Prefrontal Engagement and Reduced Default Network Suppression Co-occur and Are Dynamically Coupled in Older Adults: The Default–Executive Coupling Hypothesis of Aging

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Abstract

■ Reduced executive control is a hallmark of neurocognitive aging. Poor modulation of lateral pFC activity in the context of increasing task challenge in old adults and a "failure to deactivate" the default network during cognitive control tasks have been observed. Whether these two patterns represent discrete mechanisms of neurocognitive aging or interact into older adulthood remains unknown. We examined whether altered pFC and default network dynamics co-occur during goal-directed planning over increasing levels of difficulty during performance on the Tower of London task. We used fMRI to investigate task- and age-related changes in brain activation and functional connectivity across four levels of task challenge. Frontoparietal executive control regions were activated and default network regions were suppressed during planning relative to counting performance in both groups. Older adults, unlike young, failed to modulate brain activity in executive control and default regions as planning demands increased. Critically, functional connectivity analyses revealed bilateral dorsolateral pFC coupling in young adults and dorsolateral pFC to default coupling in older adults with increased planning complexity. We propose a default–executive coupling hypothesis of aging. First, this hypothesis suggests that failure to modulate control and default network activity in response to increasing task challenge are linked in older adulthood. Second, functional brain changes involve greater coupling of lateral pFC and the default network as cognitive control demands increase in older adults. We speculate that these changes reflect an adaptive shift in cognitive approach as older adults come to rely more upon stored representations to support goal-directed task performance. ■

INTRODUCTION

Functional brain changes are a consistent feature of neurocognitive aging. Differences in activation magnitude and spatial activation patterns are frequently reported in functional neuroimaging studies of older and younger adults during cognitive task performance (Grady, 2012; Turner & Spreng, 2012; Spreng, Wojtowicz, & Grady, 2010). However, the specific nature of these age-related changes in task-evoked response, functional connectivity, and their behavioral implications remain poorly understood (for reviews, see Grady, 2012; Turner & D'Esposito, 2011; Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Cappell, 2008).

Age-related changes in functional activation have been characterized as reduced hemispheric lateralization in older relative to younger adults, particularly during frontally mediated or executive control tasks (Cabeza, 2002). During tasks with executive control demands, enhanced bilateral pFC engagement in older adults has been associated with better performance (Daselaar et al., 2015; Stern et al., 2005; Cabeza et al., 2004; Reuter-Lorenz et al., 2000), and this pattern of supplementary recruitment appears to be a function of task demand, occurring at lower, but not higher levels of executive control challenge (Cappell, Gmeindl, & Reuter-Lorenz, 2010; Mattay et al., 2006; Reuter-Lorenz & Lustig, 2005). An alternate account of age-related functional brain changes suggests that overrecruitment is maladaptive, reflecting a loss of functional specialization within the brain. This characterization represents a neural extension of the dedifferentiation hypothesis, wherein discrete cognitive capacities in younger adults become increasing indistinct, or dedifferentiated, with advancing age (Park, Polk, Mikels, Taylor, & Marshuetz, 2001; Baltes & Lindenberger, 1997). Evidence of age-related dedifferentiation of functional brain activity has now been observed in posterior brain regions during perceptual tasks (Park et al., 2004; Grady et al., 1994) and more anterior brain regions bilaterally during memory and executive control processes (Dennis & Cabeza, 2011; Cappell et al., 2010; Gutchess et al., 2005; Cabeza et al., 2004; Morcom, Good, Frackowiak, & Rugg, 2003). At the level of the brain, dedifferentiation reflects the loss of specialized neural processors and reduced functional distinctions between brain regions leading to greater and potentially less efficient brain activity. A more recent account suggests that greater

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recruitment of lateral pFC may reflect a compensatory response to reduced white matter integrity in pFC of older adults (Daselaar et al., 2015). Although these accounts diverge in terms of their behavioral predictions, they are consistent in their prediction of age-related differences in frontal brain activity in response to executive control tasks.

Neurocognitive aging has also been studied through the lens of large-scale functional brain networks (Perry et al., 2015; Andrews-Hanna, Smallwood, & Spreng, 2014; Chan, Park, Savalia, Petersen, & Wig, 2014; Geerligs, Maurits, Renken, & Lorist, 2012; Spreng & Schacter, 2012; Meunier, Archad, Morcom, & Bullmore, 2009; Damoiseaux et al., 2008; Andrews-Hanna et al., 2007; Grady, Springer, Hongwanishkul, McIntosh, & Winocur, 2006; Lustig et al., 2003). In this network-based approach, executive control is characterized as an emergent property of functional connections among spatially distributed brain regions that are intrinsically organized into large-scale, interacting networks (Spreng, Sepulcre, Turner, Stevens, & Schacter, 2013; Vincent, Kahn, Snyder, Raichle, & Buckner, 2008; Fox et al., 2005; Corbetta & Shulman, 2002). Investigations of changes in network activation, functional connectivity, or interactivity are beginning to generate new hypotheses to explain age-related declines in executive control (Madden et al., 2010; Sambataro et al., 2010; Persson, Lustig, Nelson, & Reuter-Lorenz, 2007; Lustig et al., 2003).

Studies of age-related changes in functional brain networks suggest that the default network may be particularly vulnerable to changes in older adulthood (Spreng & Turner, 2013; Grady et al., 2010; Sambataro et al., 2010; Damoiseaux et al., 2008; Andrews-Hanna et al., 2007; Persson et al., 2007; Buckner, 2004). The default network is a collection of intrinsically connected brain regions including the posterior cingulate cortex (PCC), medial pFC (MPFC), inferior parietal lobule, and medial and lateral temporal lobes. This collection of brain regions has been implicated in internally directed cognitive processes, including access to stored knowledge representations and experiences (Andrews-Hanna et al., 2014), which are typically suppressed during performance of externally directed attention tasks (Andrews-Hanna et al., 2014; Buckner, Andrews-Hanna, & Schacter, 2008).

Age-related changes in the default network include attenuated suppression during externally directed cognitive tasks (Hansen et al., 2014; Persson et al., 2007; Lustig et al., 2003), reduced within-network functional connectivity during task (Geerligs, Maurits, Renken, & Lorist, 2012; Grady et al., 2010; Sambataro et al., 2010) and rest (Geerligs, Renken, Saliasi, Maurits, & Lorist, 2015; Damoiseaux et al., 2008; Andrews-Hanna et al., 2007), and altered connectivity between default and other functional brain networks (Geerligs et al., 2015; Chan et al., 2014; Spreng & Schacter, 2012; Sambataro et al., 2010). Consistent with previous accounts of age-related overrecruitment, changes in the default network also appear to depend on the level of task challenge, with greater reductions in task-related suppression associated with increased cognitive demand (Persson et al., 2007). These changes in the default network have been associated with reduced cognitive performance (e.g., Geerligs et al., 2012; Sambataro et al., 2010; Miller et al., 2008; Andrews-Hanna et al., 2007; Persson et al., 2007). However, this "task-negative" view of the default network has recently been questioned (see Spreng, 2012, for a discussion). There is early evidence that activation of these brain regions may support cognition in a context-specific manner, at least in younger adults (e.g., Spreng et al., 2014; Meyer, Spunt, Berkman, Taylor, & Lieberman, 2012), and that task appropriate activation, such as during an autobiographical task, is similar in young and older adults (e.g., Spreng & Schacter, 2012).

Altered recruitment of frontal brain regions and default network changes are two purported cortical mechanisms of neurocognitive aging, yet there has been scant consideration of whether or how these two patterns of age-related functional brain change interact. Recent studies suggest that they may not be entirely dissociable. Age-related increases in functional connectivity among default and frontally mediated brain networks were observed during a visual attention task (Geerligs et al., 2012). Similarly, frontal-parietal and default brain regions failed to decouple in older, but not younger, adults during externally directed working memory tasks (Spreng & Schacter, 2012; Sambataro et al., 2010). Age-related increases in frontal–default coupling in older adults has also been reported in resting-state functional connectivity studies assessing whole-brain patterns of network interactions (Geerligs et al., 2015; Chan et al., 2014). Cognitively, reduced default network suppression, which is associated with off-task behaviors and distractibility in young adults (Chadick & Gazzaley, 2011; Christoff, Gordon, Smallwood, Smith, & Schooler, 2009; Mason et al., 2007), may require engagement of additional executive control processes to overcome distraction in older adults. Supplemental recruitment of frontal brain regions, associated with executive control, would be necessary to suppress distractions and maintain robust, goal-relevant representations online in support of ongoing task performance. Older adults also demonstrate reduced modulation of activity in lateral pFC regions in the context of increased executive control demands, demonstrating both increased and reduced recruitment of these regions in response to increasing task demand (Grady, 2012; Cappell et al., 2010; Reuter-Lorenz & Cappell, 2008; Mattay et al., 2006). This suggests a putative link between default network activity and lateral pFC activation during goal-directed cognition in older adulthood.

Here, we propose the default–executive coupling hypothesis of aging (DECHA). The DECHA model predicts that reduced modulation of prefrontal brain regions in the context of increased executive control demand will co-occur with reduced suppression of the default network. Furthermore, these age-related changes in activation of default and executive regions would be associated with

greater coupling of activation patterns between these brain areas as task demands increase. We propose that this neurobiological DECHA model parallels the cognitive aging framework of declining executive control resources, associated with changes in frontal brain structures (e.g., Park & Reuter-Lorenz, 2009), precipitating greater reliance on stored representational knowledge structures and experiences, mediated by the default network (Andrews-Hanna et al., 2014). In this framework, stored representations assume an increasingly central role in goal-directed cognition in older adults (Craik & Bialystok, 2006).

To validate the DECHA model, we use a common goal-directed planning task, the Tower of London (TOL; Shallice, 1982). Functional neuroimaging investigations have previously implicated prefrontal brain regions, particularly lateral and anterior aspects (Wagner, Koch, Reichenbach, Sauer, & Schlosser, 2006; Newman, Carpenter, Varma, & Just, 2003; van den Heuvel et al., 2003; Baker et al., 1996; Morris, Ahmed, Syed, & Toone, 1993) in performance on this task. More recently, the TOL task and an autobiographical planning analog were used to demonstrate age-related reductions in the modulation of functional network interactions during internal and external mentation (Spreng & Schacter, 2012). Here we utilize the TOL paradigm to examine age-related functional brain changes in younger and older adults. Critically, we will use a parametric task manipulation (three, four, five, and six move planning puzzles) to assess frontal–default network interactions across four levels of executive control challenge.

Consistent with DECHA, we hypothesize that performance on the TOL task will be associated with activation in lateral aspects of pFC and suppression of the default network in younger adults. Moreover, these differences will be amplified at higher levels of planning challenge. We predict that older adults will fail to show this pattern of task-dependent enhancement and suppression. Specifically, older adults will fail to parametrically enhance activity in frontal brain regions as planning demands increase, and this will be coincident with reduced default network suppression, relative to the younger participants. As modulation of lateral pFC activity changes with advancing age (e.g., Reuter-Lorenz & Cappell, 2008; Persson et al., 2007), we predicted (i) reduced default network suppression and (ii) increased default-to-lateral pFC coupling, particularly for greater task challenge. These predictions, if observed, would provide preliminary support for the DECHA.

METHODS

Participants were 18 young adults (mean age = 22.8 ± 2.4 years, range = 19–27, nine women) and 18 old adults (mean age = 71.4 ± 4.0 years, range = 63–78, nine women) with normal or corrected-to-normal visual acuity and no history of psychiatric, neurological, or other medical illness that could compromise cognitive functions. Most participants were right-handed; one male participant in each group was left-handed. Older adults were high functioning, with a healthy mental status, normal neurocognitive functioning, and not depressed (see Table 1 for demographics and neuropsychological status). All participants gave written informed consent in accordance with the Harvard Institutional Review Board. This study is a novel reanalysis of previously published data (Spreng & Schacter, 2012).

Table 1. Demographic and Neuropsychological Profiles

	Old	*Young*
Gender (male/female)	9/9	9/9
Years of age	71.4 (4.0)	22.8 (2.4)
Years of education	15.9 (1.9)	15.9 (1.1)
Mini-Mental State Exam	28.4 (1.5)	–
Geriatric Depression Scale	0.8 (0.9)	–
Digit span backwards	7.6 (3.2)	–
Mental control (WMS)	23.5 (5.4)	–
WCST (categories)	4.9 (1.6)	–
Verbal fluency (FAS)	46.6 (13.2)	–

Group means and standard deviations (in parentheses) for demographic variables and neuropsychological test scores for younger and older adults. Normative performance was assessed using age- and (where available) education-matched normative data published with each measure or in Spreen and Strauss (1998).

Tasks

Using a standard TOL testing protocol, visuospatial planning was investigated by presenting participants with two configurations on a single screen: the "goal" position and the "initial" position. Both configurations consisted of three equally sized colored discs placed on three vertical rods. The objective of this task was for the participant to determine the minimum number of moves to accomplish the goal state. Participants were informed that only one disc could be moved at a time and that it can only be the top disc on each rod. Sometimes counterintuitive moves are necessary to reach the goal. A button was pressed when the lowest number of moves is determined. All participants were initially trained with a physical TOL apparatus and demonstrated mastery of the rules before practice on a digital version of the task, which was also presented in the scanner. For a comparison condition, we used a counting task adapted from previous studies of the TOL (Wagner et al., 2006; van den Heuvel et al., 2003). In this control condition, the goal state was replaced with the instruction to count vowels, followed by the appearance of random letter sequences in the discs during the execution phase. Participants also completed an autobiographical planning task, which is discussed elsewhere (Spreng & Schacter, 2012). Participants were scanned during the pseudorandom presentation of

TOL and counting trials in six experimental runs. The runs included four TOL and four counting trials. For each trial, the start position was presented separately for 5 sec to orient the participant to the goal. The goal position and the initial position were then paired in the self-paced execution phase of the trial for a maximum of 20 sec. Participants then had 5 sec to make a button press response indicating a multiple choice selection for the minimum number of moves to solve the TOL task or the number of vowels counted.

MRI Data Collection and Preprocessing

Brain imaging data were acquired with a 3.0-T Siemens TimTrio MRI scanner with a 32-channel head coil. Anatomical scans were acquired using a T1-weighted multi-echo volumetric MRI (repetition time = 2530 msec; echo time = 1.64, 7.22 msec; 7° flip angle; 1.0 mm isotropic voxels). Six 7-min task BOLD functional scans were acquired with a T2*-weighted EPI pulse sequence (repetition time = 2500 msec; echo time = 30 msec; 85° flip angle; 39 axial slices parallel to the plane of the AC–PC; 3.0 × 3.0 × 2.5 mm voxels with a 0.5-mm skip).

All fMRI data were preprocessed using standard AFNI preprocessing procedures. The first four volumes in each run were excluded from analyses to allow for T1-equilibration effects. Data were corrected for slice-dependent time shifts and for head motion within and across runs using a rigid body correction. We further analyzed group-wise head motion during our task blocks. This analysis failed to identify significant differences in motion between our two age cohorts. To compare brain data across age groups, all data were normalized to a combined young–old brain template that approximated Montreal Neurological Institute (MNI) atlas space. This target template included the variation of the population under study (e.g., blurring of the ventricular boundaries due to inclusion of unatrophied young and atrophic old adults), thus facilitating valid between-group comparison (Buckner et al., 2004). The volumetric time series was then resampled at 3-mm cubic voxels and spatially smoothed with a 10-mm FWHM Gaussian kernel. All coordinates are reported in MNI space.

Behavioral Data

Accuracy was calculated for each group at each level of planning challenge for the TOL task and counting set size for the control task. Univariate statistical analyses were conducted to determine main effects of group, task, and set size and to identify interaction effects.

fMRI Data Analysis

Task-based analyses were performed using the multivariate technique partial least squares (PLS), which is sensitive to distributed network activity (McIntosh, Chau, & Protzner, 2004). PLS determines a set of orthogonal latent variables (LVs) that optimally relate BOLD signal and the experimental design. The statistical significance of the detected patterns is assessed through permutation testing, whereas reliability is determined in an independent step by iterative bootstrap resampling with replacement.

PLS is a multivariate functional neuroimaging analysis technique used to identify whole-brain patterns of activity that are correlated with tasks. PLS is a robustly validated (Krishnan, Williams, McIntosh, & Abdi, 2011; McIntosh et al., 2004) and widely used analysis technique that has also been used extensively to assess age-related changes in neural activity (e.g., Spreng & Schacter, 2012; Grady et al., 2006, 2010; Stevens, Hasher, Chiew, & Grady, 2008). PLS is sensitive to a distributed voxel response, rather than the activity of individual voxels per se, and assesses the covariance between brain voxels (BOLD signal) and the experimental design to identify a limited number of orthogonal components (LVs) that optimally relate the two. This data-driven approach determines orthogonal whole-brain patterns of activity that covary with the experimental design.

Each trial was treated as a block, and duration was determined by trial length following the presentation of the goal and terminated with the button press response. Activity for each voxel was averaged across blocks for each condition and normalized to activity at fixation preceding the goal. The data matrix was then expressed as a voxel-by-voxel deviation from the grand mean across the entire experiment. This matrix is then analyzed with singular value decomposition to derive the optimal effects in the data. Here, we applied PLS analysis to block fMRI data, and the results identify a set of brain regions wherein activity is reliably related to the task conditions for each LV. Each brain voxel is given a singular value weight, known as a salience (akin to a component loading in principle components analysis), which is proportional to the covariance of activity with the task contrast on each LV. Multiplying the salience by the BOLD signal value in that voxel and summing the product across all voxels give a composite brain activity score for each participant on a given LV. These scores can be used to examine similarities and differences in brain activity across conditions, as greater activity in brain areas with positive (or negative) weights on an LV will yield positive (or negative) mean scores for a given condition.

In addition to the task contrasts, a functional connectivity analysis was performed using seed PLS (Krishnan et al., 2011; McIntosh, 1999). Seed PLS is a data-driven multivariate statistical technique that reveals functional activity across the entire brain that correlates with activity in a seed region. The covariance between activity in the seed and all other brain voxels is decomposed into LVs that can identify multiple patterns of functional connectivity. The advantage of block seed PLS is that potential movement confounds associated with age are substantially reduced. In this analysis, a seed region in left dorsolateral pFC (DLPFC) demonstrating a significant group by planning interaction (MNI coordinate: −45, 33, 36; and

26 neighboring voxels) was extracted and correlated across participants with all other brain voxels; PLS was used to identify patterns of functional connectivity that differed between young and old adults.

Confidence intervals (95%) for the mean composite brain activity score and functional connectivity score in each condition and group were calculated from the bootstrap, and differences in activity between conditions were determined via a lack of overlap in these confidence intervals. The significance of each LV as a whole was determined by permutation testing, using 500 permutations. This was accomplished by randomly reassigning the order of the conditions for each participant. PLS is recalculated for each permutation sample, and the frequency in which the permuted singular value exceeds the observed singular values is determined and expressed as a probability. In a second, independent step, the reliability of the saliences for the brain voxels across participants, characterizing each pattern identified by an LV, was determined by bootstrap resampling, using 100 iterations, to estimate the standard errors for each voxel. Clusters larger than 100 mm^3 comprising voxels with a ratio of the salience to the bootstrap standard error values (i.e., the "bootstrap ratio" [BSR]) greater than 3 ($p < .002$) were reported. The local maximum for each cluster was defined as the voxel with a BSR higher than any other voxel in a 2-cm cube centered on that voxel. PLS identifies whole-brain patterns of activity in a single analytic step; thus, no correction for multiple comparisons are required.

As a complement to the multivariate PLS analyses, we performed additional univariate analyses. First, we performed ROI analyses on the DLPFC, MPFC, and PCC to assess the magnitude of BOLD response at each level of planning challenge. Second, we examine how the MPFC and PCC are functionally coupled with the DLPFC at each level of planning challenge. Finally, we assessed whether modulation was correlated across high and low task challenge for the MPFC and PCC with the DLPFC and if modulation scores were correlated with the magnitude of coupling between MPFC and PCC with the DLPFC.

First, ROI analyses were conducted to directly assess BOLD signal associated with the task conditions. BOLD signal change was extracted from three ROIs: (1) a left DLPFC region that emerged in both LV patterns (MNI coordinate: −45, 33, 36; and 26 neighboring voxels), as well as core default network nodes (2) MPFC (MNI coordinate: −6, 52, −2; and 26 neighboring voxels) and (3) PCC (MNI coordinate: −8, −56, 26; and 26 neighboring voxels). Peak default network seeds were from Andrews-Hanna, Reidler, Sepulcre, Poulin, and Buckner (2010). The interaction of Age (2 groups) with Parametric planning conditions and counting (5 conditions) was assessed in three 2 × 5 mixed-model repeated-measures ANOVAs. Simple main effects were adjusted for multiple comparisons using the Bonferroni correction ($\alpha = .05$).

Second, we assessed the functional coupling between the DLPFC and key nodes of the default network, the PCC and MPFC, as a function of task demand (MNI coordinates are above). To do so, we correlated the change in BOLD activity across time, from 2.5 to 25 sec posttrial onset, during the TOL conditions for the PCC and MPFC with that of the DLPFC in each participant. Using Fisher's r-to-z transform, we conducted a 2 × 4 repeated-measures ANOVA with Group as a between-subject factor and TOL moves (3–6) as within-subject factors to assess differences in the magnitude of correlation of these default network nodes with the DLPFC across levels of planning difficulty. Simple main effects were adjusted for multiple comparisons using the Bonferroni correction ($\alpha = .05$). Using a simple *t* test, these r-to-z correlation values were also compared with zero in each group to estimate the magnitude of coupling. We predicted greater levels of coupling between the DLPFC with the MPFC and PCC in older adults, consistent with prior observations of resting-state fMRI (Keller et al., 2015).

We performed additional analyses to assess the direct functional association between modulation of the DLPFC and the default network. We examined whether BOLD modulation of activity in the DLPFC was related to modulation in the MPFC and PCC by calculating modulation values between "low" (three and four moves) and "high" (five and six moves) levels of planning challenge and assessing their correlation. We also examined whether modulation scores predicted the extent of MPFC and PCC to DLPFC coupling by correlating the *z*-scores (described above), which were also collapsed into low and high planning challenge.

RESULTS

Behavioral Results

Accuracy and RT for the four-move trials in the TOL were assessed with a 2 × 4 mixed-measures ANOVA with simple main effects Bonferroni corrected for multiple comparisons (alpha = .05). Means, *SD*, and auxiliary independent samples *t* and *p* values are presented in Table 2. For accuracy, there was a significant effect of Number of moves ($F(3, 32) = 13.72, p < .001$) and a trend towards a Group × Move interaction ($F(3, 32) = 2.51, p = .076$). Although equivalent on the easiest, three-move trials, performance of younger adults exceeded that of old adults on trials with four, five, and six moves. Performance of both groups declined as planning difficulty increased, although this was only significant in the young group (see Table 2). For RT, there was a significant effect of Number of moves ($F(3, 32) = 5.69, p < .01$) and a Group × Move interaction ($F(3, 32) = 2.93, p < .05$). RT differences between groups did not survive adjustment for multiple comparisons. However, the trend in the Age × RT effect is accounted for by differences at the easiest 3-move puzzle. RT in both groups increased as planning difficulty increased, although this was only significant in the young group. It should be noted, however, that most participants used the full 20 sec

Table 2. TOL Task Performance

	Percent Accuracy				*RT (msec)*			
Number of Moves	*Old*	*Young*	*t*		*Old*	*Young*	*t*	
Three	74 (23)	82 (8)	1.40	*ns*	18864 (3294)	15752 (4887)	2.24	$p < .05$[a]
Four	48 (26)	72 (20)	3.16	$p < .01$	19317 (2016)	17628 (3855)	1.65	*ns*
Five	50 (29)	70 (15)	2.71	$p < .05$	19404 (2214)	18362 (2568)	1.30	*ns*
Six	31 (25)	65 (31)	3.59	$p < .01$	19403 (2531)	19323 (1297)	0.12	*ns*

Group means and standard deviations (in parentheses) for TOL task percent accuracy and RT. *ns* = nonsignificant.

[a]Not significant when Bonferroni adjusted for multiple comparisons.

to complete the TOL trials, and thus, RT is largely at ceiling. Accuracy and RT for the counting trials were assessed with independent samples *t* tests. Accuracy on the counting task was significantly greater in the young group ($t = 5.40$, $p < .001$; Young mean .95 ± .06; Old mean .78 ± .11). Three old adults complained that it was difficult to distinguish letters within the blue discs in this condition. This difficulty was not encountered during pilot sessions outside the scanner. RT for the counting conditions did not differ ($t = 1.07$, $p = .29$; Young mean 18616 ± 2709 msec; Old mean 19480 ± 2105 msec).

fMRI Results

Activation Patterns

Two significant LVs identified planning by age group interactions. The first identified a pattern of brain activity that differentiated the TOL conditions (5 and 6 moves in young adults, 3, 4 and 5 moves in old adults) from the counting condition (LV1: accounting for 73.20% of the covariance in the data; $p < .001$). The second LV differentiated brain activity in older participants based on the level of planning challenge. Brain activity during easier puzzles was distinguished from activity observed during the most difficult puzzles (LV2: accounting for 8.57% of the covariance; $p < .026$). Brain regions distinguishing planning from control tasks (LV1: Figure 1A, B; Table 3) included anterior and posterior lateral pFC regions bilaterally, dorsal anterior cingulate, superior and inferior parietal lobes, precuneus, as well as MPFC and insular cortex. Brain regions distinguishing high and low planning challenge in older adults (LV2: Figure 1C, D; Table 3) included left anterior DLPFC, posterior regions of superior frontal gyrus bilaterally, precentral gyrus, posterior aspect of left STS, as well as medial and lateral parietal cortices.

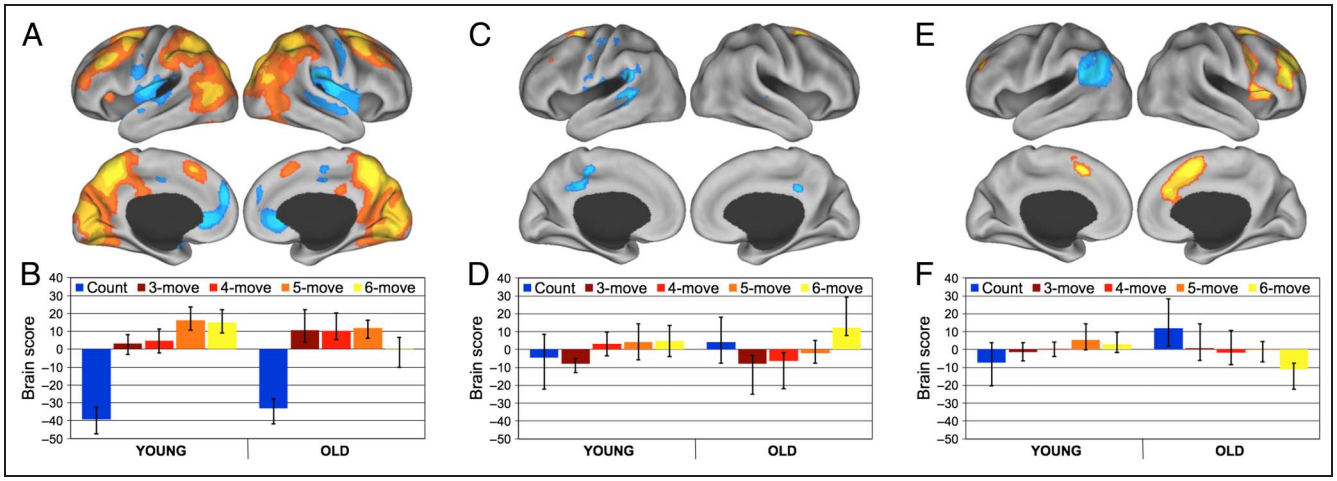

Figure 1. Task activation analysis. Three significant patterns of brain activity were identified. (A) LV1 distinguished TOL planning conditions from the Counting control condition. This pattern interacted with age such that high complexity puzzles (5–6 moves) in Young and lower complexity puzzles (3–5 moves) in Old were maximally dissociated from the Counting condition. (C) LV2 also distinguished levels of planning challenge and age interactions with the TOL task. Low complexity puzzles in Young and Old were maximally dissociating from the six-move condition only in the Old. (E) LV3 maximally dissociated the Counting condition from the six-move planning condition only in the Old. In the top panels, data are displayed on the lateral and medial surfaces of the left and right hemispheres of a partially inflated surface map using CARET software (Van Essen, 2005). Bottom panels (B, D, F) report composite brain activity scores for each LV (A, C, E, respectively). These convey the association between experimental conditions in brain activity related to each task condition and group. Brain image color scales indicate regions that positively (warm colors) or negatively (cool colors) reflect the corresponding brain score patterns. Color intensity indicates reliability of the patterns based on bootstrap resampling values (see Methods for details and Table 3 for peak coordinates).

Table 3. Task Activation

Hemis	Region	MNI Coordinates			BSR
		x	*y*	*z*	
LV1					
B	Dorsal precuneus	−9	−57	57	12.62
L	DLPFC	−42	33	33	11.44
R	FEFs	24	6	69	11.38
L	FEFs	−24	9	60	10.92
L	Intraparietal sulcus	−33	−51	42	10.57
R	Superior lateral occipital cortex	21	−90	21	10.14
L	Superior lateral occipital cortex	−24	−87	30	9.97
R	Intraparietal sulcus	33	−48	45	9.52
B	Occipital pole	3	−90	0	9.46
B	Dorsal anterior cingulate	−3	18	51	7.82
R	DLPFC	45	15	45	7.81
L	Rostrolateral pFC	−33	54	15	5.71
R	Thalamus	15	−27	15	5.05
L	Thalamus	−18	−27	15	4.74
L	Anterior insula	−33	24	3	4.74
L	Caudate	−15	9	15	4.14
R	Parietal operculum cortex	57	−27	24	−6.49
B	Ventromedial pFC	0	36	−12	−6.00
L	Central operculum cortex	−63	−15	12	−5.69
R	STS	60	−27	6	−5.16
B	Posterior middle cingulate cortex	6	−15	51	−4.60
LV2					
R	Superior frontal gyrus	27	9	66	5.51
L	Superior frontal gyrus	−24	9	63	5.19
L	DLPFC	−45	33	36	3.93
L	Posterior STS	−63	−39	−3	−4.92
L	Angular gyrus	−57	−45	27	−4.71
B	PCC	−3	−39	39	−3.84
L	Precentral gyrus	−45	−12	63	−3.48
LV3					
B	Dorsal ACC	6	15	51	5.68
L	Rostrolateral pFC	−24	42	21	4.95
R	Rostrolateral pFC	39	42	33	5.29
R	Superior frontal gyrus	21	3	60	4.61

Table 3. (*continued*)

Hemis	Region	MNI Coordinates x	y	z	BSR
R	BG	18	0	0	4.43
R	Anterior insula	36	18	12	4.49
L	TPJ	−60	−51	30	−5.85

Brain regions demonstrating reliable activation patterns for the task analysis. Clusters with a minimum size of 100 mm^3 and BSR greater than 3 ($p < .002$) are reported. Hemis = hemisphere; L = left; R = right.

In the multivariate analysis of brain activity, a third LV was expressed only in the older adult group. This pattern identified a difference in the counting task versus the six-move TOL condition (accounting for 7.47% of the covariance, $p < .042$; Figure 1E, F; Table 3). The counting task was associated with greater lateral pFC (right > left) and dorsal anterior cingulate activity, whereas the most difficult puzzle condition was associated with greater left temporal-parietal brain activity in the older group.

The multivariate results confirmed that planning demands were associated with age-related differences in brain activity that included both frontoparietal control and default network brain regions. We next examined whether these changes reflected age-related differences in the enhancement or suppression of activity in key ROIs identified by the multivariate pattern. The DLPFC and PCC ROIs showed an Age × Task interaction ($F(4, 31) = 2.93$, $p < .05$; $F(4, 31) = 5.56$, $p < .01$, respectively). This interaction approached significance for the MPFC ($F(4, 31) = 2.32$, $p < .08$). Both age groups showed activation changes in the expected directions (enhanced DLPFC and reduced default network activation) during planning relative to the control task. However, unlike younger adults, older adults failed to modulate brain activity in DLPFC as planning complexity increased. In younger adults, activity in the frontal ROIs increased (DLPFC) and decreased (MPFC) monotonically with increasing puzzle moves. Activities in these regions were not modulated by planning task complexity in older adults (Figure 2C, D). In contrast, activation in PCC was not modulated by the level of planning task demand in the young group but appeared to follow a curvilinear pattern in older adults increasing from three

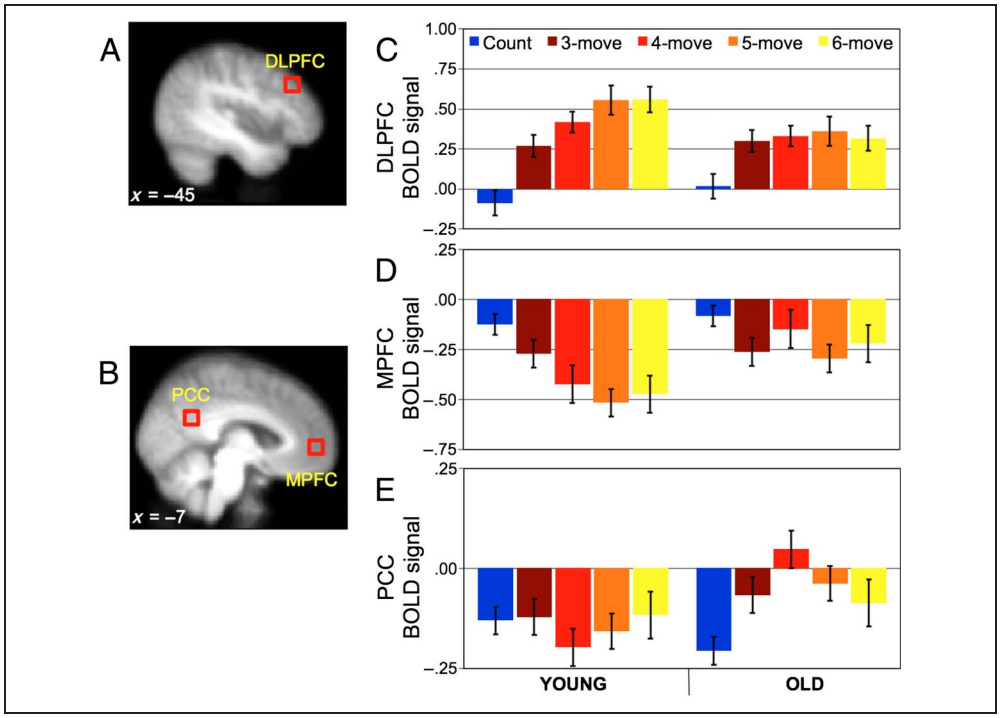

Figure 2. ROIs. Mean and standard error of task-related BOLD signal changes during TOL and Counting conditions in (A) left DLPFC and (B) MPFC and PCC. (C) DLPFC displays a parametric increase in BOLD signal across all levels of planning challenge in the Young; in the Old, a dichotomous, task-dependent increase, differentiating counting from all planning conditions. (D) MPFC displays a parametric decrease in BOLD signal in the Young with increasing planning challenge and a dichotomous, task-dependent decrease in the Old, discriminating counting from all planning conditions. (E) In the Young, PCC displays a task-based decrease in BOLD signal, differentiating counting from all planning conditions; in the Old, PCC activity is dependent on levels of planning challenge with greater suppression during low and high planning challenge and least suppression at moderate challenge levels.

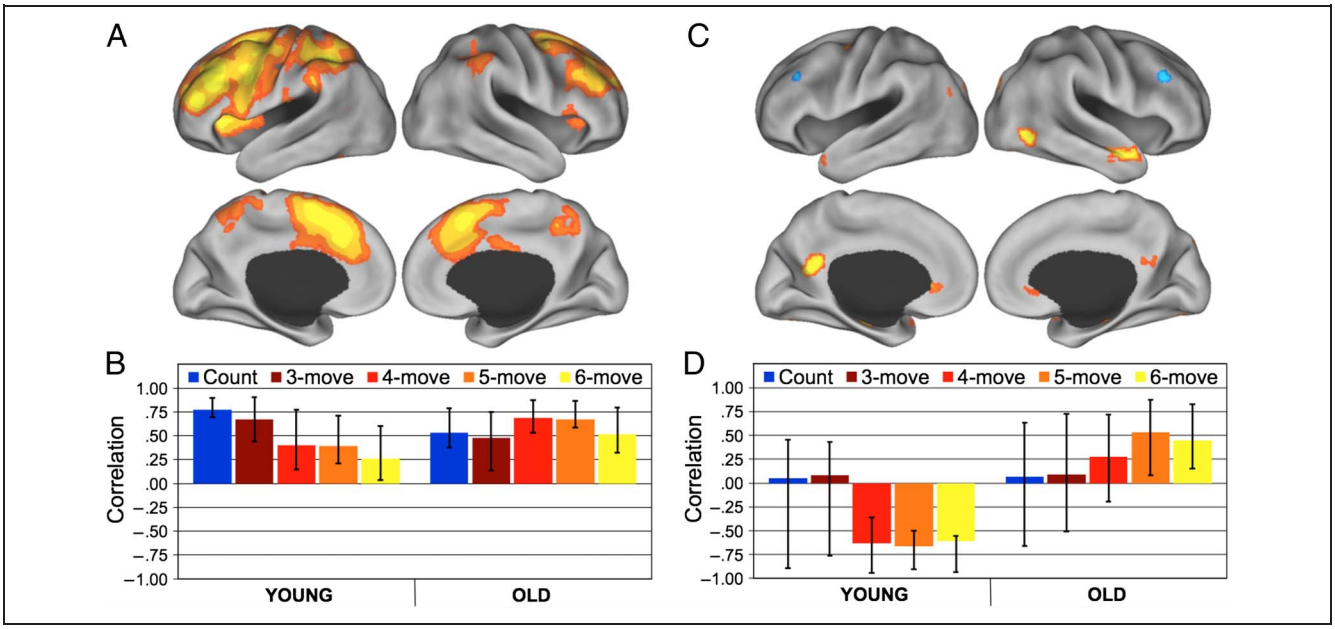

Figure 3. Task-related functional connectivity identified condition- and group-wise patterns of connectivity with a left dorsolateral seed region. (A) LV1 demonstrates an age- and task-invariant pattern of connectivity with the seed region including lateral pFC, dorsal ACC, and posterior parietal regions. (C) LV2 demonstrates an Age × Task dependent interaction of functional connectivity with the left DLPFC seed. Younger adults show coupling with a homologous region of right lateral pFC at the highest levels of planning challenge (4–6 moves) and a negative pattern of connectivity with default network regions including MPFC and PCC. Older adults show positive left DLPFC coupling with default network structures, including MPFC and PCC (see also Table 4 for full results). The bottom row depicts mean correlations between seed region activity and the distributed pattern of BOLD response in A or C, respectively, with confidence intervals calculated from the bootstrap across conditions and age groups. Color scales and intensities are as in Figure 1.

to four move puzzles and decreasing for five and six move conditions (Figure 2E).

Task-related Functional Connectivity

We next examined how the functional connectivity of the left DLPFC brain region changed across planning tasks in both groups. Two statistically significant patterns emerged depicting (1) covarying patterns of brain activity common to both groups and all task conditions and (2) distinct patterns of functional connectivity with the left DLPFC seed region for younger and older adults. The first LV (representing 54.55% of the overall variance, $p < .001$; Figure 3A, B) reflected a pattern of functional connectivity between left DLPFC and regions of the extended control network, including bilateral pFC, dorsal ACC, anterior insula, bilateral FEFs, superior parietal and anterior inferior parietal lobes, and dorsal precuneus that was common across all conditions in both groups. A second LV (representing 18% of overall variance, $p < .03$; Figure 3C, D; Table 4) demonstrated a significant age by condition interaction. This LV reflected contralateral right DLPFC connectivity and ipsilateral pFC connectivity during four, five, and six move TOL puzzles in younger adults. In older adults, left DLPFC was functionally coupled with core regions of the default network, including the MPFC, PCC, and left angular gyrus, for the hardest five- and six-move planning trials (please see Table 4 and Figure 3 for a full description and illustration of these findings).

Next we used univariate functional connectivity measures to examine group-wise differences in MPFC and PCC to DLPFC connectivity (Figure 4A, B) using two Group × Move repeated-measures ANOVAs. We addressed two primary questions: (i) Does DLPFC and default connectivity differ between groups and across levels of planning challenge? (ii) Are DLPFC and default network regions reliably functionally connected across the two age groups? Group × Move interactions for MPFC or PCC to DLPFC connectivity were not significant ($F_{MPFC}(3, 32) = 2.11$, $p = .12$; $F_{PCC}(3, 32) = 1.24$, $p = .31$). Planned comparisons revealed a main effect of Group for both analyses (Figure 4A, B). For DLPFC to MPFC coupling, we observed a significant difference between groups ($F(1, 34) = 9.99$, $p < .01$), with post hoc tests revealing differences on the most difficult five and six moves puzzles. For DLPFC to PCC coupling, we also observed a significant difference between groups ($F(1, 34) = 12.21$, $p < .001$): Post hoc tests revealed that functional coupling was significantly different between the young and old on the three, five, and six move puzzles.

To confirm the reliability of DLPFC to default region functional connectivity, we conducted simple t tests to estimate the magnitude of DLPFC–MPFC and DLPFC–PCC coupling (r-to-z transformed correlations). These t tests revealed that DLPFC–MPFC coupling in young adults was significantly negative for three, four, five, and six move puzzles but did not differ from zero in old adults. Additionally, simple t tests of DLPFC–PCC coupling in young

Table 4. Task-related Functional Connectivity

		MNI Coordinates			
Hemis	*Region*	*x*	*y*	*z*	*BSR*
LV1					
L	DLPFC (seed region)	−45	33	36	1696.55
B	Dorsal ACC	−3	18	51	10.88
L	Rostrolateral pFC	−39	42	12	9.44
L	Superior parietal lobule	−33	−48	45	9.94
L	Anterior insula	−42	15	9	8.49
L	Ventral precentral gyrus	−45	3	27	8.40
R	Anterior inferior parietal lobule	51	−39	45	6.54
R	DLPFC	42	39	27	6.92
B	Dorsal precuneus	3	−45	51	5.68
R	Anterior insula	30	27	−3	4.73
L	Occipital cortex	−30	−81	24	3.46
LV2					
L	Hippocampus	−30	−18	−24	7.40
L	Middle frontal gyrus	−30	−6	51	6.62
L	Lateral occipital cortex	−27	−90	33	6.22
R	Temporal pole	57	3	−27	5.89
L	Temporal pole	−45	18	−24	5.31
B	Ventromedial pFC	−9	48	−9	5.23
R	Lateral occipital cortex	21	−87	39	5.20
B	PCC	0	−54	27	5.18
L	MPFC	−12	60	9	5.06
L	Lateral occipital cortex	−45	−78	33	4.88
R	Inferior temporal gyrus	51	−60	−9	4.81
R	Occipital fusiform gyrus	33	−75	−15	4.16
L	Occipital fusiform gyrus	−33	−72	−18	4.09
R	Hippocampus	21	−9	−21	3.77
R	Lingual gyrus	12	−75	−12	3.71
L	DLPFC (seed region)	−45	33	36	−2023.34
L	Rostrolateral pFC	−39	42	12	−5.21
R	DLPFC	51	30	36	−5.19
R	Inferior temporal lobe	60	−33	−15	−5.12
L	Parietal operculum	−51	−24	21	−4.49

Brain regions demonstrating reliable functional connectivity patterns with a left DLPFC region. For LV2, left DLPFC connectivity is positive in older adults with regions designated with a positive BSR. Left DLPFC connectivity is positive in young adults with regions designated with a negative BSR. Clusters with a minimum of size of 100 mm^3 and a BSR greater than 3 ($p < .002$) are reported. See Table 3 caption for abbreviations.

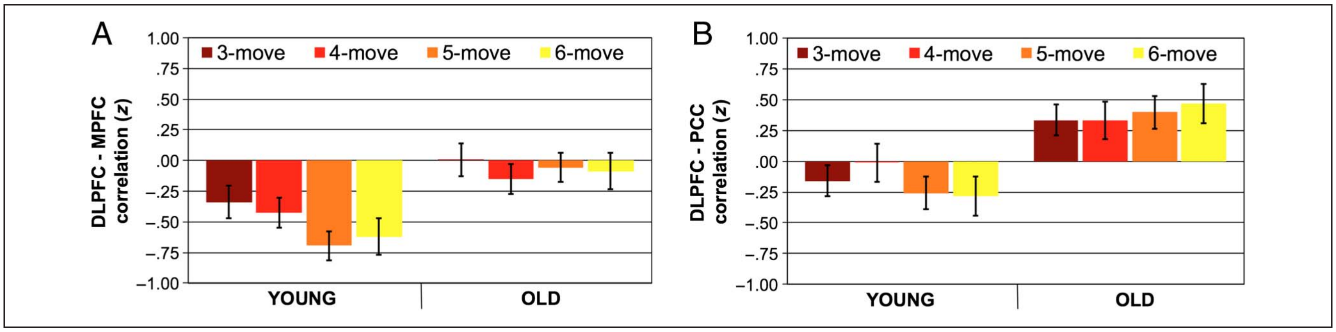

Figure 4. Task-related functional connectivity between the DLPFC and default network brain regions. Bar graphs depict the mean and *SEM* magnitude of correlation between (A) MPFC and (B) PCC, with the DLPFC as a function of age group and number of planning moves.

adults approached significant negative values for the five and six move puzzles (ps $< .08$). In the old, DLPFC–PCC coupling was significantly positive for three, five, and six move puzzles and approached significance for four moves ($p < .06$). Overall, the univariate results are consistent with the multivariate findings in showing more positive (or less negative) correlations between DLPFC and default network structures in older, compared to younger, adults —particularly at higher levels of task challenge.

Finally, we assessed whether modulation was correlated across high and low task challenge for the MPFC and PCC with the DLPFC and whether modulation scores predicted the magnitude of coupling between MPFC and PCC with the DLPFC. Correlations between modulation scores were not significant (all ps $> .05$). DLPFC modulation did predict coupling in the higher challenge puzzles, with significant correlations observed for DLPFC–MPFC ($r = .47$, $p < .01$) and DLPFC–PCC ($r = -.37$, $p < .05$). When controlling for age, the association between DLPFC modulation and DLPFC–MPFC coupling during more difficult puzzles held (pr $= -.32$, $p < .05$, single-tailed). However, within group correlations (ns $= 18$) were not significant (all ps $> .05$).

DISCUSSION

In this study, we introduce the DECHA model, which predicts that reduced modulation of lateral pFC activity and reduced suppression of the default network co-occur and may serve as a mechanism of age-related cognitive decline. Consistent with this model, we observed that recruitment of lateral pFC in older adults during performance of a goal-directed planning task, the TOL, was not modulated with difficulty level. We also observed reduced default network suppression in older adults across all levels of planning challenge. Functional connectivity analyses suggest that these changes are coupled in older adulthood, particularly at the highest levels of planning challenge.

As predicted by the DECHA, patterns of brain activity revealed by task-based multivariate analyses, encompassed both lateral pFC and default network brain regions. Activity in left DLPFC, a region implicated in TOL performance in young adults (Wagner et al., 2006; van den Heuvel et al., 2003) was increased for planning relative to a control task in both age groups (Figure 2C). However, unlike young adults, older adults did not increase activation in this region as planning demands increased (Figure 2C; see also Persson et al., 2007). Activity in MPFC, a central default network region, was suppressed relative to the control condition for both groups. But again, unlike young adults, older adults did not parametrically suppress activity in this region as task challenge increased (Figure 2D). In contrast, the young adults uniformly suppressed activity in PCC across levels of planning challenge. In the old group, PCC was not reliably suppressed, indicative of an absence of deactivation in this core default network region (Figure 2E).

To assess age- and task-related alterations in pFC–default coupling, we conducted a task-based functional connectivity analysis using the left DLPFC seed region that emerged from our task-activation analyses. This region has been implicated in parametric manipulations of planning challenge in younger adults using the TOL paradigm (van den Heuvel et al., 2003). Two significant connectivity patterns emerged. The first reflected an age- and condition-invariant pattern of functional connectivity between the left DLPFC seed region and a large collection of regions implicated in visual attention and cognitive control (Figure 3A). This suggests that these regions are functionally coupled across tasks and age groups, consistent previous investigations of TOL (van den Heuvel et al., 2003), and visual attention more generally (Corbetta & Shulman, 2002). The second pattern identified a robust group difference in functional connectivity of the DLPFC as planning complexity increased. Whereas younger adults demonstrated functional connectivity with homologous regions of right DLPFC, older adults showed robust coupling between the left DLPFC seed and regions of the default network (Figure 3C, Table 4). Thus, whereas younger adults showed greater bilateral connectivity and negative coupling with default structures as planning challenge increased, older adults showed greater coupling between DLPFC and default brain regions. Converging evidence for these effects was also observed with univariate analyses, as DLPFC activity was more positively coupled with default network activity in older adults than younger adults at the highest levels of task challenge

(Figure 4). We did not observe a significant correlation between DLPFC and default network modulation, a prediction of the DECHA model. DLPFC modulation from low to high planning challenge was associated with DLPFC–default coupling across study groups. This suggests that task-driven changes in DLPFC and default brain regions are related; however, small sample sizes in the current study may be limiting the statistical power to detect within-group correlations.

Taken together, these findings suggest that as executive control capacity is challenged (or exceeded), default network structures may be recruited to access stored representational knowledge to support ongoing task performance. This is consistent with a default–executive coupling hypothesis, wherein representational knowledge increasingly comes to the fore to support executive control processes as they decline across the lifespan (Craik & Bialystok, 2006). At the level of the brain, this is also consistent with our recent findings that recruitment of default network can support executive control processing when access to stored representations is congruent with task goals (Spreng et al., 2014). Our results are also consistent with recent resting-state functional connectivity data suggesting that differentiation among functional networks decreases in older adults. In these studies, internetwork connections are strengthened and intranetwork connections decline (Geerligs et al., 2015; Chan et al., 2014). By adopting a task-based approach, we were able to parametrically manipulate task difficulty and demonstrate a task-dependent increase in frontal and default network coupling in older, but not younger, adults.

A critical test of the DECHA model will be to determine whether this pattern of default–executive modulation reflects a compensatory or deleterious pattern of brain change (e.g., Daselaar et al., 2015). Regrettably, insufficient trials in the current sample preclude an analysis of successful versus unsuccessful task performance and our current sample size precluded an adequately powered analysis of brain–behavior correlations (Cummings, 2012). It may be the case that the default–frontal executive modulation patterns observed here reflect the commitment of greater executive control resources to sustain goal focus in the face of increased internal distractions as default network brain regions are more active (Chadick & Gazzaley, 2011). This would be consistent with a recent study of resting state correlations in younger and older adults, where a more robust negative correlation between DLPFC and MPFC was associated with better working memory performance in young adults. However, greater DLPFC and MPFC coupling was not associated with working memory performance in old adults (Keller et al., 2015), leaving the question as to whether this shift is adaptive unanswered.

Investigating whether DECHA represents an adaptive compensatory strategy of default network response to access semantic or experiential knowledge in support of ongoing cognition will be an important avenue of future research. Recent conceptualizations of default network activation during complex cognition suggest that these regions are not merely "task negative" but can support ongoing goal-directed behaviors when access to internal representations is adaptive and task relevant (Spreng et al., 2014; Spreng, 2012). Viewed from this perspective, greater engagement (i.e., reduced suppression) of the default network in older adults may reflect greater reliance on stored representational knowledge to support cognitive control processes. Strategic recruitment of encoding, retrieval, and monitoring processes to access mnemonic representations would coactivate prefrontal and default brain regions, as predicted by the DECHA model. If this interpretation is correct, suppression of default network brain regions could potentially hamper older adult performance, particularly at higher levels of task demand. However, overreliance on past experience may also impede flexible responding to shifting environmental contingencies (Craik & Bialystok, 2006). Thus, it may not be the coupling per se but rather the context-dependent, dynamic range of interactivity between executive and default brain regions that may best predict successful aging. Recent work elucidating the importance of variability within and between brain networks for cognitive functioning in older adulthood (e.g., Garrett, Kovacevic, McIntosh, & Grady, 2013) is consistent with this idea.

The DECHA model might also help to inform the design of interventions to preserve functional independence in older adulthood. In a recent review of training-related functional brain changes in younger adults, we reported greater activation of default network brain regions posttraining—irrespective of the specific training domain (Patel, Spreng, & Turner, 2013). This suggests that accessing stored representational knowledge or experience, associated with engagement of default brain regions, may be a neural marker of training-related performance gains. However, executive control training in older adulthood has recently emphasized strategies to reduce distractions and enhance default network suppression (Anguera et al., 2013; Chadick & Gazzaley, 2011). Again, it may not be the magnitude but rather the dynamic and contextually dependent range of default and executive region coupling that is a neural marker of training success.

The present results are consistent with a growing body of research suggesting that older adults are unable to enhance recruitment of lateral pFC in the context of increasing task challenge. These data suggests that there is a similar modulation deficit within the default network. There has been little investigation of how these two mechanisms dynamically interact in the service of goal-directed cognition. Here we provide preliminary evidence that these functional brain changes may interact and are coupled in older adulthood, consistent with a DECHA model. This integrated model of age-related functional brain change may facilitate understanding and

improve intervention strategies to maintain goal-directed cognition in older adults. Such a unified account better characterizes age-related functional brain changes, incorporating both regional activation differences and large-scale network dynamics.

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