and Control trials. Valid trials, like Lure trials, require relational encoding and source memory processes. In our data, we did not find a significant difference between Valid and Control trials, whereas we did find differences between Lure and Control trials. Thus, we believe that a source memory deficit hypothesis cannot explain our pattern of results.

What drives the ability to suppress irrelevant information from memory, and why is this compromised in the older adults? The left VLPFC has been shown to be uniquely activated in the Suppress task but not in the Ignore task (Nee & Jonides, 2008, 2009). Numerous studies have associated the VLPFC with the resolution of proactive interference. Jonides and colleagues (2000), for example, showed that older adults had reduced VLPFC activations and increased interference effects relative to younger adults in a task in which proactive interference resolution is required. Nee, Jonides, and Berman (2007) replicated Jonides and colleagues (2000) in younger adults, showing left VLPFC involvement during the recent-probes task, and extended these findings, showing that this area was also activated in a directed forgetting task. An fMRI study of the Suppress task that assessed performance in patients with schizophrenia (who have known prefrontal dysfunction) helped to further localize the nature of inhibitory control processes, showing that whereas healthy control participants had reductions in posterior-VLPFC activity after the instruction cue, commensurate with ridding working memory of irrelevant information, the patients did not, implying that they did not inhibit items from memory. At the time of the probe, the patients also showed divergent patterns of brain activity in mid-VLPFC. A mediation analysis revealed that this strain on interference-resolution processes at the time of the probe resulted in increased behavioral errors (Eich et al., 2014). For the older adults in the current study, it is possible that a similar neural mechanism is driving the results we see behaviorally in the Suppress task. Indeed, several prominent theories of age-related cognitive dysfunction emphasize a preferential role of prefrontal brain function in accounting for cognitive change due to senescence (Braver & Barch, 2002; Buckner, 2004; Rajah & D'Esposito, 2005; Raz et al., 1997; Rossi et al., 2004; Salat et al., 2004; West, 1996). Future work using brain imaging to investigate the neural basis of the time point–localized inhibitory deficits in the Suppress task in older adults would help to shed light on the neural basis of this age-related change to memory.

Along with the finding of impaired inhibition in the Suppress task for the older relative to the younger adults, we also found that older adults showed a reduced Lure–Control difference scores relative to younger adults in the Ignore task. As was discussed in the introduction, negative priming effects arise when reactions to items that were previously ignored and later tested are slowed, presumably due to lasting perceptual inhibition of these items (Tipper, 2001). Previous work has shown reductions in negative priming effects in older adults, which has been taken as evidence of impaired perceptual inhibition (Hasher et al., 1991; Kane et al., 1994). Our results fit nicely with these findings. The increased latencies to the Lure trials that we see in younger relative to older adults suggest that older adults fail to perceptually inhibit the to-be-ignored items. For the younger adults, perceptual inhibition of these items carries over to the probe, and, when the probe is a Lure, responses are slowed. For the older adults, on the other hand, responses are not slowed, as the items do not have to be released from inhibition in order to be encoded at the time of the probe. The accuracy data reveal that these differences in RT are not a result of a speed-accuracy trade off. Indeed, both younger and older adults achieve very high accuracy rates on the Lure trials, and their difference scores between Lure and Control trials are nearly identical. Thus, it is not that the older adults are less accurate. Instead, they are equally accurate, but relatively faster than younger adults.

It is important to note, however, that the Ignore task and negative priming paradigms diverge in several noteworthy ways. Often (see Mayr & Buchner, 2007), but not always (cf. Neill, Valdes, Terry, & Gorfein, 1992), the to-be-attended stimulus is superimposed on the to-be-ignored item, unlike in our paradigm where the to-be-attended and to-be-ignored items were in nonoverlapping spatial positions. Further, the stimuli presentation times in a negative priming task are typically much shorter than those in our paradigm and are generally based upon the minimum viewing time necessary to correctly identify a stimulus. The brief nature of the presentation reduces “the possibility of switching attention to the ignored object after selection of the attended object” (Tipper, 1985, p. 577). Finally, the critical measure of inhibition in the negative priming task results from differences in accepting a previously ignored versus nonpresented item, rather than rejecting it, as in our task.

Older adults smaller Ignore Inhibition Index could also be due to the fact that they simply did not attend to the noncued color words in the first place. Younger adults, by contrast, may have attended to both the target words and the distractors, perceptually inhibited the distractors, and, as a result, showed a perceptual interference effect for Lure probes. However, work on visual working memory has shown that older and younger adults are equally captured by distractors, although they show differences in the time point at which perceptual filtering is expressed. Jost and colleagues (2011), for example, found that age-related differences in perceptual filtering were expressed in the early stages of encoding, consistent with the work of Gazzaley and colleagues (2005, 2008). Further, the reading of familiar words, such as the ones used in the current paradigm, is presumably fast and automatic (Kahneman & Chajczyk, 1983), and in our paradigm, the memory set was displayed for a relatively long duration (4.5 s). Given this, it seems unlikely that all of the words were not read and that perceptual representations were not formed for all words. Future studies testing recognition of all items, using eye tracking, and varying the stimulus-onset asynchrony between the memory set and the probe could help determine the locus of the smaller difference score in the Ignore task.

Conclusions

Memory tasks used to assess age-related memory decline, including many of the tasks commonly used in neuropsychological batteries, often do not take into consideration the nonunitary mechanisms that can lead to memory decline, and thus may fail to correctly assess what exactly has been affected by age. In the current study, we found that older and younger adults differed in their ability to inhibit items both during encoding and when items had to be inhibited in memory but that these age differences were exaggerated when information had to be inhibited from memory. Understanding inhibitory deficits in memory on a component process level will enable us to determine precisely which aspects are and are not impaired in older adults. With this knowledge will come greater accuracy in differentiating healthy from pathological aging, which could lead to the development of therapeutic strategies to diminish the effects of interference in memory, thus enhancing quality of life in older adults.

Funding

Support for this publication was provided by the Dr. Rita G. Rudel Foundation and the U.S. Department of Health and Human Services–National Institutes of Health–National Institute of Mental Health (T32 MH020004) to T.S. Eich, the CAPES Foundation, Ministry of Education of Brazil, Brazil to B. M. M. Gonçalves, and the U.S. Department of Health and Human Services–National Institutes of Health–National Institute on Aging (R01 AG-026158) to Y. Stern.

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