

Deficit in switching between functional brain networks underlies the impact of multitasking on working memory in older adults

Wesley C. Clapp, Michael T. Rubens, Jasdeep Sabharwal, and Adam Gazzaley¹

Departments of Neurology, Psychiatry, and Physiology, The W. M. Keck Foundation Center for Integrative Neuroscience, University of California, San Francisco, CA 94158

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Multitasking negatively influences the retention of information over brief periods of time. This impact of interference on working memory is exacerbated with normal aging. We used functional MRI to investigate the neural basis by which an interruption is more disruptive to working memory performance in older individuals. Younger and older adults engaged in delayed recognition tasks both with and without interruption by a secondary task. Behavioral analysis revealed that working memory performance was more impaired by interruptions in older compared with younger adults. Functional connectivity analyses showed that when interrupted, older adults disengaged from a memory maintenance network and reallocated attentional resources toward the interrupting stimulus in a manner consistent with younger adults. However, unlike younger individuals, older adults failed to both disengage from the interruption and reestablish functional connections associated with the disrupted memory network. These results suggest that multitasking leads to more significant working memory disruption in older adults because of an interruption recovery failure, manifest as a deficient ability to dynamically switch between functional brain networks.

Working memory (WM), the ability to store and manipulate information in the mind over brief periods of time, is critical for a wide variety of cognitive abilities and real life activities (1). It has been demonstrated that WM performance is negatively impacted by the presence of external stimuli that are outside the focus of our memory goals (2, 3). This interference occurs whether there is an attempt to ignore these stimuli (i.e., distractions), or attend to them as a component of a concurrent, secondary task (i.e., interruptions, or multitasking) (4). We recently showed that older adults experience a more negative impact by distraction on WM performance compared with younger adults, and an even greater impairment when multitasking (5). There is extensive literature indicating that older adults are highly susceptible to distraction and that this leads to impairment in performance (for review, see refs. 6 and 7). In terms of a greater impact of multitasking on WM in aging, this finding is consistent with the detrimental influence that multitasking has been shown to have on a wide range of activities in older individuals (8–10). Research directed at understanding the basis of age-related interference effects is becoming increasingly important, as older adults remain engaged in the work force later in life (11), which itself is evolving into a more demanding, high-interference environment (12).

To explore the neural basis of age-related WM disruption by distractions, we previously conducted a series of experiments using electroencephalography (EEG) and functional MRI (fMRI) recordings. Functional MRI measures revealed that older individuals inappropriately direct excessive attention toward processing visual stimuli that are entirely irrelevant (i.e., distractions), and that this correlates with diminished WM performance (13). EEG studies further showed that this occurs early during visual processing (<200 ms after stimulus onset), whether or not individuals are prepared for the distractor (5, 13–15). Moreover, the degree that both distractors and interruptors are processed correlates with reduced WM performance in both younger and older

adults (4, 5). Based on these findings, we had hypothesized that the more negative impact on WM performance by interruptions in older adults was because of their directing excessive attention and overprocessing interrupting stimuli compared with younger adults. However, a recent study revealed that this was not the basis of the aging interruption effect (5). Using a well-characterized EEG marker of visual stimulus processing and attentional modulation (i.e., N170 latency index), this study showed that in the setting of an interrupting secondary task, older adults did not process the interrupting stimuli more than younger adults, suggesting that a different mechanism underlies the impact of interruptions on WM performance in aging.

The goal of the present study was to use fMRI to elucidate the neural mechanisms that underlie the greater impact of interruption on WM performance in older compared with younger adults. To accomplish this, the same fMRI experiment that was used to assess WM and interference in younger adults (4) was performed in older adults and direct comparisons were made between the two datasets. In brief, participants were instructed to remember a natural scene image, maintain it in mind for 14.4 s, and then respond by indicating whether or not a probe stimulus matched the encoded image. External interference was introduced during the middle of the maintenance period of the delayed recognition task either as a distracting face (participants were instructed to ignore) or an interrupting face (participants were instructed to make a sex/age decision). There were also “no interference” and “passive viewing” conditions that served as baseline tasks (Fig. 1). Each of these conditions was presented in blocks.

We posited three hypotheses for the neural basis of the aging interruption effect, which were systematically evaluated in the present fMRI study: (i) Older adults do direct excessive attention to interrupting stimuli and process them more than younger adults, resulting in greater interference effects, and this was not detected using EEG measures in the previous study. (ii) Neural processes of task re-engagement occurring immediately after interruptions are compromised in aging. In the recent fMRI study on younger adults, we showed that interrupting stimuli during WM maintenance disrupt ongoing prefrontal cortex-visual cortex functional connectivity. This connectivity is then re-established in the delay period following the interruption, and this is associated with successful WM performance. We interpret this network reinstatement as reflecting successful task switching from the interruptor task back to the memory task. (iii) Task switching involves two processes: disengagement from the interrupting task and re-engagement of the original task (16). Our third hypothesis is that older adults do not effectively disengage from the interrupting stimuli, resulting in extended retroactive interference

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¹To whom correspondence should be addressed. E-mail: adam.gazzaley@ucsf.edu.

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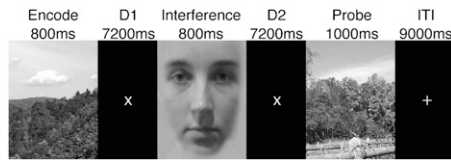


Fig. 1. Experimental paradigm. Participants performed four blocked and counterbalanced tasks. For interrupting stimuli (IS), distracting stimuli (DS), and no interference (NI), an encode scene was followed by a delay and a probe scene at the end of each trial. For IS and DS, an interfering face stimulus appeared middelay, requiring attention only in IS. For NI, an equal-length delay replaced the interfering face. For passively viewed (PV), participants were told to passively view the scene and face, and the probe consisted of responding to the direction of an arrow.

effects. Of note, older adults have been shown to exhibit impaired task-switching abilities (17, 18), which may be a consequence of any of these possibilities.

Results

Behavioral Data. To investigate age-related changes in susceptibility to interference, we first compared WM accuracy across tasks. Older participants performed significantly worse in the presence of interference. They achieved the highest accuracy in the no interference task (NI) (96%), which declined in the presence of distracting stimuli (DS) [93%, $t(16) = 3.43$, $P < 0.005$], and further when confronted with interrupting stimuli (IS) [88%, $t(16) = 5.222$, $P < 0.00005$] (Table S1). WM performance was also significantly worse on the IS task compared with the DS task [$t(16) = 2.92$, $P < 0.01$]. This same pattern of results was observed in older adults who performed a similar version of this experiment, with faces used as both the encoded and interfering stimuli (5). The data from the older adults were directly compared with accuracy results from younger adults who engaged in the identical fMRI experiment (Table S1) (4), using an ANOVA with task (NI, DS, IS) as the within-participant factor and age (younger, older) as the across-participant factor. This analysis revealed a main effect of task [$F(2,70) = 12.341$, $P < 0.05$], no effect of age [$F(1,35) < 1$, $P > 0.05$], and a task by age interaction [$F(2,70) = 3.162$, $P < 0.05$]. To further evaluate this interaction and the impact of interference on WM accuracy, we compared the reduction in task performance from the NI condition across age groups (i.e., NI-IS and NI-DS). This comparison revealed that the impact of interruption on WM was greater for older adults [$t(35) = 2.060$, $P < 0.05$], but the impact of distraction did not differ between age groups [$t(35) < 1$, $P > 0.05$]. There was also no age difference between the IS-DS contrast [$t(35) = 1.17$, $P > 0.05$].

Reaction time data revealed that older adults responded fastest during NI (1,210 ms, SE 122), and this was not significantly different from DS (1,226 ms, SE 127), but faster than IS (1,281 ms, SE 133) ($P < 0.05$). The younger adults exhibited the following reaction times: NI (1,089 ms, SE 86), DS (1,072 ms, SE 87), and IS (1,063 ms, SE 75) (Table S1). Comparing reaction times across age groups revealed no main effect of condition [$F(2,70) = 1.3$, $P > 0.05$] or age [$F(1,35) = 3.86$, $P = 0.057$], but an age by condition interaction [$F(2,70) = 3.3$, $P < 0.05$]. This interaction was driven by a significant difference between the age groups only in the interruption task ($P < 0.05$).

Thus, the reaction time and accuracy data converge to reveal that WM recognition performance in older adults was both slower and less accurate in the presence of interruption compared with younger adults. Also of note, all participants exhibited accuracy of greater than 90% in responding to the sex/age interruption task (i.e., reporting males over 40 y of age).

Neural Data. Hypothesis 1: Older adults process interruptors more than younger adults. To investigate if older adults direct more resources to processing interrupting stimuli compared with younger adults, we assessed the blood-oxygen level-dependent (BOLD) response

in the region of the visual cortex maximally selective to the interrupting stimulus category (i.e., faces) during the time period when these stimuli were present. The fusiform face area (FFA) is selectively responsive to faces (19), and activity in this region is modulated by top-down attentional processes (13). Analysis of the current data revealed that FFA activity in response to interfering face stimuli differed depending on the task. Consistent with what was determined for younger adults, BOLD response in older adults to interruptors (IS) was higher than for distractors (DS) [$t(16) = 2.45$, $P < 0.05$] and passively-viewed intervening stimuli (PV) [$t(16) = 2.25$, $P < 0.05$] (Fig. 2). Direct comparisons to fMRI data from younger participants showed a main effect of condition [$F(2,70) = 11.9$, $P < 0.05$], but no effect of age [$F(1,35) = 2.31$, $P > 0.05$] and no condition by age interaction [$F(2,70) = 1.89$, $P > 0.05$]. Thus, these fMRI results support previous conclusions that older adults do not direct more attention to processing interrupting faces compared with younger adults (5).

To evaluate the relationship between activity modulation to interrupting stimuli and WM performance in older adults, fMRI modulation indices from the FFA (IS-PV; see *Materials and Methods*) and WM accuracy data were subjected to an across-participant regression analysis. This analysis showed a significant negative correlation between enhancement of interruptors and WM accuracy in older adults, revealing that participants who allocated greater visual processing resources to the interruptor, performed worse on the WM task ($R = -0.6$, $P < 0.05$) (Fig. 2). This finding was also true for younger participants performing this same fMRI experiment ($R = -0.54$, $P < 0.05$) (4) (Fig. 2) [with no difference in correlations between age groups ($z = 0.25$, $P = 0.8$)], as well as both younger and older participants engaged in a similar version of the experiment using EEG markers of attention modulation (i.e., N170 latency indices) (5). Although not the focus of the present study, a strong correlation between the suppression index (DS-PV) and WM performance ($R = 0.51$, $P < 0.05$) exists, where those participants who exhibited the most suppression, had the highest WM accuracy in the DS task.

In summary, the relationship between the degree that interruptors were processed and the impact that this processing had on WM performance is preserved in aging. This finding converges with data from our previous EEG experiment (5), thus processing of the interruptors does not account for the age-related interruption effect (rejection of hypothesis 1).

Hypothesis 2: Older adults exhibit impairment in reactivating representations of the memoranda after interruption. A previous fMRI study in younger adults revealed that a region of the prefrontal cortex, the right middle frontal gyrus (MFG), and the visual cortical region that selectively represents scene memoranda [parahippocampal place area (PPA) (20)] remained functionally connected throughout the maintenance period in tasks with no interference, as well as when a face was a distractor, but that connectivity dropped significantly in the presence of a face interruptor (4). This finding was interpreted as a disruption in the maintenance of scene memoranda when attention was directed toward the interruptor. Data suggested that representations of the scene memoranda were reactivated in the delay period following the interruption, as reflected by a re-establishment of significant MFG-PPA functional connectivity [$t(16) = 5.79$, $P < 0.00001$].

To assess these same measurements in older adults, an identical functional connectivity analysis was conducted for the older participants. The approach involved first collapsing the data from the encoding stages of all three WM conditions (IS, DS, and NI) and identifying regions within the prefrontal cortex that were most strongly correlated with the PPA. In older adults, this analysis revealed a single area in the prefrontal cortex significantly correlated with the PPA (i.e., right MFG). Of note, this MFG region identified in older adults was 8.40 mm from the right MFG region identified and evaluated in younger adults [Montreal Neurological Institute (MNI) coordinates: Younger (46, 36.1, 28.6), Older (41.7, 31.1, 23.4)] (4). Average z -scores were then extracted from each participant's correlation maps from the right MFG region during four stages of each condition (encode, delay

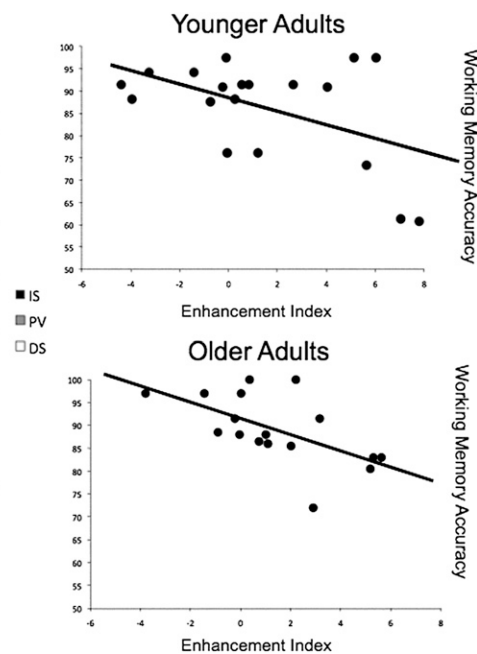
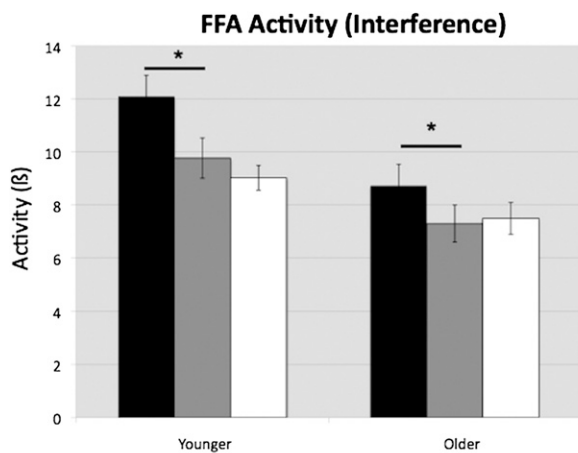


Fig. 2. Visual association cortex activity. BOLD response in the FFA shows modulation based on task instructions; that is, activity is highest in the interruptor condition (IS vs. PV and IS vs. DS, $P < 0.05$). The amount of attention that participants allocate toward an interruptor (IS, enhancement) correlates negatively with their WM performance (younger: $R = -0.54$, $P < 0.05$; older: $R = -0.6$, $P < 0.05$).

1, distractor, and delay 2). Comparisons next focused on the interference period in older adults, and showed that MFG-PPA functional connectivity was significantly diminished in the interruptor condition (IS) compared with the same time period when no interfering stimulus was present (NI) [$t(16) = 3.22$, $P < 0.05$] or when a distractor was present (DS) [$t(16) = 2.95$, $P < 0.05$] (false-discovery rate correction for multiple condition and interval comparisons) (Fig. 3, *Upper*). Furthermore, at the time of interference, connectivity was only significant in DS and NI conditions [$t(16) = 2.56$, 2.83 $P < 0.05$], and not in IS [$t(16) = 1.25$, $P > 0.05$]. This pattern was identical to the functional connectivity findings in the interference period in younger adults (4), and suggests that the rehearsal of the memoranda in both age groups is disrupted by the interruptor.

However, unlike younger adults, where significant MFG-PPA connectivity was re-established in the delay period following interruption (delay 2), functional connectivity in older adults did not return to significant levels (Fig. 3, *Upper*). Additionally, it remained reduced relative to both DS and NI levels [$t(16) = 2.95$, 3.18 , $P < 0.05$], also in contrast to the pattern in younger adults, where there was no difference between the three conditions in delay 2 (4). These results suggest that reactivation of internal representations of the scene memoranda following interruption was impaired in older adults. Further investigation to directly assess whether older adults differed from younger adults in their re-engagement of the WM network (i.e., the change in MFG-PPA connectivity between the interruption and the post-interruption delay period), involved a two-way ANOVA with age (younger, older) and stage (interruption, delay 2) as factors. This analysis revealed a significant effect of stage [$F(1,35) = 9.73$, $P < 0.05$], age [$F(1,35) = 9.49$, $P < 0.05$], and an age X stage interaction [$F(1,35) = 4.15$, $P < 0.05$]. Post hoc t tests revealed that during interruption there was no significant difference between age groups [$t(35) = 1.19$, $P > 0.05$], whereas younger adults showed significantly higher connectivity (i.e., re-engagement) during the postinterruption delay period compared with older adults [$t(35) = 3.59$, $P < 0.05$]. Evidence for the behavioral relevance of this finding was generated by a whole-brain analysis, which showed that in both younger and older adults, MFG-PPA connectivity in delay 2 correlated with subsequent WM accuracy (both $P < 0.05$, corrected for multiple comparisons) (4). These findings suggest that those participants who were best able to reactivate the stored memoranda postinterruption (via restora-

tion of MFG-PPA connectivity) performed with the highest WM accuracy, highlighting the importance of assessing individual differences even in age-comparative studies (21). However, as a group, older participants were unable to attain levels achieved by the younger participants, which suggests an age-related reactivation deficit (support for hypothesis 2).

Hypothesis 3: Older adults continue to process interruptors after they are no longer present or relevant. To assess age-related differences in functional connectivity associated with the face interruptor, we evaluated connectivity measures between the right MFG region identified in the previous analysis and the FFA across the stages of each WM task in both younger and older adults. The results for both age groups indicated that there was no significant MFG-FFA connectivity for any task during the encoding (cue) period or delay 1 period. In the interference stage of the WM task, connectivity in the IS condition was significantly greater than in the DS [$t(16) = 3.09$, $P < 0.05$] and NI conditions [$t(16) = 2.98$, $P < 0.05$]. This finding was also true in younger adults [IS > DS: $t(19) = 2.87$, $P < 0.05$; IS > NI: $t(19) = 2.94$, $P < 0.05$]. These results were expected because IS was the only condition in which participants were instructed to direct attention toward the faces (Fig. 3, *Lower*). Further analysis revealed that there was no significant difference in MFG-FFA connectivity between age groups during the interruption period [$t(35) = -0.112$, $P > 0.05$]. These connectivity findings thus offer supporting evidence of the previous conclusion based on univariate FFA activity that both younger and older adults allocate the same degree of attention to processing the interrupting face (rejection of hypothesis 1).

In assessing the second delay period (postinterruption), younger participants' connectivity between the right MFG and FFA diminished to nonsignificant levels and did not differ from the connectivity measures in DS or NI ($P > 0.05$), but connectivity in older participants remained significantly elevated, and to a greater degree than DS and NI [$t(16) = 3.05$, 3.19 $P < 0.05$] (Fig. 3, *Lower*). Moreover, older adults showed significantly higher MFG-FFA connectivity in the postinterruption delay period compared with younger adults [$t(35) = -2.77$, $P < 0.05$]. PPA-MFG and FFA-MFG connectivity did not correlate across participants in the postinterruption period ($R = 0.36$, $P = 0.16$).

Thus, younger participants disengage the functional network associated with processing the interruptor during the second delay period, and older adults do not disengage during this time period (support for hypothesis 3).

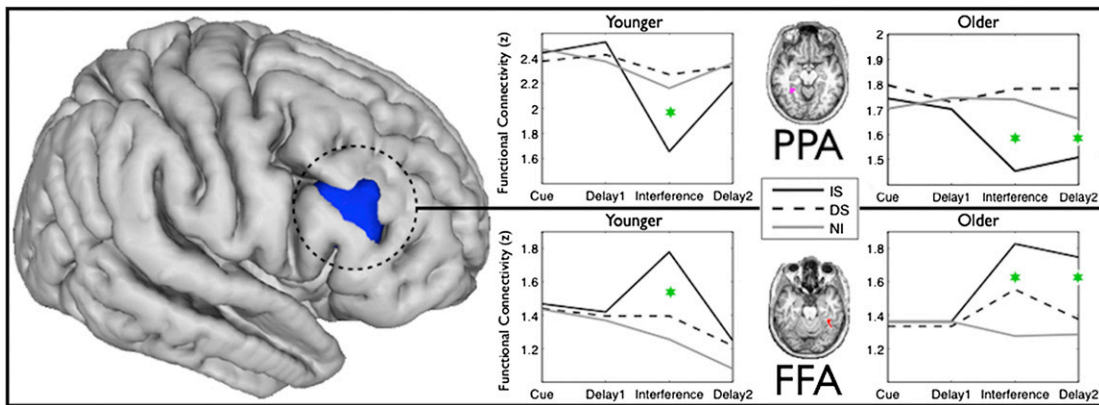


Fig. 3. MFG functional connectivity with PPA and FFA during WM maintenance. (*Upper*) In both younger and older adults, PPA connectivity with the MFG is maintained in all tasks in delay 1 (D1). In both NI and DS, connectivity is maintained in the interference period, whereas in IS connectivity declines significantly during interruption. Of note, during the second delay (D2), younger participants exhibit a return of significant connectivity between the MFG and the PPA, whereas the older participants do not. (*Lower*) FFA connectivity with this MFG region occurs only during the interruption period in both age groups, and remains elevated in the D2 period only in older adults. PPA and FFA regions in the axial slice are from a representative participant. Asterisks signify a significant difference between IS and NI (or DS).

Discussion

The goal of the present study was to determine the neural basis of the disproportionate impact that multitasking has on WM performance in older adults. To accomplish this goal, older participants performed an identical experiment using fMRI recordings to that recently performed in younger individuals (4). A comparison of the behavioral data between age groups revealed that WM performance was more disrupted by interruption in older adults than it was in younger adults, thus replicating previous findings obtained using a similar task and EEG recordings (5). Given the fundamental role of WM in higher-order cognition, it is expected that this deficit has an impact on a wide range of life activities. This result contributes to a growing literature documenting the consequences of multitasking on cognitive performance in older adults (8–10).

In considering the neural mechanism of this behavioral effect, three nonmutually exclusive hypotheses were addressed. The fMRI data in the present study supports the results of our recent EEG study that concluded the age-related interruption effect was not the result of older adults processing interrupting stimuli more than younger adults. This conclusion, which is based upon both univariate FFA activity and MFG-FFA connectivity during the interruption stage of the delayed recognition task, and the convergence of findings across two recording techniques in distinct groups of participants, leads us to reject hypothesis 1. Rather, functional connectivity data assessed during the delay period following the interruptor support both hypotheses 2 and 3, which suggest that older adults have a diminished ability to reactivate internal representations of the stored memoranda following an interruption, as well as extended processing of interrupting stimuli.

The ability to dynamically update WM stores is critical for cognitive performance. Reactivation refers to the ability to return to mind memory representations of information that are no longer active (22). Functional connectivity data suggests that in younger adults, reactivation occurs in the delay period following interruption, such that after an individuals' attention is diverted toward a secondary task, it is reallocated to the memoranda that was temporarily released (4). The current findings suggest that older adults have a deficit in this ability to reactivate information following interruption. Further investigation is necessary to determine if this relates to a deficit in refreshing information, a process that increases or prolongs activity of still-active representations (23, 24), or deficits in reviving representations that are no longer active [i.e., recall (25), reactivation or retrieval (19)], which have been reported to occur in older adults.

The underlying mechanism of how memoranda remain internalized during the interruption period, such that is available for

reactivation, was not explicitly investigated. We hypothesize that when active maintenance is disrupted by an interruption (as evidenced by diminished MFG-PPA connectivity during the interruption period), neural processes and networks involved in long-term memory are engaged (e.g., medial temporal lobe structures). Long-term memory consolidation processes may also have been engaged during encoding, and perhaps persist throughout the trial, in anticipation of the disruptive impact of interruption on the ability to rehearse. This view is supported by a recent study that showed hippocampal lesion patients exhibit diminished WM performance only when delayed-recognition tasks were manipulated to reduce their ability to actively rehearse the memoranda (i.e., interference and long delay periods) (26). Following interruption, the PFC is involved in the reactivation of the representation of stored memoranda, as suggested by the connectivity data from younger adults in the present study and supported by other fMRI studies (27–29). Additionally, it has been shown that the medial temporal lobe (i.e., parahippocampus) is also involved in the reactivation of information following interruption of rehearsed material (30).

The functional connectivity data obtained in the present study further suggest that older participants remain engaged in processing interrupting stimuli after the secondary task was completed (delay period 2), whereas younger adults disengage during this period. Continued representation of interrupting information results in an extended source of interference to the memory decision required at the time of the probe. It seems likely that this finding is related to the proposed role of “deletion” in optimal WM performance (6): “Inhibition also controls what is in active memory by deleting or suppressing the activation of any marginally relevant or irrelevant information, along with the activation of any information that becomes irrelevant information because... goals have shifted.” Consistent with this view, the act of disengagement from a task that was just performed has been described as “backward inhibition” (31–33). Behavioral studies using both garden-path sentence completion tasks and directed forgetting paradigms conclude that older adults have a deficit in the deletion process compared with younger adults (6). From this perspective, our neural findings of persistent connectivity for the interruptor may reflect inadequate deletion of information that is no longer relevant. Therefore, this disengagement deficit seems to represent yet another example of failed inhibition in older adults, which has been extensively characterized as a deficit in suppressing distracting information (5, 13, 15). Thus, this finding serves as a conceptual bridge to unite age-related distraction and interruption effects under a common mechanism. In the setting of distraction, the underlying deficit is suppressing irrelevant in-

formation that it is present, and in the setting of interruption, the deficit is suppressing information that is no longer present and no longer relevant. Further investigation will be necessary to assess if there are overlapping neural mechanisms that govern these aspects of suppression and associated age-related changes (34).

fMRI data from the present study reveals that an age-related interruption effect is not the result of excessive attention and overprocessing of the interrupting stimulus, but rather a diminished ability to both reactivate the memoranda after interruption and disengage from processing the interruptor. A direct relationship between these two phenomena is unclear given the current dataset. A failure in one of these processes may cause the other, or there may be no causal connection. Of relevance, PPA-MFG and FFA-MFG connectivity did not correlate across participants in the postinterruption period. This finding suggests that the relationship between these networks and WM performance is more complex than a simple push-pull exchange of resources and will be investigated further.

There have been an increasing number of studies investigating functional connectivity changes in older adults (e.g., refs. 35 and 36) and it has been proposed that age-associated declines in WM and long-term memory are a result of reorganization in the functional integration of brain regions, in addition to general dysfunction of specific regions and white matter connections (37–39). For example, Grady et al. (40) showed that functional connectivity between the hippocampus and prefrontal cortex differs between younger and older adults, such that older adults exhibit connectivity to more dorsolateral areas (rather than ventral areas) in the prefrontal cortex. Our findings, in identifying an almost identical region in the right MFG for older adults compared with younger adults (assessed independently for each age group), and no other significant prefrontal regions identified, suggests that the age-related effects reported here are a result of changes in switching between networks, rather than a global reorganization.

In conclusion, a number of theories exist as to why older adults struggle with multitasking (8), including: multiple tasks increase task difficulty/complexity (41), resource capacity limitations (42), increased crosstalk conflict (43), and greater bottleneck-processing limitations (44). The present results offer yet another mechanism for the impact of multitasking on cognitive performance in older adults. It will be important to evaluate how widespread interruption recovery failure, as mediated by deficits in the disengagement and reengagement of functional networks, is in older adults.

Materials and Methods

Participant Data. Twenty healthy older participants (mean age 69.1 ± 7.2 y, seven males) took part in the experiment. All participants had normal or corrected-to-normal vision, gave consent, and were monetarily compensated for participation in the study. Participants were considered healthy as determined by a battery of neuropsychological tests and a phone questionnaire. Data from three participants were excluded from all analyses because two participants had excessive motion in the scanner, and one participant did not perform the task correctly. To investigate age-related effects we compared the results from this study to a recent fMRI study performed with younger adults engaged in an identical task (4). All analyses and experimental parameters in this study were identical to the study with younger participants. The younger group consisted of 22 young, healthy adults (ages 18–32 y, mean: 24.57, 13 males) that were neurologically normal and had normal or corrected-to-normal vision. Twenty of these younger participants were used in this analysis, and two participants were removed because of not performing the task correctly.

Neuropsychological Test. After determining eligibility, older participants were screened on a separate day of testing to ensure intact executive and memory function. Eleven neuropsychological tests were used, including: the Mini-Mental State Exam (45), geriatric depression (46), 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 making test A and B (47, 48)], phonemic fluency (words beginning with the letter “D”), semantic fluency (animals), calculation ability (arithmetic), executive functioning (Stroop interference test), WM, and incidental recall (backward digit span and digit symbol, Wechsler Adult Intelligence Scale-

Revised (49)). Intact function was assessed as within 1.75 SDs of the norm on each of the tests listed above (Table S2). Of note, the older participants performed at a high level on neuropsychological testing, as well as on the experimental tasks. Thus, the implications are even greater when deficits are found in such high-performing older adults compared with younger adults, as for the present study. It would be expected that these effects would be even more exaggerated across the whole healthy older population.

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

Paradigm. The paradigm used was the same delayed-recognition WM tasks that were performed by younger adults (4) (Fig. 1). To summarize, participants were shown a picture of a scene during the encoding period (800 ms) and told to hold this image in mind. This was followed by a delay period (7,200 ms), an interfering stimulus (800 ms), a second delay period (7,200 ms), and finally a probe period (1,000 ms) in which participants were asked to make a match/no-match decision. There were three different WM conditions: no interference, distracting stimulus, and interrupting stimulus. 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.

In the NI condition, no interfering stimuli were present during the trial. Instead, the interference period acts as an extension of the delay. In both the DS and IS conditions, participants were presented with a picture of a face for 800 ms during the interference period. In the DS condition, participants were told that this face was irrelevant and should be ignored, but in the IS condition they were told to determine whether or not the face was of a male over the age of 40. In 10% of the trials, the face was a picture of a male over the age of 40; in these cases participants were asked to press both buttons on the button box (otherwise they were instructed to not press anything). The trials that had button responses were discarded because of motor artifact. An additional two trials were included in the IS to balance for these trials. A fourth condition, PV, was included in the experiment. This condition was not a WM task. Participants were shown a picture of a scene during the cue period and a face during the interference period, and were instructed that neither stimulus needed to be remembered. During the probe period the participant responded to the direction of an arrow. The participants were instructed to make all decisions as quickly as possible without sacrificing accuracy. Each task was counterbalanced and repeated twice, with 16 trials in each run. These parameters were chosen to collect 32 trials of data for each task.

fMRI Acquisition and Processing. All images were acquired on a Siemens 3T Trio Magnetom. Images were collected with a 2-s repetition time and $1.78 \times 1.78 \times 3.5$ voxel size. For functional data, 33 3.0-mm oblique axial T2*-weighted gradient-echo slices (repetition time, 2,000 ms; echo time, 25 ms; 90° flip angle and 250-mm² field-of-view in a 128×128 matrix) were collected. Images were corrected for slice timing, motion artifacts, and Gaussian-smoothed to 5-mm FWHM. Data were modeled using a general linear model (GLM) in SPM5 in participant-native space. Group whole-brain maps were calculated from MNI-normalized data. In addition, high-resolution anatomical (T1-MPRAGE) datasets were collected.

Region of Interest Localization. An independent localizer task was used to identify face-selective areas in the visual association cortex, the FFA (19), and scene-selective areas, the PPA (20). In this task, participants performed 10 blocks of a one-back task. Each block consisted of a 16-s presentation of face stimuli, scene stimuli, or rest. Participants were instructed to indicate when a match (one-back) occurred within a block with a simple button press. Blocked-face and scene-stimuli regressors were contrasted to generate SPM[T] images, and from these contrasts, regions of interest (ROIs) were identified. A face-selective ROI (FFA) was then identified as the cluster of 35 contiguous voxels with the highest *t*-value within the right fusiform gyrus of each participant; the right FFA has been shown to be most strongly activated by faces; thus, it was used as a seed in all β -series correlations (19, 50). A scene-selective ROI (PPA) was also identified as the cluster of 35 contiguous voxels (388 mm³), with the highest *t*-value within the left parahippocampal gyrus of each participant. The left PPA has been shown to be the most selective for

scenes (20), and was used in all β -series correlations. The decision of the ROI voxel extent was based on the methodology of similar studies (13, 51–53) and was used to achieve a reasonable balance between regional specificity (diminished by the use of a larger cluster) and susceptibility to noise (a problem with smaller nodes).

fMRI Univariate Analysis. BOLD responses were modeled as events convolved with the canonical hemodynamic response function. The onsets of temporally adjacent covariates were spaced at least 3.6 s apart to minimize the contamination of residual activity and autocorrelation (54). The faces presented as interfering stimuli were separated from scene stimuli by 7.2 s, thus allowing us to assess signals in the FFA selectively associated with faces. All responses were included in the GLM, although trials when participants failed to respond to the probe were modeled separately and not included in the final analysis.

fMRI Functional Connectivity Analysis. Whole-brain maps of functional connectivity were generated by extracting β -values for each stage of every trial from each participant's ROI and correlating these values across trials with each voxel in a whole-brain analysis (52, 53). A new GLM design matrix was

constructed in which each trial stage (cue, delay 1, interference, delay 2, and probe) from each trial was coded with a unique covariate. This process resulted in a total of 640 covariates of interest being entered into the GLM (5 task stages per trial \times 32 trials per condition \times 4 task conditions).

Indices of Attentional Modulation. The same attentional indices were used in the present analyses as in previous studies (4, 5): enhancement, defined as the difference between activity measures associated with interruptors and passively viewed intervening stimuli (IS-PV), and suppression, defined as the difference between activity measures associated with passively viewed intervening stimuli and distractors (PV-DS). These measures were calculated such that a positive value always indicated greater enhancement above baseline or greater suppression below baseline.

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