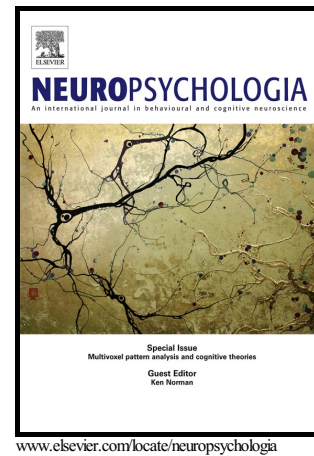


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Effects of Task Complexity and Age-Differences on Task-Related Functional Connectivity of
Attentional Networks

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ABSTRACT

Studies investigating the strength and membership of regions within multiple functional networks primarily focus on either resting state or single cognitive tasks. The goals of the current study were to investigate whether task-related functional connectivity changes with task complexity, and whether this connectivity-complexity relationship is age-sensitive. We assessed seed-to-voxel functional connectivity for the default mode network (DMN) and two attentional networks [cingulo-opercular (CO), fronto-parietal (FP)] in three cognitive control tasks of increasing complexity (Single task, Dual task, and Memory Updating), across younger and older adults ($N=52$; $N_{Young}=23$; $N_{Old}=29$). The three tasks systematically varied in cognitive control demands due to differing maintenance, switching, and updating requirements. Functional connectivity for all networks, resulting from task > rest contrasts, increased with greater task complexity, irrespective of age and gray matter volume. Moreover, between-network connectivity for DMN, CO, and FP regions was greatest for working memory updating, the most complex task. Regarding age-related differences in accuracy, none were observed for Single or Dual tasks, but older adults had poorer accuracy in Memory Updating. More anterior frontal clusters of functional connectivity were observed for older, compared to younger, adults; these were limited to seeds of the two attentional networks. Importantly, increased connectivity in these additional frontal regions in older adults were non-compensatory, because they were associated with detrimental task performance, especially Memory Updating. For the Memory Updating > Rest, the younger > older contrast resulted in greater DMN seed connectivity to regions in the other two attentional networks, implicating increased reliance on between-network connectivity for the DMN seeds during complex cognitive tasks. Our results also implicate functional connectivity between attentional networks and the cerebellum during cognitive control. Reliability of multiple seeds in the seed-to-voxel connectivity is also discussed.

Keywords: task-related functional connectivity, age-related differences, task demands, attentional networks, default mode network

1. Introduction

The human brain is capable of executing a diverse number of thoughts and behaviors with ease. To do so, different brain regions must interact to successfully complete a common goal. In line with this knowledge, specific functional networks have been defined based on the co-activation of regions during task and at rest (Fox et al., 2005; Smith et al., 2009). Research on task-related functional connectivity suggests that different tasks recruit different spatial patterns from the same functional network. However, there is also considerable spatial overlap between networks during a single task. Therefore, to better understand the fundamental properties of task-related functional networks, we need to investigate how the variability in recruitment of these networks, both within a network and between different networks, is affected by task complexity. The current study was designed to investigate such connectivity-complexity relationships in cognitive control tasks, and any age-related differences in those relationships.

1.1 Task Complexity in Cognitive Control

Imaging studies vary considerably regarding the levels of complexity used as in-scanner tasks. The current study employed task-switching and working memory updating to recruit mechanisms of cognitive control. The manipulation demands of cognitive control are typically maintenance, switching, and updating of information units or task-rules (Basak & Verhaeghen, 2011a; Carpenter, Just, & Reichle, 2000; Miyake et al., 2000). Studies on cognitive control vary the amount of task complexity by requiring different combinations of these manipulations. For example, consider task-switching paradigms, where the participants must maintain multiple independent task-based rules and switch between them (Basak, Voss, Boot, & Kramer, 2008; Monsell, 2003; Verhaeghen, Steitz, Sliwinski, & Cerella, 2003). The baseline condition of task-switching, that is, the single task condition, requires participants to maintain only one rule at a time, which requires very nominal demands on cognitive

control. The more complex condition, that is, the dual task condition, requires maintenance of two task-based rules and unpredictably switching between them, thus requiring greater cognitive control than the single task (Monsell, 2003).

In working memory updating paradigms, in addition to maintenance and switching between multiple items in memory, the items need to be updated (Basak & Verhaeghen, 2011a; Garavan, 1998; Oberauer, 2002, 2006). At any given moment, only one item can be immediately accessed in the limited focus of attention for subsequent updating; hence focus-switching is required to switch an item into the focus of attention from the outer store of working memory (Garavan, 1998; Verhaeghen & Basak, 2005). A commonly used working memory updating paradigm is the N-back task, where focus-switch expectancies are predictable (Verhaeghen & Basak, 2005; Verhaeghen, Cerella, & Basak, 2004; Vaughan, Basak, Hartmann, & Verhaeghen, 2008). Yet if focus-switch expectancies are made unpredictable in this task (Basak & Verhaeghen, 2011b; Oberauer, 2006), similar to the aforementioned unpredictable task-switching paradigms, greater cognitive control is required compared to a standard N-back task where switch expectancies are predictable (Basak & O'Connell, 2016; Basak & Verhaeghen, 2011b). Unlike task-switching, these unpredictable updating paradigms require both unpredictable switching as well as continuous memory updating. In contrast, there are no memory updating demands in task-switching paradigms. Therefore, it is plausible that unpredictable memory updating paradigms would require greater cognitive control demands than task-switching paradigms, provided both paradigms have the same number of information units to switch between.

In the present study, functional connectivity was assessed for three tasks of varying degrees of complexity: Single task, Dual task, and an unpredictable N-back task (Memory Updating task). To our knowledge, this is the first study to investigate task-related functional connectivity across multiple tasks, where cognitive control demands of maintenance, switching, and updating were systematically added

from one task to the next, such that the Single task required minimal cognitive control demands whereas the Memory Updating task required the most cognitive control demands. The Single task was limited to task maintenance (Basak et al., 2008), whereas the Dual task included both task maintenance and switching between two streams of information (Basak et al., 2008). Finally, the Memory Updating task included all three types of cognitive control mechanisms: maintenance, switching, and updating of two streams of information (Basak & O'Connell, 2016; Basak & Verhaeghen, 2011b). In sum, we used an additive approach to define task complexity (Single task: maintenance, Dual task: maintenance + switching, and Memory Updating: maintenance + switching + updating) to investigate how increasing cognitive control demands will affect the connectivity of attentional networks.

A meta-analysis conducted by Niendam and colleagues (2012) on fMRI tasks of different types of cognitive control suggests that collectively these different tasks recruit a unitary “network” of regions that overlap with the cingulo-opercular (CO) and fronto-parietal (FP) networks (e.g. right insula, right inferior parietal lobes). These results are in line with other unitary models of cognitive control in the brain (e.g., Duncan, 2010). Based on this unitary network of cognitive control, we hypothesized that increasing cognitive control demands during a task will result in increased connectivity within CO and FP regions. The results of the meta-analysis, however, also suggested that different types of cognitive control activated independent brain regions in addition to the unitary network. For example, both flexibility (or switching) and working memory (or updating) tasks recruited additional, but distinct, prefrontal, occipital, and temporal regions. Moreover, working memory (or updating) tasks additionally recruited subcortical regions (caudate, thalamus, cerebellar declive, putamen). Therefore, it is plausible that CO and FP regions show additional functional connectivity to mechanism-specific brain regions; for example, additional connectivity to subcortical regions during Memory Updating can be expected based on findings from the meta-analysis (Niendam et al., 2012).

1.2 Attentional Networks Underlying Cognitive Control Mechanisms

Neural activation during cognitive control tasks have previously been found within regions of the fronto-parietal (FP) network, the underlying network involved in working memory performance and cue-response mapping adaptation (Dosenbach et al., 2007; Laird et al., 2011; Owen, McMillan, Laird, & Bullmore, 2005). For example, a study conducted by Klingberg, O'Sullivan, and Roland (1997) measured regional activation during three tasks with increasing cognitive control -- a simple pattern match task, a delayed matching task, and a delayed alternating-matching task. Results indicated significant activation in frontal and parietal regions for the two matching tasks, compared to the control task. Furthermore, the alternating-match task, compared to the simpler match task, resulted in recruitment of more fronto-parietal regions than other contrasts (e.g., match>control). Strong fronto-parietal network connectivity was also found during a 2-back task (Leech, Kamourieh, Beckmann, & Sharp, 2011). These and other results suggest that recruitment of fronto-parietal regions, which underlie cognitive control, increase with task-difficulty (Dove, Pollmann, Schubert, Wiggins, & Yves von Cramon, 2000; Klingberg, O'Sullivan, & Roland, 1997). Graph theory expands on the role of the FP network by indicating its highly flexible nature, with changes of both within- and between-network connectivity during 64 complexity levels of the same task (Cole et al., 2013). Increased between-network connectivity as a function of task demands for the FP seeds to other network seeds was evident for the CO network and the DMN. This suggests that FP network connectivity may not only be more robust for the more difficult task but may also have different connectivity patterns during different tasks.

The cingulo-opercular (CO) network has also been found to underlie cognitive control mechanisms, specifically the stable, top-down processing of information, which remains active for the purpose of task-related attentional mechanisms (Dosenbach et al., 2007; Voss et al., 2012). Intercommunication between the FP and CO networks seem to underlie most cognitive control

processes, such that change in stimulus modality, value, or other features prompt activation for top-down control in the task. Communication between these two networks has been found during the switch condition of a cue-based task-switching paradigm (Stelzel, Basten, & Fiebach, 2011). The communication between these two cognitive control networks is argued to represent stable attention (CO) and changing attention to the target (FP) during a task, and this communication works in an interacting loop (Dosenbach et al., 2007).

1.3 Default Mode Network

The third network investigated in this study was the default mode network (DMN), which has been extensively studied during rest (Buckner, Andrews-Hanna, & Schacter, 2008; Greicius, Krasnow, Reiss, & Menon, 2003). Results from resting-state and task-related functional connectivity analyses have prompted two independent hypotheses regarding the function of the DMN, the most well studied being the Default Mode Hypothesis (Andrews-Hanna, Reidler, Huang, & Buckner, 2010). The Default Mode Hypothesis suggests that DMN activation represents internal mentalization, that is, task-independent thought and reflection (Gilbert, Bird, Frith, & Burgess, 2006). It has been supported by studies on passive fixation during rest (Binder et al., 1999; Buckner et al., 2008) and task-related anti-correlations between regional changes in activity within the DMN and task performance (Fox et al., 2005). This suggests that the DMN circuit is suppressed during task execution, and if active, may be detrimental to task performance (Hampson, Driesen, Skudlarski, Gore, & Constable, 2006; Leech et al., 2011). Leech et al. (2011) investigated changes in activation and connectivity for the DMN and FP networks between a basic task (0-back task, comparable to our Single task, however, requiring only single-handed response) and a more difficult task (2-back task, comparable to our Memory Updating paradigm, however, with predictable stimuli presentation). The results indicated that as task complexity

increased from 0-back to 2-back, FP activation and within-network connectivity also increased, whereas DMN activation and within-network connectivity decreased.

The second hypothesis, Cognitive Control Hypothesis, regarding the functions of the DMN suggests that DMN connectivity underlies some cognitive control mechanisms, specifically in attentional maintenance to help predict environmental demands (Raichle & Snyder, 2007). Leech et al. (2011) argued that the different connectivity patterns observed for regions of the DMN (specifically posterior cingulate cortex [PCC] seed location) was due to external vs. internal focus of attention. Further support for this hypothesis comes from increased PCC activation during an unpredictable perceptual-detection task, which found greater PCC activation during trials where attention switched to peripheral regions of the screen (Hahn, Ross, & Stein, 2007). Although these findings were on brain activation, not functional connectivity, they were specific to the unpredictable version of the scanned task, which involved greater attention to future events due to variable expectancies of when and where to allocate attention. Furthermore, support for the attention-based hypothesis is found in task-based connectivity for the DMN during a 3-back task where significant within-network connectivity was found between the middle frontal gyrus and PCC regions (Hampson et al., 2006). Connectivity between these regions (during both rest and task) was positively correlated to task performance, suggesting that positive within-network DMN connectivity was beneficial to task performance. Further support for Cognitive Control Hypothesis comes from positive DMN-FP network correlations found both during autobiographical planning (Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010) and following training in a high cognitive control video-game (Voss et al., 2012). Higher control video-game training, compared to lower control, resulted in increased DMN-attentional networks (brain regions that overlapped with regions of FP and CO networks) connectivity and faster game learning (Voss et al., 2012), suggesting a symbiotic relationship between cognitive control and DMN connectivity.

We predict two different patterns of between-network DMN connectivity based on the two hypotheses. The Default Mode Hypotheses would result in a negative monotonic connectivity-complexity relationship, such that connectivity between the DMN seeds and the attentional network regions would decrease with increased task complexity. In contrast, there would be a positive monotonic connectivity-complexity relationship according to the Cognitive Control Hypothesis, such that connectivity between the DMN seeds and the attentional network regions would increase with task complexity. Such a positive connectivity-complexity relationship would suggest that between-network connectivity for the DMN seeds with frontal-based attentional networks support top-down control needed for external task demands (Raichle & Snyder, 2007; Spreng et al., 2010), as well as unpredictable switching of attention to the target (Hahn et al., 2007) for the more complex tasks.

1.4 Age-related Differences in Functional Connectivity

The current study included adult participants of a broad age range, allowing for investigation of the relationship between network recruitment and task complexity in a population with known age-related changes in functional connectivity. For example, DMN connectivity has been found to be significantly weaker for older, compared to younger, adults (Dennis & Thompson, 2014; Esposito et al., 2008). These decreases in default mode connectivity have been related to poorer cognition in older adults (Andrews-Hanna et al., 2007; Damoiseaux, 2017; Damoiseaux et al., 2008; Persson, Lustig, Nelson, & Reuter-Lorenz, 2007). Not only do older adults have decreased global connectivity in relation to younger adults in anterior and posterior regions associated within the DMN, but this has also been shown within the FP network during switch trials of a cognitive control task (Andrews-Hanna et al., 2007; Campbell, Grady, Ng, & Hasher, 2012; Grady et al., 2010; Madden et al., 2010). Therefore, we hypothesized that older adults would have less functional connectivity compared to younger adults in all

three networks, that is, the DMN and the two frontal-based networks, with support from a recent review of age-related changes in functional connectivity (Damoiseaux, 2017).

We also hypothesized that changes in functional connectivity with increases in task-complexity would be more robust for younger, compared to older, adults. Our prediction was based on past research on age-related differences in cognitive control, where older adults, compared to younger adults, either showed a lesser degree of neuromodulation of the fronto-parietal regions as a function of task complexity, indexed by working memory set-size (Schneider-Garces et al., 2010; Rieck, Rodrigue, Boylan, & Kennedy, 2017) or displayed non-compensatory activations in fronto-parietal regions that subserved both global and local switch costs during a multi-tasking paradigm (Nashiro, Qin, O'Connell, & Basak, 2018).

A recent analysis of network connectivity in both older and younger adults for the DMN, FP, and Dorsal Attentional Network (DAN) found that decreases in within-network connectivity for the DMN was related to increases in between-network connectivity for the FP in older, compared to younger, adults, indicating network dedifferentiation (Grady, Sarraf, Saverino, & Campbell, 2016). Similar findings of lesser within-network and greater between-network connectivity was also found for DMN and DAN (Spreng, Stevens, Viviano, & Schacter, 2016). Furthermore, graph theory analytic approaches resulted in less network modularity and segregation for older adults compared to younger adults (Chan, Park, Savalia, Peterson, & Wig, 2014; Geerligs, Rubinov, & Henson, 2015). The accumulation of findings suggesting increased coupling of DMN regions with attentional network regions for older adults has prompted the formalization of the proposed default-executive coupling hypothesis of aging (Ng et al., 2016; Turner & Spreng, 2016). We, therefore, predicted that older adults would show greater network connectivity between the DMN and the two attentional networks based on past findings (Grady et al., 2016).

To summarize, in the current experiment, we first investigated the relationships between task complexity and seed-to-voxel functional connectivity during these tasks for three cognitive networks, two attentional networks (FP, CO) and the DMN. Second, we investigated age-related differences in these complexity-connectivity relationships by directly comparing older adults and younger adults. This novel study is designed to understand how our brains process different levels of task complexity indexed by cognitive control demands, and how longevity-related differences may affect the recruitment of these neuronal mechanisms.

2. Methods

2.1 Participants

Fifty-six individuals were recruited from the University of Texas at Dallas and the surrounding communities by flyers and advertisements in local newspapers. Four individuals were excluded from the analysis due to technical recording errors during the MRI scans. Thus, the analyses were conducted on 23 younger adults ($M_{\text{age}}=25.70$, $SD_{\text{age}}=4.15$, $M_{\text{education}}=17.57$, $SD_{\text{education}}=1.75$, $N_{\text{females}}=14$) and 29 older adults ($M_{\text{age}}=66.03$, $SD_{\text{age}}=6.83$, $M_{\text{education}}=15.79$, $SD_{\text{education}}=1.82$, $N_{\text{females}}=17$). During the fMRI scanning of one participant, the experimenter failed to press the key that recorded the behavioral data. This participant therefore was not included in any behavioral analyses ($N_{\text{Young}}=22$, $N_{\text{Old}}=29$). All individuals completed an interview regarding demographic information, handedness, and MRI compatibility. Inclusion criteria included right-handedness, normal or corrected vision, and no major history of medical or psychological illnesses. Additionally, the older adult participants needed to score a minimum of 26 on the Mini-Mental Status Examination (MMSE; Folstein, Folstein, White, & Messer, 2010; Folstein, Folstein, & McHugh, 1975) in order to exclude participants with markers of dementia. All participants signed an informed consent approved by the University of Texas at Dallas and the University of Texas Southwestern Medical Center Institution Review Boards. Participants were

compensated \$40/h for imaging sessions and \$10/h for behavioral sessions. All demographic information and behavioral performances are included in Table 1.

2.2 Scanning Procedure

Functional and anatomical images were collected from each participant during a 45-minute scan. Two in-scanner tasks were completed by each participant, resulting in the three levels of task complexity investigated in the current analysis. Both tasks had hybrid block and event-related design (Braver, Reynolds, & Donaldson, 2003); however, for the current analysis only the blocked design was used. The tasks were programmed in E-prime 2.0 software (Psychology Software Tools, Pittsburgh, PA).

The Task Switch paradigm consisted of one run that began with 30 s of a resting block and subsequently alternated between resting and task blocks (Braver et al., 2003). Each task block had 30 trials, where the digit was presented for 3 s. The stimuli were separated by a jittered fixation interval of 1, 3 or 5 s. This resulted in a 154 s duration for each task block, whereas resting blocks were a 30 s duration. During the task blocks, the participants were presented with a digit (one to nine, excluding five) on either a blue or a pink background; the background color indicated the task rule. A blue background meant that the participant had to indicate whether the digit was higher or lower than 5. A pink background meant that the participant had to indicate whether the digit was odd or even. A higher/even decision was made using the right button box, whereas a lower/odd decision was made using the left button box. To remove any memory demands from the task, decision rules were always presented at the bottom left (lower/odd) and bottom right (higher/even) of the screen. Participants first completed two blocks of the Single tasks; first a block of the higher/lower judgement task (blue cue trials), followed by a block of the odd/even judgment task (pink cue trials). Participants then completed two blocks of the Dual task, where they were presented with a random mix of blue and pink trials. Half of these trials were non-switch, where the trial type was repeated (e.g. blue followed by blue) and the

other half of the trials were switch (e.g. blue followed by pink). The Dual task blocks necessitate greater cognitive control than the Single task blocks due to the increase in cognitive control demands, such that a participant had to simultaneously maintain and randomly switching between the task rules. Therefore, out of the three tasks used in the current study, the Single task blocks were considered the least complex and the Dual task blocks were considered to be moderately complex.

The Memory Updating paradigm is comparable to an unpredictable 2-back task (Basak & Verhaeghen, 2011b; Oberauer, 2006) and consisted of two runs of alternating resting and task blocks. Each run started and ended with a resting block with seven 30 s resting and six 30 s task blocks. Each task block had 20 trials. In each trial, a digit was presented for 1450 ms, followed by a 50 ms inter-trial interval. A pink or yellow digit was presented in the center of the screen and the participant had to indicate whether the current number was the same (left button box) or different (right button box) than the previous number presented in the same color. The Memory Updating task required, in addition to maintenance, the switching and updating of two information streams in working memory. When the probed digit changed from yellow to pink (or vice versa), it was a switch trial. When the probed digit was different from the previous one in the same color, it was an update trial. Since the Memory Updating task required all three types of cognitive control mechanisms (maintenance, switching and updating), it was considered to be the most complex of the three tasks. Previous studies that have used a similar N-update paradigm found 1-update to be less cognitively demanding and complex than 2-update (Basak & O'Connell, 2016; Basak & Verhaeghen, 2011b).

The three tasks did not vary regarding the stimuli domain and switch cues. Specifically, all stimuli were verbal in nature (i.e., digits) and the switch cues were represented by different colors. In the two tasks that required switching, i.e., Dual task and Memory Updating, a non-switch trial was represented by repeated presentation of the same color cue, whereas the change in color cue from one

trial to the next represented a switch trial. In total, we had 60 trials for the Single task, 60 trials for the Dual task, and 240 trials for Memory Updating.

2.3 fMRI Data Acquisition, Image Preprocessing, and Connectivity Analysis

Imaging was performed on a Philips Achieva 3T scanner (Philips Medical Systems, Andover, MA, USA) with a 32-channel head coil. Anatomical images were acquired using a transverse MPRAGE T1-weighted sequence (160 slices; TR = 8.1 ms; TE = 3.7 ms; flip angle = 12°; 256 x 204 mm FOV, voxel size = 1 mm³). Protocol for our two in-scanner tasks differed due to an a priori established jittered fixation in the Task Switching paradigm and fixed fixation in the Memory Updating paradigm. In spite of these differences, participants had a 2000 ms response window in both tasks. Functional images during the Task Switch paradigm were acquired using an echo-planar sequence (39 slices; TR = 2000 ms; TE = 30 ms; flip angle = 70°; 64 x 64 mm FOV, voxel size = 3.44 x 3.44 x 4 mm). Functional images during the Memory Updating paradigm were acquired using an echo-planar sequence for each run; two runs in total (29 slices/run; TR = 1500 ms; TE = 30 ms; flip angle = 60°; 64 x 64 mm FOV, voxel size = 3.44 x 3.44 x 5 mm).

Data was preprocessed using SPM12 (<http://fil.ion.ucl.ac.uk/spm/software/spm12/>). All functional images were slice-timed and motion corrected, realigned to the first volume using a six-parameter rigid body transformation, normalized to a study-specific template, and smoothed with a 6 mm FWHM Gaussian kernel. To create the study-specific template, an equal number (20/age-group) of older and younger adults' high-resolution structural images were registered to the standard 152 T1 MNI template, and the resulting images were subsequently smoothed and averaged into a composite image. Anatomical images were normalized and segmented into gray matter, white matter, and cerebral spinal

fluid (CSF) masks. Motion correction was applied via an artifact detection tool (ART) for global mean and motion outliers (http://www.nitrc.org/projects/artifact_detect/).

2.3.1 Seed Selection and Functional Connectivity

Seed-to-voxel based functional connectivity analyses were conducted using the *Conn* functional connectivity toolbox v14 (Whitfield-Gabrieli & Nieto-Castanon, 2012; <http://www.nitrc.org/projects/conn>). *Conn* uses a noise reduction method called CompCor, which extracts principal components from white matter and CSF time series (Behzadi, Restom, Liau, & Liu, 2007). The six realignment parameters, the main effect of the different blocks, and the scrubbing parameters were also used to remove any possible confounds of noise. A high pass filter of .008 Hz was implemented. Two individual regressors were added to the first-level general linear models: first, the two specific ART parameters that were outliers in global mean signal intensity and motion, and second, the realignment parameters. Bivariate-correlations for the relationship between the mean BOLD time series for each seed and the mean BOLD time series for all other voxels were computed for task > rest contrasts. A Fisher Z transformation was applied to convert our bivariate correlations to a normal distribution. These individual maps were entered into the second-level analysis, where group level differences in network activation was explored.

Three networks were chosen to investigate task-related functional connectivity in three tasks of varying degrees of cognitive control. Two of these networks were attentional networks, cingulo-opercular (CO) and fronto-parietal (FP), and the third was the default mode network (DMN). Two seeds for each of these networks were chosen for their relatively low betweenness centrality (i.e. more network segregation; Spreng et al., 2013) and regions of correspondence between these network seeds to the task-defined systems (Dosenbach et al., 2007; Power et al., 2011). For additional information, see

the *seed selection* in Supplementary Materials. Selection of two seeds was intended to limit the possibility of seed selection bias.

In seed-to-voxel analyses, a seed is defined as the average time-series within the selected region of interest and correlated with the time-series from all other voxels in the brain. Therefore, we used a total of six regions of interest, resulting from 2 seeds x 3 network, in the current study. Seeds were created using an 8 mm sphere surrounding the specified region's peak MNI X, Y, Z coordinates. These peak coordinates were selected from Dosenbach et al. (2007) and Power et al. (2011). The seeds for CO were the dorsal anterior cingulate cortex (dACC: MNI -1, 10, 46) and left anterior insula/frontal operculum (aI/FO: MNI -35, 14, 5). The FP seeds were the right dorsal lateral prefrontal cortex (dlPFC: MNI 46, 28, 31) and the left anterior inferior parietal lobe (aIPL: MNI -53, -50, 39). The DMN seeds were the posterior cingulate cortex (PCC: MNI 1, -51, 29) and right lateral temporal gyrus (MNI 61, -21, -12).

In the first set of analyses, we investigated the task > rest functional connectivity maps for each of the three networks (CO, FP, and DMN) during the Single task, Dual task, and Memory Updating conditions. Standardized scores for total gray matter volume and age were entered as a continuous regressors within our general linear model to control for the effects of neurocognitive aging on functional connectivity. A significant correlation was observed between age and total gray matter volume ($r = -.60, p < .001$). Previous findings by Fox et al. (2006) and Fair et al. (2007), who investigated the use of a block-design fMRI tasks to measure resting state connectivity, suggested that task-related activity is a "linear addition" of task on top of the persistent spontaneous baseline activity involved in the resting blocks. Therefore, in tasks that interleave rest and task blocks (like our current design), Fair and colleagues (2007) found that looking at the results of the rest > task blocks gave more or less a continuous state of resting behavior that the authors were interested in. The focus of the current study

was not on resting behavior, but on task-related functional connectivity. Therefore, we investigated a similar contrast, but in the opposite direction (task > rest), for all three tasks in order to remove any persistent activity related to the rest blocks. Such task > rest connectivity maps have been used in other studies investigating task-related functional connectivity using block design (Bluhm et al., 2010; Elton & Gao, 2014). We also conducted additional analyses where the effects of rest blocks are not removed from the task blocks. Results from these additional analyses are provided in the Supplementary Materials.

The second set of analyses investigated the age-related differences in functional connectivity of the three networks during the three different task complexities. Age-group was an independent variable where participants were either separated into younger or older adults, allowing us to conduct the following two contrasts, younger > older and older > younger, for the three different tasks across the six different network seeds. Results from all analyses are reported in Tables 2 and 3.

It is important to note that the atlas-defined location of the peak voxel for some of the clusters differed from the atlas-defined location of the majority of the voxels in that cluster. Therefore, if the tables list two cluster locations, the first location indicates where the peak voxel is located (indicated by a ‘+’ in Tables 2 and 3), and the second location indicates where the majority of the voxels are located in the cluster (indicated by a ‘*’ in Tables 2 and 3). Moreover, we used the larger corpus of network nodes by Power et al. (2011) to define the network of the resulting clusters, in order to deem the significant connectivity as within-network or between-network. To do so, we created 6 mm seeds from Power et al. (2011) MNI coordinates for our three networks of investigation, resulting in 14 seeds for the cingulo-opercular network, 25 seeds for the fronto-parietal network, and 56 seeds for the default mode network. These networks seeds were overlaid on the resulting *t*-maps to visually compare our resulting clusters to the regions from previous network analyses. CO seeds are in yellow, FP in green, and DMN in red; for

the particular network that the seeds under investigation (in seed-to-voxel analyses) belong, the Power et al. nodes are shown in black (see Figure 1 and Figure 2).

3. Results

3.1 Task Complexity and Aging: Accuracy and Cognitive Control Costs

A 2 x 3 repeated-measures Analysis of Variances (ANOVA), with age-group (young vs. old) as a between-subjects factor and complexity (Single task, Dual task, Memory Updating) as a within-subjects factor, were conducted on accuracy (see Table 1 and Supplementary Figure 1). A significant main effect for complexity was observed, $F(2, 96) = 63.73$, $MSE = .002$, $p < .001$, $\eta_p^2 = .57$, suggesting that as task complexity increased, accuracy decreased. Sidak post-hoc comparisons indicated a significant difference in accuracy between the Single task and Memory Updating ($p < .001$) as well as between Dual task and Memory Updating ($p < .001$), signifying that Memory Updating was the most difficult task to perform. Single task and Dual task did not differ in accuracy ($p = .88$). The main effect of age group was significant, $F(1, 48) = 14.55$, $MSE = .005$, $p < .001$, $\eta_p^2 = .23$, with older adults expectedly performing worse than younger adults. Importantly, a significant age group by complexity interaction, $F(2, 96) = 12.83$, $MSE = .002$, $p < .001$, $\eta_p^2 = .21$, indicated that the decline in accuracy with increases in task complexity was more rapid for older adults than for younger adults.

Additionally, we also calculated two types of cognitive control costs, mixing costs [$RT(\text{Dual task}) - RT(\text{Single task})$] and switch costs [$RT(\text{Switch}) - RT(\text{Non-switch})$]. Mixing costs allowed us to evaluate whether maintaining two tasks was more difficult than maintaining one task. A one-sample t-test found the mixing costs to be significantly higher than zero, $t(50) = 17.23$, $p < .001$, 95% CI [247.01, 312.19], suggesting that responding to dual tasks was more difficult than responding to a single task. Switch costs were calculated for both Dual task and for Memory Updating, since both tasks had switch and non-switch trials. Therefore, we could evaluate whether switching between tasks during task switching was

similar to switching between two streams of information in working memory. Switch costs for both tasks were significantly greater than zero; Dual task: $t(50) = 4.33, p < .001, 95\% \text{ CI } [29.86, 81.54]$; Memory Updating: $t(50) = 6.30, p < .001, 95\% \text{ CI } [54.78, 106.06]$. Importantly, using a paired samples t-test, we found that there were no differences between switch costs for Dual task and switch costs for Memory Updating, $t(50) = -1.54, p = .13, 95\% \text{ CI } [-57.07, 7.62]$. The results suggest that switch costs are similar across the two types of tasks: task switching and memory updating.

3.2 Functional Connectivity Analyses

All analyses were corrected for multiple comparisons using cluster p-FWE at a p -value of .05 and a p -uncorrected voxel threshold at a p -value of .001 (Friston et al., 1994). Peak voxels in significant clusters were identified using the xjView toolbox (<http://www.alivelearn.net/xjview>). Table 2 and 4 include cluster coordinates and localization. If the peak voxel of each cluster and the location of the majority of voxels in a cluster differed in the defined brain regions, we included both regions. Figures 1 and 2 include our network seeds as defined by Dosenbach et al. (2007) and Power et al. (2011) for resulting cluster comparison.

3.2.1 Task Complexity and Seed-to-Voxel Functional Connectivity in CO, FP and DMN

Networks

Comparisons across the multiple GLMs for task complexity and the three networks of interest, after controlling for age and total gray matter volume, suggested that as task complexity increased (from Single to Dual to Memory Updating), the overall number of significant voxels for task > rest connectivity also increased. See Table 2 and Figure 1 for resulting significant clusters of connectivity for the six seeds, two seeds for each network.

For the Single task > Rest contrast, the dACC seed of the CO network was correlated to a cluster of voxels within the same network, whereas the right dlPFC seeds of the FP network was correlated to a

cluster of voxels in the CO network. For the DMN network, both seeds, the PCC and right lateral temporal gyrus, were significantly correlated to clusters of voxels within-network as well as to FP regions.

For the moderately complex task (Dual task > Rest contrast), only seeds from the two attentional networks were significantly correlated to voxels both between-network and within-network. Neither of the two DMN seeds were significantly connected to voxels from other brain regions. The seeds of the CO network were broadly connected to regions in the FP network, the DMN, and the cerebellum. Furthermore, there was considerable overlap between the resulting within-network clusters across the two CO seeds. In contrast, only one of the FP seeds, the right dlPFC, showed significant connectivity to voxels from other brain regions. Its resulting spatial map was more restricted than that of the CO seeds, with within-network connectivity to two clusters in the supramarginal gyrus and postcentral gyrus and between-network connectivity to one cluster in the hippocampus.

For the Memory Updating > Rest contrast, the most complex of the three task conditions, significant connectivity to different clusters of voxels were observed in all three networks: CO, FP and DMN. Furthermore, all six network seeds resulted in significant within- and between-network connectivity. The CO network seeds again resulted in significant between- and within-network connectivity, but with broader spatial extent than resulting from the Dual task > Rest contrast. Again, the two seeds noticeably overlapped in their resulting significant *t*-maps of significant connectivity for this particular contrast (Figure 1). Connectivity for the dACC was extensively connected to regions in all three networks, as well as in additional regions (cerebellum and caudate nucleus). The left anterior insula seed also resulted in significant connectivity to within-network regions and to regions in the DMN and FP networks. Connectivity for the FP network seeds were more posterior than the resulting connectivity for the CO network seeds; however, resulting *t*-maps encompassed all three networks. The

resulting significant clusters for left aIPL seed were much larger than those found for right dLPFC seed, but the connectivity patterns across the two seeds were similar for the regions within the FP network, posterior regions of the DMN and regions in the visual cortex. DMN seed connectivity resulted in both within-network clusters as well as between-network clusters to regions of both the FP and CO networks. The clusters for the PCC seed were much larger than those found for the right lateral temporal seed; however, the connectivity patterns across the two seeds were similar for regions within the DMN, the FP network, and in the visual cortex (Figure 1).

3.2.2 Functional Connectivity Values Predicting Task Performance

We further evaluated whether the between- and within-network connectivity during the three contrasts (Single task > Rest, Dual task > Rest, Memory Updating > Rest) were related to task performance by conducting separate multiple regression analyses for each task. In each set of hierarchical regressions, one for each task, age and total gray matter volume were entered in the first model (Table 3). In the second model, connectivity values (beta-coefficients) for the respective task > rest contrasts were entered in a stepwise manner. Beta-coefficients of connectivity clusters only survived as regressors in the model if their probability-of- F -to-enter was less than or equal to .05. The dependent variable for each hierarchical regression was based on the appropriate performance measures (Single task reaction time, Dual task reaction time, and Memory Updating accuracy). Age and total gray matter volume, which were entered into the first stage of analysis, accounted for a significant amount of variance in performance for all three tasks (Single task reaction time, $R^2 = .18$, $F(2, 48) = 5.30$, $p = .008$; Dual task reaction time, $R^2 = .18$, $F(2, 48) = 5.22$, $p = .009$; Memory Updating accuracy, $R^2 = .46$, $F(2, 47) = 20.16$, $p < .001$). No connectivity clusters significantly predicted Single task reaction time, after accounting for the effects of age and total gray matter volume (Table 3). In contrast, for Dual task reaction time, three connectivity pairs survived the stepwise criterion, right dLPFC to left supramarginal

gyrus ($\beta_{\text{standardized}} = .33$), left anterior insula to left declive ($\beta_{\text{standardized}} = .41$), and left anterior insula to right inferior parietal lobe ($\beta_{\text{standardized}} = -.28$), and accounted for a significant amount of variance above and beyond the effects of age and total gray matter volume, $\Delta R^2 = .28$, $F(5, 45) = 7.54$, $p < .001$. For Memory Updating accuracy, four connectivity pairs survived the stepwise criterion: right lateral temporal gyrus to left supplementary parietal lobe ($\beta_{\text{standardized}} = .25$), dACC to right Uvula ($\beta_{\text{standardized}} = -.29$), right dlPFC to right medial superior frontal gyrus ($\beta_{\text{standardized}} = -.29$), and dACC to middle cingulate gyrus ($\beta_{\text{standardized}} = .24$). Together they accounted for a significant amount of variance above and beyond the effects of age and total gray matter volume, $\Delta R^2 = .26$, $F(6, 43) = 18.81$, $p < .001$.

3.2.3 Task Complexity and Functional Connectivity in CO, FP and DMN Networks: Age-related Differences

By controlling for age and total gray matter volume in our previous analyses, we investigated the overall pattern of connectivity for three different networks across three different task complexities. It is possible though that the pattern of task-based change in strength and membership of functional connectivity is different for older and younger adults. Therefore, we directly investigated the specific seeds and tasks where younger adults had greater connectivity than older adults (younger > older contrast), and vice-versa (older > younger contrast; see Figure 2 and Table 4). For the Single task > Rest contrast, younger adults showed significantly greater connectivity than older adults between the left anterior insula seed of the CO network to a cluster in the visual cortex, whereas older adults showed significantly greater connectivity than younger adults between the PCC seed of the DMN to both middle frontal gyrus and caudate.

Connectivity for the Dual task > Rest contrast resulted in a notably greater number of significant within-network clusters for the FP seeds for the younger > older contrast, whereas the older > younger

contrast yielded two clusters of FP-DMN between-network connectivity (FP to occipital fusiform gyrus, and FP to paracingulate gyrus).

Connectivity for the Memory Updating > Rest contrast resulted in more significant clusters for younger, compared to older adults, for both CO and DMN seeds. For the CO seeds, younger adults, compared to older, yielded significant connectivity to regions in the DMN and occipital lobe, whereas older adults showed greater connectivity than younger adults to frontal regions of the DMN (e.g. superior frontal gyrus). For the DMN seeds, both younger and older adults showed greater connectivity to both within-network regions (superior temporal regions for both young and old; precuneus for just old) and between-network posterior FP regions (inferior parietal lobe for both young and old). For the FP seeds, only the left anterior IPL seed resulted in any significant age-related clusters, such that the older > younger contrast yielded both within-network connectivity (anterior cingulate gyrus, precentral gyrus) and connectivity to one DMN region (paracentral lobe).

Overall, older adults, compared to younger, showed increased connectivity to anterior frontal regions for all three networks across all tasks, except for the DMN seeds for the Memory Updating > Rest contrast. In contrast, younger adults, compared to older, showed more robust within-network connectivity (FP for Dual task > Rest; DMN for Memory Updating > Rest) as well as between-network connectivity to posterior brain regions for the Memory Updating > Rest contrast for the DMN and CO network.

3.2.3 Functional Connectivity Values for Older > Younger Contrasts Predicting Performance

To assess whether the regions where older adults resulted in greater connectivity than younger adults (older > younger) helped or hindered their behavioral performance, a series of individual linear regressions were conducted to see if any of the beta-coefficients from the older > younger contrasts (for all three task > rest conditions; see Table 4) significantly interacted with age to predict task

performance. Single task reaction time, Dual task reaction time, and Memory Updating accuracy were used as the respective dependent variables in the regression models. The interaction terms between age and connectivity for both Single task and Dual task did not significantly predict performance in the respective task (see Table 5). However, many functional connectivity values interacted with age to significantly predict Memory Updating accuracy at a Bonferroni adjusted alpha level of .006¹. Memory Updating accuracy was significantly predicted by the interaction of age and six functional connectivity pairs (see Table 5): left anterior insula to left superior frontal gyrus ($\beta_{standardized} = -.44$, $t(48)=-3.43$, $p=.001$), left aIPL to anterior cingulate gyrus ($\beta_{standardized} = -.55$, $t(48)=-4.54$, $p<.001$), left aIPL to paracentral lobe ($\beta_{standardized} = -.51$, $t(48)=-4.09$, $p<.001$), left aIPL to left precentral gyrus ($\beta_{standardized} = -.48$, $t(48)=-3.77$, $p<.001$), PCC to right inferior parietal lobe ($\beta_{standardized} = -.47$, $t(48)=-3.65$, $p=.001$), and right lateral temporal gyrus to superior temporal gyrus ($\beta_{standardized} = -.51$, $t(48)=-4.16$, $p<.001$). All coefficient estimates are negative, therefore, increased functional connectivity in these regions with older age predicts lower accuracy in memory updating.

4. Discussion

One of the goals of the current study was to investigate how task complexity affects functional connectivity in three different networks. Another goal was to determine any age-related differences in task-related functional connectivity and how it may interact with task difficulty. To our knowledge, investigation of functional connectivity for tasks that are systematically manipulated on maintenance, switching, and updating in an additive manner is novel. In the current study, task complexity was defined by the number of cognitive control mechanisms involved in the task. The easiest task (Single task), where only one task rule had to be maintained, required minimal cognitive control. In the moderately complex task (Dual task), two different task rules had to be maintained, resulting in increased cognitive control demands. Moreover, an ability to unpredictably switch attentional focus

between these two rules was needed to successfully perform this task. In the most complex task (Memory Updating), not only did two different streams of information have to be maintained and unpredictably switched in and out of the focus of attention, but these information streams also had to be continually updated in working memory. Therefore, we hypothesized that task complexity increased from Single task to Dual task to Memory Updating. Behavioral results from accuracy and mixing cost supported our hypothesized directional increase of task complexity across the three tasks.

However, the switch costs, calculated from the difference in response times of the non-switch trials from the switch trials, did not vary across two types of task: Dual task vs. Memory Updating. In Dual task, the switch costs reflected switching between two types of task judgments with no memory demands, whereas in Memory Updating, the switch costs reflected switching between two streams of information in working memory, although the task judgment remained same. These results suggest that cue-driven switching is similar across different types of cognitive control tasks. Therefore, we conclude that the reason Memory Updating is more difficult than Dual task, as reflected by decreased accuracy, is due to the added updating mechanism.

Furthermore, we only found age-group differences during Memory Updating, such that the addition of updating demands detrimentally affected the accuracy of older adults significantly more than younger adults. That is, older adults showed a steeper decline in accuracy from Dual task to Memory Updating, supporting past results that have claimed that updating in working memory is a cognitive marker of aging (Basak & Verhaeghen, 2011b; Verhaeghen & Basak, 2005).

After establishing that task complexity increased from Single task to Dual task to Memory Updating, and that age-group differences increased with task complexity, based on performance measures, we investigated our two primary hypotheses. The first hypothesis was that as the complexity of the cognitive tasks increased due to more demands on cognitive control, task-related functional

connectivity in the attentional networks, when controlling for rest-blocks, would also increase. The second hypothesis was that older adults would exhibit less task-related connectivity in the attentional networks, compared to the younger adults, but greater between-network connectivity for the DMN.

4.1 Task Complexity and Functional Connectivity in the two well-known Attentional Networks, FP and CO

The increase in functional connectivity in our two, known, attentional networks, cingulo-opercular (CO) and the fronto-parietal (FP), during the three levels of task complexity supported our first hypothesis (see Table 2 and Figure 1). As expected, for the Single task > Rest contrast, which demanded minimal cognitive control, limited functional connectivity was observed across all seeds. Therefore, we conclude that the simplicity of the Single task, which primarily required rule maintenance, does not sufficiently engage the attentional networks.

In contrast, functional connectivity for the Dual task > Rest contrast, which required not only rule maintenance, but also unpredictable switching between two rules, was found to be related only to our attentional network seeds (FP and CO). The results implicated both within- and between-network connectivity for these seeds. Similar within- and between-network results were found for the Memory Updating > Rest contrast, although the resulting clusters of significance were much larger for this more complex task compared to Dual task. The CO-FP between-network connectivity is expected since functionality in both networks underlie cognitive control. Furthermore, previous research has suggested a theoretical looped interaction between the CO-FP networks (Dosenbach et al., 2007, Stelzel et al., 2011). A closed loop CO-FP interaction would suggest that task-related processing is free flowing between the two networks, whereas a parallel loop CO-FP interaction would suggest that the two networks are distinct, yet interact for task completion (Dosenbach et al., 2007). The current study does not support one loop over another. However, our results suggest a greater CO-FP interaction during

tasks that demand more cognitive control, such as Dual task compared to Single task. This CO-FP interaction, indexed by between-network connectivity, was found to be even more robust for the Memory Updating > Rest contrast, which required even greater cognitive control due to the accumulation of maintenance, unpredictable switching, and updating of two streams of information.

Additionally, the CO network was significantly connected to regions of the cerebellum and DMN for both the Dual task > Rest and Memory Updating > Rest. FP seeds were also significantly connected to DMN regions, particularly during Memory Updating > Rest. The implications of such increasingly strong association between the attentional network seeds and DMN regions with increased demands of cognitive control are detailed later (see section 4.3). Although the between-network connectivity between the CO seeds and cerebellum were not hypothesized, the cerebellum has previously been implicated in tasks of cognitive control (for a review see Bellebaum & Daum, 2007), including task-switching (Collette et al., 2005) and working memory (Chen & Desmond, 2005; Kirschen, Chen, Schraedley-Desmond, & Desmond, 2005; Schumacher et al., 1996). The cortico-cerebellar white matter circuits are especially strong for the prefrontal cortex in humans (Ramnani et al., 2006). These white matter fronto-cerebellar projections lend support to the role of the cerebellum in cognitive control. Previous studies have also suggested that the temporo-parietal white matter projections to the cerebellum may be related to the phonological loop for rehearsal and storage in verbal working memory (Justus, Ravizza, Fiez, & Ivry, 2005). It is also possible that motor control, the most developed functional attribute of the cerebellum, may be related to the automaticity of actions needed during cognitive control tasks, such as switching between hands for different task-responses (Lang & Bastian, 2002). Thus, the increased between-network connectivity of the CO seeds and cerebellum may reflect the cognitive challenges faced during response selection.

Importantly, we find great overlap between the resulting *t*-maps of the two CO seeds (dorsal anterior cingulate cortex and left anterior insula) for Dual task > Rest and Memory Updating > Rest, suggesting strong reliability across the two seeds. The seeds of FP and DMN also show great overlap between theory resulting *t*-maps, with significantly larger maps for one seed encompassing the map of the other seed. Therefore, we suggest that future research takes into account multiple seeds to represent a network in task-related seed-to-voxel functional connectivity analysis, to better evaluate the reliability of the seeds.

4.2 Age-related Differences in Task Complexity and Functional Connectivity in the FP and CO

Networks

Research regarding age-related changes in regions supporting cognitive control mechanisms suggest that younger adults would exhibit greater connectivity for the attentional networks than older adults (Madden et al., 2010). Results from all three cognitive control tasks found that age-related differences in task-related functional connectivity predominantly favored the young. These results are in line with previous studies, where older adults have exhibited less connectivity in attentional networks (Andrews-Hanna et al., 2007; Campbell et al., 2012; Esposito et al., 2008; Grady et al., 2010; Madden et al., 2010). Specifically, we found that younger adults, compared to older adults, showed more within-network connectivity for the FP for the Dual task > Rest contrast, and more between-network connectivity for the CO and DMN seeds for the Memory Updating > Rest contrast. Conversely, older adults, compared to younger adults, had significantly greater connectivity to clusters in the anterior regions of the brain for seeds from the attentional networks for the Dual task > Rest and Memory Updating > Rest contrasts, and to one anterior cluster for a DMN seed for the Single task > Rest contrast. It is important to determine whether this increased connectivity in anterior brain regions is compensatory or detrimental to task performance. The accuracies in Single and Dual tasks were similar across the two age groups, however,

the multiple regression analyses between the appropriate connectivity-age results and behavioral performance were not significant. Therefore, we cannot determine whether increased connectivity of the DMN seeds (for Single task) and FP seeds (for Dual task) to the anterior brain regions in older adults is compensatory in nature. In contrast, older adults had significantly lower accuracies than younger adults during the Memory Updating task, and when these accuracies were predicted by the interaction between age and significant connectivity measures for the older > younger contrasts, we found negative relationships between these connectivity values and performance. This suggests that increased connectivity for the CO and FP seeds to other brain regions in older adults were non-compensatory.

The greater posterior connections for younger adults and greater anterior connections for older adults for these attentional network seeds are in compliance with the age-related posterior to anterior shift in task activations (Davis, Dennis, Daselaar, Fleck, & Cabeza, 2007). Over-activation of anterior regions in older adults is not necessarily an efficient or compensatory response, because such over-activations are often accompanied with worse task performance not only for memory paradigms (Kim, 2011; Maillet & Rajah, 2014), but also in tasks of cognitive control that entail switching between two task rules (Nashiro et al., 2018). Our results support this non-compensatory view, particularly for the most complex task, Memory Updating, because older adults' greater connectivity of almost all additional anterior regions for all network seeds during Memory Updating significantly predicted worse performance. However, for less demanding cognitive control tasks, where no age-related differences in accuracy were observed (e.g., Single and Dual tasks), older adults showed greater connectivity to anterior clusters for the FP and DMN seeds, but we cannot conclusively state that these age-related increases in connectivity were compensatory.

4.3 Task Complexity and Functional Connectivity in the DMN

The two primary hypotheses, the Default Mode Hypothesis and the Cognitive Control Hypothesis, that surround the default mode network are based on patterns of activation and deactivation of DMN regions (Buckner et al., 2008; Fransson & Marrelec, 2008; Greicius et al., 2003; Hampson et al., 2006). Functional connectivity analyses, which rely upon the correlation of time-series between two regions, are unable to distinguish between these two hypotheses because positive correlations between two DMN regions (as observed in the current study) could result from either two regions activating at the same time or deactivating at the same time.

Unlike DMN regions that activate or deactivate, regions of the fronto-parietal network and cingulo-opercular network have consistently been found to activate during tasks of cognitive control and working memory (Dosenbach et al., 2007; Owen et al., 2005). Therefore, between-network connectivity for the DMN to these attentional networks would either increase (Cognitive Control Hypothesis) or decrease (Default Mode Hypothesis) with increased task complexity, depending upon whether the DMN region activates or deactivates, respectively. We found positive connectivity between the DMN seeds and voxels within the attentional networks for the Dual task > Rest and Memory Updating > Rest contrasts. The positive connectivity was more robust and widespread for the Memory Updating > Rest contrast. DMN and prefrontal regions of the attentional networks were positively correlated during both encoding and retrieval phases of working memory (Piccoli et al., 2015). Furthermore, activation of our DMN seeds have been related to mental search, episodic memory, and signaling environmental change (Fransson & Marrelec, 2008; Mayes, 2000; Pearson, Heilbronner, Barack, Hayden, & Platt, 2011), all of which are needed in memory updating. Hence, our results indicate the need for increased connectivity between the DMN and attentional networks to successfully perform a cognitively demanding task. The CO/FP-DMN positive relationships and positive DMN within-network correlations during both Dual task and Memory Updating both support the Cognitive Control Hypothesis. Further support for the

Cognitive Control Hypothesis of DMN comes from the relationship between seed-to-cluster connectivity from the Memory Updating > Rest contrast and accuracy in that same task. Our results suggest that, during Memory Updating, individuals with greater DMN connectivity to a cluster in the FP network also had higher accuracy in this most complex task (Table 3). Together, the positive connectivity-complexity (Figure 1) and the positive connectivity-performance relationships (Table 3) suggests that between-network connectivity for the DMN seeds with the attentional networks, specifically the FP network, supports the top-down control needed for external task demands (Raichle & Snyder, 2007; Spreng et al., 2010), unpredictable switching of attention to the target (Hahn et al., 2007), and updating and retrieval of stored information (Piccoli et al., 2015).

4.4 Age-related Differences in Task Complexity and Functional Connectivity in the DMN Network

Age-related differences in connectivity for the DMN seeds were found to be task-related. Connectivity for the older > younger adult contrast resulted in a series of significant clusters during the Single task > Rest contrast, however no significant clusters resulted from the younger > older contrast. One may hypothesize that older adults' increased DMN connectivity during this task is helping to equate their performance to younger adults, however, our connectivity-behavioral analyses (Table 5) did not support this hypothesis. Younger adults did not require any additional DMN connectivity to support their Single task and Dual task performance. In contrast, connectivity for the younger > older adult contrast resulted in many clusters for the PCC seed during Memory Updating. Although previous findings found the DMN to be engaged during cognitive control mechanisms (Leech et al., 2011; Spreng, 2012), our results suggest that this complexity-DMN relationship could be age-specific. That is, for regions where younger adults had greater connectivity than older adults, Memory Updating accuracy was significantly predicted by the interaction between age and connectivity values between PCC to left superior temporal gyrus ($\beta_{\text{standardized}} = .53$, $t(48)=4.35$, $p<.001$), PCC to right IPL ($\beta_{\text{standardized}} = .32$,

$t(48)=2.32, p=.03$) and PCC to left middle cingulate gyrus ($\beta_{\text{standardized}} = .41, t(48)=3.07, p=.004$). This suggests that younger adults increasingly rely on the DMN network as demands on cognitive control increase, particularly when switching and updating are required. In contrast, greater connectivity for DMN seeds for older adults, compared to younger adults, were detrimental to task performance. The interaction between age and connectivity values for the PCC to right IPL ($\beta_{\text{standardized}} = -.47, t(48)=-3.65, p=.001$) and right lateral temporal gyrus to left superior temporal gyrus ($\beta_{\text{standardized}} = -.51, t(48)=-4.16, p<.001$) negatively predicted performance in Memory Updating.

Overall, we find that additional connectivity for older adults for the attentional network seeds as well as DMN seeds are detrimental to performance of the most cognitively demanding task. The results are in line with the findings supporting the default-executive coupling hypothesis of aging (Ng et al., 2016; Turner & Spreng, 2016). It is to be noted that coupling between DMN and other networks favoring younger adults were also observed for the most complex task, but such coupling indicated a beneficial, symbiotic relationship between default-executive networks.

4.5 Conclusion

In conclusion, we found that task-related functional connectivity increased in FP and CO attentional networks with increased cognitive control demands (i.e., task complexity). These connectivity patterns were observed in the anterior brain regions for older adults, compared to younger adults, suggesting a posterior to anterior shift with aging. We conclude that greater task-related functional connectivity in the anterior brain regions for the Memory Updating > Rest contrast for older adults reflects sub-optimal strategy use, resulting in lower task performance. In the DMN network, between-network connectivity to regions of the two attentional networks, were observed for both the Dual task > Rest and Memory Updating > Rest contrast, irrespective of age and total gray matter volume. These interactions were more robust and widespread for the most complex task, and the

strength of these interactions were positively related to task performance, suggesting the need for DMN coactivation to successfully perform cognitive control tasks. This was further supported by increased within- and between-network DMN connectivity in younger adults, compared to older adults, that were related to better performance in the most complex task. Task-related connectivity is methodologically less common than resting-state connectivity, especially when multiple seeds are investigated to determine the resulting spatial patterns. It is, however, a useful way to investigate specific functional brain networks that respond to the interactions between task-specific and age-specific demands. Such studies should also explore whether age-related increases in connectivity is detrimental to their performance or is maintaining their performance.

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Footnotes

¹ We corrected for multiple comparisons using Bonferroni adjustments: $\alpha [PT] = \frac{\alpha [PF]}{C}$, with C equal to the number of comparisons being made. Thus, for the eight regressions conducted to predict Memory Updating accuracy from interaction between age and beta-coefficients, the Bonferroni adjusted p -value was .006 ($= \frac{.05}{8}$). The beta-coefficients were extracted from the significant older > younger clusters during Memory Updating.

Figure Captions

Figure 1. Significant t-maps for Task Complexity (task > rest) across the three networks, controlling for age and total gray matter volume. Multiple seed-to-voxel general linear models (GLM) were conducted across three tasks (Single task > Rest, Dual task > Rest, and Memory Updating>Rest) and three networks (CO, FP, and DMN), while controlling for age and gray matter volume. Significant connectivity is much greater for the Memory Updating task, across all three networks; this task is the most complex of our three in-scanner tasks (see Table 1 for region localization of significant voxels). The color of resulting clusters indicates the network of seed selection for the analysis: CO (yellow), FP (green), DMN (red). The resulting maps from the task > rest contrasts are overlaid on Power et al. (2011) network seeds to differentiate between within- and between-network connectivity. For the seed-to-voxel connectivity maps of a particular network (e.g. CO), the Power et al. seeds for that particular network are displayed in black and the other two network seeds from Power et al. are displayed in their respective colors. CO seeds are colored in yellow, FP seeds are colored in green, and DMN seeds are colored in red, if they are overlaid over results from seeds of the other two networks.

Figure 2. Age-related differences in significant t-maps for Task Complexity (task > rest) across the three networks. Multiple seed-to-voxel general linear models (GLM) were conducted across three tasks (Single task > Rest, Dual task > Rest, and Memory Updating>Rest) and three networks (CO, FP, and DMN) for two separate contrasts: younger > older (YA > OA) and older > younger (OA > YA). Results indicate that older adults had significantly greater connectivity to clusters in the anterior regions of the brain for the attentional network seeds, compared to younger adults. The resulting maps from the age-related contrasts are overlaid on Power et al. (2011) network seeds to differentiate between within- and between-network connectivity. For the seed-to-voxel connectivity maps of a particular network (e.g. CO), the Power et al. seeds for that particular network are displayed in black and the other two network

seeds from Power et al. are displayed in their respective colors. CO seeds are colored in yellow, FP seeds are colored in green, and DMN seeds are colored in red, if they are overlaid over results from seeds of the other two networks.

Table 1. Demographics, Accuracy, and Cognitive Control Costs for each Age-group

	Younger Adults	Older Adults	<i>p</i> -value
<i>Age</i>	25.70(4.15)	66.03(6.83)	<.001
<i>Education</i>	17.57(1.75)	15.79(1.82)	.001
<i>No. Females</i>	23	29	
<i>Health Rating</i>	4.26(0.81)	4.29(0.66)	.889
<i>Physical Fitness Rating</i>	3.42(1.12)	3.76(1.08)	.303
<i>Single task Accuracy</i>	0.97(0.01)	0.96(0.06)	.559
<i>Dual task Accuracy</i>	0.97(0.03)	0.95(0.08)	.199
<i>Memory Updating Accuracy</i>	0.92(0.04)	0.81(0.07)	<.001
<i>Mixing Cost</i>	274.22(97.59)	283.67(129.59)	.776
<i>Switch Cost (Dual task)</i>	27.64(78.39)	76.98(96.84)	.144
<i>Switch Cost (Memory Updating)</i>	58.90(58.45)	96.75(107.87)	.057

Note. A series of independent samples t-tests between younger and older adults were conducted at $p < .05$. Both the Health Rating and Physical Fitness Rating were on a 1-5 Likert scale.

Table 2. Significant clusters for Task Complexity (task > rest) across the three networks, controlling for age and total gray matter volume. Multiple seed-to-voxel general linear models (GLM) were conducted across three tasks, over and beyond connectivity during rest block (Single task > rest, Dual task > rest, and Memory Updating>Rest) and three networks (CO, FP, and DMN) resulting in all significant clusters surpassing a p -FWE corrected p -value of .05.

Task/Network/Seed/Clusters	BA	x	y	z	No. Voxels	t-value
Single Task						
CO						
<i>dACC/msFC</i>						
left Frontal Lobe		-30	-34	30	75	5.36
<i>Left anterior Insula</i>						
--						
FP						
<i>Right dlPFC</i>						
right Inferior Frontal Gyrus ⁺ , Insula*		42	20	-2	163	4.95
<i>Left aIPL</i>						
--						
DMN						
<i>PCC</i>						
left Superior Frontal Gyrus ⁺ , Frontal Pole*		-4	58	-8	643	6.04
left Medial Frontal Gyrus ⁺ , Frontal Pole*		-14	40	36	113	5.64
left Inferior Temporal Gyrus ⁺ , Temporal Pole*	21	-44	0	-38	99	5.64
<i>Right Lateral Temporal Gyrus</i>						
right Inferior Frontal Gyrus		54	12	20	129	5.82
right Cerebellum, Crus 2		10	-94	-34	72	5.17
Dual Task						
CO						
<i>dACC/msFC</i>						
right Fusiform Gyrus ⁺ , Occipital Fusiform Gyrus*		32	-64	-16	127	5.51
Fusiform Gyrus ⁺ , Temporal Occipital Fusiform						
left Cortex*	37	-34	-50	-18	122	5.55
right Superior Occipital Gyrus ⁺ , Lateral Occipital Gyrus*		30	-82	22	90	4.45
right Superior Parietal Lobe ⁺ , Lateral Occipital Gyrus*		30	-70	50	74	4.82
<i>Left anterior Insula</i>						
right Precuneus	7	4	-64	40	604	6.28
right posterior Cingulate Gyrus	23	6	-34	24	247	5.62
left Cerebellum, Declive		-6	-78	-22	246	6.03
right Inferior Parietal Lobe ⁺ , Lateral Occipital Gyrus*		38	-64	40	220	4.77
left Superior Parietal Lobe ⁺ , Lateral Occipital Gyrus*		-30	-74	46	181	4.28
left Inferior Frontal Gyrus, pars opercularis		-40	12	26	78	4.74

FP							
<i>Right dlPFC</i>							
left	Supramarginal Gyrus		-28	-42	36	95	5.57
left	Postcentral Gyrus ⁺ , Precuneus*		-4	-54	66	85	4.68
right	Hippocampus	28	16	-12	-16	76	5.86
<i>Left aIPL</i>							
--							
DMN							
<i>PCC</i>							
--							
<i>Right Lateral Temporal Gyrus</i>							
--							
Memory Updating							
CO							
<i>dACC/msFC</i>							
left	Superior Frontal Gyrus	8	-16	30	54	5222	9.78
left	Angular Gyrus ⁺ , Lateral Occipital Gyrus*	39	-38	-70	36	3443	10.81
left	middle Cingulate Gyrus ⁺ , Precuneus*		-2	-34	36	2892	8.21
right	Angular Gyrus ⁺ , Lateral Occipital Gyrus*	40	42	-64	44	2061	7.82
right	Inferior Temporal Gyrus ⁺ , Middle Temporal Gyrus*	21	62	-42	-18	345	5.72
left	Middle Temporal Gyrus	21	-64	-40	-12	328	6.12
left	middle Orbitofrontal Gyrus ⁺ , Frontal Pole*	10	-34	54	-4	169	5.21
right	Cerebellum, Uvula		26	-74	-34	159	6.79
right	Caudate		12	14	8	125	5.75
right	Superior Temporal Gyrus ⁺ , Middle Temporal Gyrus*		58	-10	-42	112	5.90
left	Caudate		-8	16	4	98	4.64
<i>Left anterior Insula</i>							
left	middle Cingulate Gyrus ⁺ , Precuneus*		-2	-38	34	1905	7.14
left	Superior Frontal Gyrus ⁺ , Frontal Pole*		-16	46	38	1764	8.40
left	Inferior Parietal Lobe ⁺ , Lateral Occipital Gyrus*		-44	-68	40	1147	8.18
right	Angular Gyrus ⁺ , Lateral Occipital Gyrus*	39	52	-64	24	965	6.16
left	Superior Frontal Gyrus ⁺ , Frontal Pole*		-10	60	12	336	6.05
right	Middle Frontal Gyrus	8	36	20	50	225	5.29
left	Inferior Temporal Gyrus ⁺ , Middle Temporal Gyrus*		-60	-6	-32	189	6.97
left	Superior Frontal Gyrus ⁺ , Middle Frontal Gyrus*		-36	14	54	103	5.41
right	anterior Cingulate Gyrus ⁺ , Paracingulate Gyrus*	32	6	46	12	88	4.55
left	Inferior Frontal Gyrus, pars triangularis		-54	26	-4	76	5.08
right	Middle Temporal Gyrus		60	-8	-26	73	5.40

FP							
<i>Right dlPFC</i>							
right	Middle Temporal Gyrus ⁺ , Lateral Occipital Gyrus*		40	-78	18	4983	9.20
right	Precuneus ⁺ , Lateral Occipital Gyrus*		16	-58	56	1390	6.92
	Supplementary Motor Area ⁺ , Superior Frontal Gyrus*	6	-12	-2	66	750	7.31
right	Postcentral Gyrus		66	-18	30	244	5.76
left	Precentral Gyrus		-40	-12	42	136	5.32
right	medial Superior Frontal Gyrus		2	54	24	103	4.26
<i>Left aIPL</i>							
right	Precuneus	7	14	-76	36	36892	12.52
right	Putamen		24	4	4	525	6.96
left	Amygdala		-24	2	-14	142	5.29
right	Insula		40	-6	-10	116	5.62
right	Medial Frontal Gyrus ⁺ , Frontal Pole*		20	26	36	114	5.32
DMN							
<i>PCC</i>							
right	Inferior Frontal Gyrus ⁺ , Frontal Pole*		42	42	4	24468	11.15
	Supplementary Motor Area ⁺ , anterior Cingulate Gyrus*	6	4	12	46	1644	7.39
left	Middle Temporal Gyrus		-56	-60	-6	532	6.87
right	Middle Temporal Gyrus		60	-54	-8	330	6.19
left	Cerebellum, Declive		-28	-64	-20	229	5.56
	Supplementary Motor Area ⁺ , Superior Frontal Gyrus*	6	-12	2	64	100	4.79
left	posterior Cingulate Gyrus		-14	-32	40	78	4.64
left	Cerebellum, Culmen		-48	-48	-38	77	5.79
<i>Right Lateral Temporal Gyrus</i>							
	Supplementary Parietal Lobe ⁺ , Lateral Occipital Gyrus*	7	20	-72	54	458	6.97
left	Postcentral Gyrus ⁺ , Supramarginal Gyrus*		-56	-32	42	440	6.59
right	Precentral Gyrus ⁺ , Supramarginal Gyrus*		66	-18	42	420	6.11
left	Supplementary Parietal Lobe ⁺ , Lateral Occipital Gyrus*		-20	-72	58	378	6.74
right	Lateral Occipital Gyrus	39	40	-80	26	309	5.87
left	inferior Orbitofrontal Gyrus ⁺ , Frontal Pole*		-34	38	-20	156	5.94
right	Inferior Temporal Gyrus	37	62	-52	-14	99	5.03
left	Inferior Temporal Gyrus	20	-52	-52	-18	95	5.82
left	Inferior Frontal Gyrus ⁺ , Precentral Gyrus*		-42	4	26	78	5.03
left	Lateral Occipital Gyrus		-36	-84	24	76	4.89

Note: ⁺ indicates the locations of the peak voxel

* indicates the location of the majority of voxels in the cluster

Table 3. Standardized stepwise regression coefficients for Single task reaction time, Dual task reaction time, and Memory Updating accuracy predicted by age, total gray matter volume, and beta weights for significant connectivity clusters from stepwise regression.

Variable	β	t	p	R^2	ΔR^2	F	p
Single task > Rest Contrasts							
Model 1				0.18		5.30	0.008
Age	0.34	2.05	0.05				
Total Gray Matter Volume	-0.13	-0.78	0.44				
Dual task > Rest Contrasts							
Model 1				0.18		5.22	0.009
Age	0.39	2.36	0.02				
Total Gray Matter Volume	-0.06	-0.34	0.74				
Model 2				0.46	0.28	7.54	<.001
Age	0.47	-3.28	0.002				
Total Gray Matter Volume	-0.06	2.47	0.69				
Right dlPFC to left Supramarginal Gyrus	0.33	2.99	0.005				
Left anterior Insula to left Declive	0.41	-3.50	0.002				
Left anterior Insula to right Inferior Parietal Lobe	-0.28	-3.41	0.03				
Memory Updating > Rest Contrasts							
Model 1				0.46		20.16	<.001
Age	-0.51	-3.77	<.001				
Total Gray Matter Volume	0.24	1.76	0.09				
Model 2				0.72	0.26	18.81	<.001
Age	-0.34	-3.28	0.002				
Total Gray Matter Volume	0.26	2.47	0.02				
Right Lateral Temporal Gyrus to left Supplementary Parietal Lobe	0.25	2.99	0.005				
dACC to right Uvula	-0.29	-3.50	0.001				
Right dlPFC to right medial Superior Frontal Gyrus	-0.29	-3.41	0.001				
dACC to middle Cingulate Gyrus	0.24	2.91	0.006				

Table 4. Significant clusters for age-related differences in connectivity as a function of Task Complexity (task > rest) across the three networks. Multiple seed-to-voxel general linear models (GLM) were conducted across the three tasks, over and beyond connectivity during rest blocks (Single task > rest, Dual task > rest, and Memory Updating>Rest) and the three networks (CO, FP, and DMN) for younger > older and older > younger contrasts, resulting in all significant clusters surpassing a p -FWE corrected p -value of .05.

Task/Network/Seed/Clusters	BA	x	y	z	No. Voxels	t-value
Single Task						
CO						
<i>dACC/msFC</i>						
YA>OA						
--						
OA>YA						
--						
<i>Left anterior Insula</i>						
YA>OA						
right Middle Temporal Gyrus ⁺ , Lateral Occipital Gyrus*		44	-62	10	110	6.03
OA>YA						
--						
FP						
<i>Right dlPFC</i>						
YA>OA						
--						
OA>YA						
--						
<i>Left aIPL</i>						
YA>OA						
--						
OA>YA						
--						
DMN						
<i>PCC</i>						
YA>OA						
--						
OA>YA						
right Middle Frontal Gyrus	9	32	30	38	106	5.00
right Caudate		16	6	16	72	6.20
<i>Right Lateral Temporal Gyrus</i>						
YA>OA						
--						
OA>YA						
--						

Dual Task								
CO								
dACC/msFC								
YA>OA								
OA>YA								
Left anterior Insula								
YA>OA								
OA>YA								
FP								
Right dlPFC								
YA>OA								
	right	Middle Frontal Gyrus ⁺ , Frontal Pole*	10	44	48	4	80	4.88
OA>YA								
	right	Occipital Fusiform Gyrus	19	26	-70	-14	90	4.60
Left aPL								
YA>OA								
	right	Inferior Parietal Lobe ⁺ , Superior Parietal Lobe*		32	-56	46	115	4.70
	left	Inferior Parietal Lobe ⁺ , Supramarginal Gyrus*		-48	-42	40	72	5.38
	right	Middle Frontal Gyrus ⁺ , Frontal Pole*	10	46	56	0	69	5.04
OA>YA								
	left	Paracingulate Gyrus		-10	46	20	79	4.67
DMN								
PCC								
YA>OA								
OA>YA								
Right Lateral Temporal Gyrus								
YA>OA								
OA>YA								
Memory Updating								
CO								
dACC/msFC								
YA>OA								
	right	Lingual Gyrus		6	-90	-14	162	6.00
OA>YA								

	left	Superior Frontal Gyrus ⁺ , Frontal Pole*		-20	52	18	86	5.03
Left anterior Insula								
YA>OA								
	right	Middle Temporal Gyrus ⁺ , Lateral Occipital Gyrus*		42	-64	22	126	5.50
	left	Occipital Pole	18	-8	-100	-18	87	4.69
OA>YA								
	left	Superior Frontal Gyrus ⁺ , Frontal Pole*		-24	52	12	107	5.95
FP								
Right dIPFC								
YA>OA								
		--						
OA>YA								
		--						
Left aIPL								
YA>OA								
	right	Calcarine Gyrus ⁺ , Lingual Gyrus*		24	-50	4	76	5.78
OA>YA								
	right	anterior Cingulate Gyrus	32	4	34	20	98	4.88
		Paracentral Lobe ⁺ , posterior Cingulate Gyrus*		0	-20	46	90	5.18
	left	Precentral Gyrus ⁺ , Postcentral Gyrus*		-42	-16	32	77	4.75
DMN								
PCC								
YA>OA								
	left	Superior Temporal Gyrus ⁺ , Insula*	13	-44	-12	-8	274	6.66
	right	Inferior Parietal Lobe ⁺ , Parietal Operculum Cortex*		48	-34	28	183	4.93
	right	Superior Temporal Gyrus ⁺ , Central Opercular Cortex*		58	-8	4	127	4.90
	left	Middle Cingulum ⁺ , Precentral Gyrus*	5	-2	-34	50	86	4.17
OA>YA								
	left	Precuneus	44	-8	-66	44	92	4.78
		Inferior Parietal Lobe ⁺ , Lateral Occipital						
	right	Gyrus*		34	-64	40	82	4.67
Right Lateral Temporal Gyrus								
YA>OA								
		--						
OA>YA								
	left	Superior Temporal Gyrus ⁺ , Supramarginal Gyrus*		-46	-46	20	87	5.56

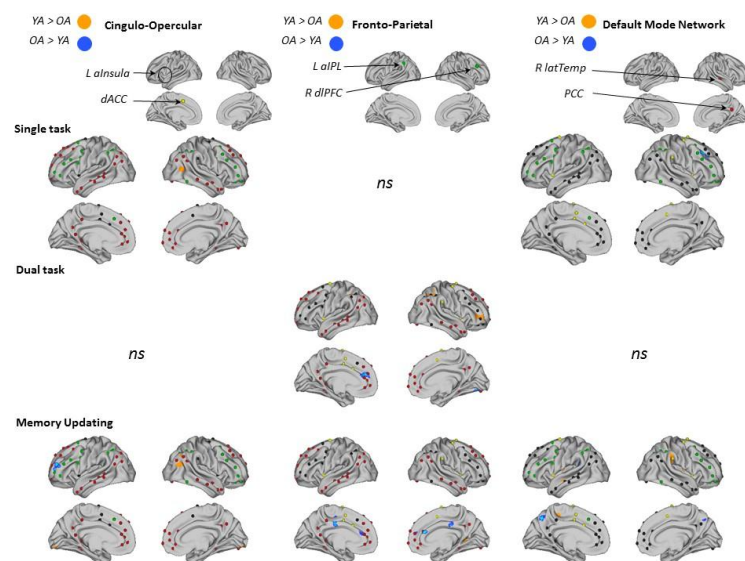
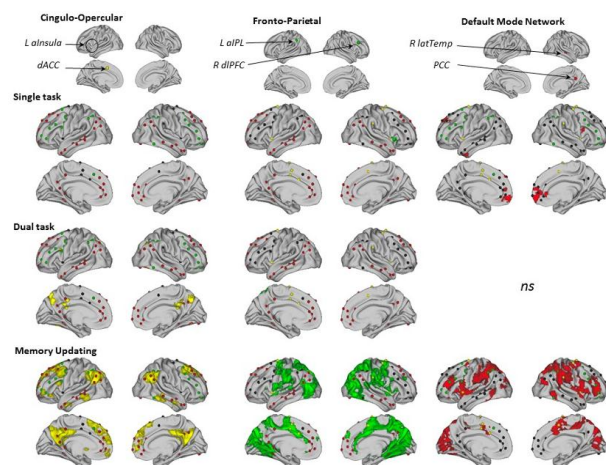
Note: ⁺ indicates the locations of the peak voxel

* indicates the location of the majority of voxels in the cluster

Table 5. Standardized linear regression coefficients of age X variable interaction terms, predicting performance in one of the three scanner tasks. Tests of these comparisons were conducted using Bonferroni adjusted alpha levels (for example $\alpha = .006$ for Memory Updating, * for significant regression analyses).

Variable	β	SE	$t(48)$	p
<i>Single task Reaction Time</i>				
PCC to right Middle Frontal Gyrus	-0.06	1.86	-0.40	0.69
PCC to right Caudate	0.16	2.32	1.16	0.25
<i>Dual task Reaction Time</i>				
Right dlPFC to right Occipital Fusiform Gyrus	0.04	1.48	0.26	0.80
Left aIPL to Paracingulate Gyrus	0.16	1.41	1.10	0.28
<i>Memory Updating Accuracy</i>				
dACC to left Superior Frontal Gyrus	-0.26	0.002	-1.83	0.07
Left anterior Insula to left Superior Frontal Gyrus	-0.44	0.003	-3.43	0.001*
Left aIPL to anterior Cingulate Gyrus	-0.55	0.002	-4.54	<.001*
Left aIPL to Paracentral Lobe	-0.51	0.002	-4.09	<.001*
Left aIPL to left Precentral Gyrus	-0.48	0.002	-3.77	<.001*
PCC to left Precuneus	-0.07	0.002	-0.51	0.61
PCC to right Inferior Parietal Lobe	-0.47	0.002	-3.65	0.001*
Right Lateral Temporal Gyrus to left Superior Temporal Gyrus	-0.51	0.002	-4.16	<.001*

Note: The Single task and Dual task analyses are predicting reaction time, whereas the Memory Updating analyses are predicting accuracy.



Highlights

- FP, CO and DMN network connectivity were examined during 3 cognitive control tasks
- Both within- and between-network connectivity increased with task complexity
- Older adults had more connectivity to anterior brain regions from FP and CO seeds
- Such age-related increases in connectivity were linked to poorer task performance