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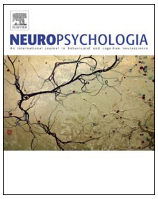

Semanticized autobiographical memory and the default – executive coupling hypothesis of aging

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ABSTRACT

As we age, the architecture of cognition undergoes a fundamental transition. Fluid intellectual abilities decline while crystalized abilities remain stable or increase. This shift has a profound impact across myriad cognitive and functional domains, yet the neural mechanisms remain under-specified. We have proposed that greater connectivity between the default network and executive control regions in lateral prefrontal cortex may underlie this shift, as older adults increasingly rely upon accumulated knowledge to support goal-directed behavior. Here we provide direct evidence for this mechanism within the domain of autobiographical memory. In a large sample of healthy adult participants (n = 103 Young; n = 80 Old) the strength of default – executive coupling reliably predicted more semanticized, or knowledge-based, recollection of autobiographical memories in the older adult cohort. The findings are consistent with the default – executive coupling hypothesis of aging and identify this shift in network dynamics as a candidate neural mechanism associated with crystalized cognition in later life that may signal adaptive capacity in the context of declining fluid cognitive abilities.

1. Introduction

A fundamental shift occurs in the architecture of cognition across the human lifespan. With age, experience and knowledge of oneself and the world continues to accrue, while fluid, or controlled, cognitive abilities decline (Craik and Bialystok, 2006; Park et al., 2001; Park and Reuter-Lorenz, 2009). This shift likely has a profound impact on real-world functional abilities. Recent and accumulating evidence suggests that goal-directed behaviors, such as decision-making, become increasingly determined by accumulated knowledge and experience as cognitive control processes decline with older age (Li et al., 2013; Samanez-Larkin and Knutson, 2015). Older adults may rely less on declining control processes, or less successfully recruit these processes, thereby relying more on crystalized intellectual capacities to support goal-directed behaviors. However, the neural mechanisms associated with this putative age-related shift in cognitive architecture remain under-specified.

This transition from controlled to crystalized cognition is readily apparent in the domain of autobiographical memory. Young adults rely on controlled retrieval processes to construct detailed recollections of their personal past (Wheeler et al., 1997). In contrast, older adult recollections are composed of less episodic and more semantic information, as control processes decline and specific details are replaced by more gist- or fact-based recollections (Levine et al., 2002). Here we use autobiographical memory as a lens to investigate whether the shift from controlled to crystalized cognition in older adulthood is associated with specific changes in the functional network architecture of the brain.

We recently proposed a novel neural mechanism associated with this shift towards more crystalized cognition in older adults: The Default to Executive Coupling Hypothesis of Aging (DECHA) (Turner and Spreng, 2015). The model integrates two widely reported trends in neurocognitive aging. First, greater task-related activity is observed in lateral prefrontal cortex (LPFC). Increased LPFC activity is associated with greater controlled processing demands (Koechlin et al., 2003) and suggests poor modulation of this region by task context (Cabeza et al., 2002; Cappell et al., 2010; Grady et al., 1994; Reuter-Lorenz et al., 2000). Second, the default network, a set of brain regions implicated in associative and mnemonic processes (Andrews-Hanna et al., 2014; Bar et al., 2007; Buckner, 2004), is less suppressed, and again poorly modulated by task demands in older adults (Buckner, 2004; Buckner et al., 2008; Damoiseaux, 2017; Miller et al., 2008; Park et al., 2010;

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Sambataro et al., 2010). The DECHA proposes that these two processes, reduced modulation of LPFC and the default network, are functionally coupled (Turner and Spreng, 2015).

Support for this account was provided in a recent lifespan study where LPFC (among other "task-positive" regions) and default network brain regions were functionally coupled, and poorly modulated, during a spatial distance judgment task in older adults (Rieck et al., 2017). Further, the strength of this coupling was negatively associated with fluid reasoning, suggesting these changes have direct implications for cognitive functioning in older adulthood. Similar findings were reported in a recent longitudinal study, where increased default – executive coupling was observed with advancing age. Critically, the rate of increase in default – executive coupling in older adulthood predicted slower processing speed (Ng et al., 2016).

Default to executive coupling in older adulthood has now been observed across multiple goal-directed cognitive tasks (e.g. Rieck et al., 2017; Sambataro et al., 2010; Spreng and Schacter, 2012; Turner and Spreng, 2015). If this connectivity pattern is a neural marker of cognitive aging during goal-directed cognitive tasks, then increased coupling of executive and default network brain regions should be increasingly entrained within the intrinsic network architecture of the aging brain and observable in the absence of specific task demands. Functional connectivity, measured at rest, is assumed to reflect repeated covarying patterns of brain activity during active cognitive processes (Stevens and Spreng, 2014). This intrinsic architecture of the brain is measureable using resting fMRI methods (Biswal et al., 1995). To test the DECHA hypothesis as an enduring, and task independent, marker of cognitive aging here we use resting-state fMRI methods to derive estimates of network interactivity.

Behaviorally, we chose to evaluate the DECHA model using a measure of autobiographical memory – the Autobiographical Interview (AI, Levine et al., 2002). The shift from controlled to crystalized cognitive processes has been repeatedly demonstrated within the domain of memory where there is lifespan transition from controlled, episodic retrieval to more semanticized recollective experiences (Craik and Bialystok, 2006). To characterize the putative age-related shift from controlled to semanticized cognition specifically within the memory domain we took advantage of the within-task measures of controlled (i.e., episodic) and semantic (i.e., crystalized) recollection provided by the AI. This instrument is able to reliably quantify the number of episodic and semantic details provided during recollection of personal events (see Supplemental Materials and Methods). Previous research has shown that young adult memories contain more episodic detail specific to time and place, suggesting a re-experiencing of the original event. In contrast, older adult memories are more semanticized, with fewer episode-specific details and more general knowledge or personal semantic details (Levine et al., 2002). Using resting-state fMRI methods and the AI, we tested our central hypothesis: Age-related differences in network interactivity, measured as default – executive coupling, would be associated with more semanticized cognitive processing, measured as the density of semantic content during autobiographical recollection.

2. Methods

2.1. Participants

Eighty older adults (age range: 60–92 years; 45 women) and 103 younger adults (age range: 18–30 years; 63 women) participated in the current study. All participants were healthy and had no history of psychiatric, neurological, or other medical illness that could compromise cognitive functions. Participants were included with an MMSE (Folstein et al., 1975) ≥ 26. Older adults were additionally screened for depression and retained for the current study with standardized Geriatric Depression Scale (Yesavage et al., 1982) ratings ≤ 1.0. See Table 1.

Table 1
Participant demographics.

	Older Adults		Younger Adults	
	Mean	SD	Mean	SD
Age in years	68.8	6.3	22.4	3.0
Education in years	17.7	2.9	15.4	1.9
MMSE	28.2	1.3	29.2	1.0
Fluid Intelligence (National Percentage)	48.0	23.9	66.7	28.7
Autobiographical Memory				
Internal detail count	30.8	16.7	41.8	21.3
External detail count	17.7	15.9	10.3	9.2
Internal detail density	.074	.019	.099	.023
External detail density	.036	.013	.020	.009

Table Note: All differences between groups are significant (see Section 3).

2.2. Neuroimaging

All imaging data were acquired on a 3T GE Discovery MR750 scanner (General Electric, Milwaukee, United States) with a 32-channel receive-only phased-array head coil at the Cornell Magnetic Resonance Imaging Facility in Ithaca. Each participant obtained an anatomical scan acquired during a 5 m 25 s run using a T1-weighted volumetric MRI magnetization prepared rapid gradient echo [repetition time (TR) = 2530 ms; echo time (TE) = 3.4 ms; inversion time (TI) = 1100 ms; flip angle (FA) = 7°; bandwidth = 195 Hz/pixel; 1.0 mm isotropic voxels, 176 slices]. Anatomical scans were acquired with 2× acceleration with sensitivity encoding. Participants additionally completed two 10m06s resting-state multi-echo BOLD functional scans with eyes open, blinking and breathing normally in the dimly lit scanner bay. These scans were acquired prior to engagement in any cognitive task fMRI experiment. Resting-state functional scans were acquired using a multi-echo echo planar imaging (ME-EPI) sequence with online reconstruction (TR = 3000 ms; TE's = 13.7, 30, 47 ms; FA = 83°; matrix size = 72 × 72; field of view (FOV) = 210 mm; 46 axial slices; 3.0 mm isotropic voxels). Functional scans were acquired with 2.5x acceleration with sensitivity encoding.

Multi-echo fMRI has been developed as a data acquisition sequence to facilitate removal of noise components from resting fMRI datasets (Kundu et al., 2013, 2012). This method relies on the acquisition of multiple echoes, allowing direct measurement of T2* relaxation rates. Blood-oxygen level dependent (BOLD) signal can be then distinguished from non-BOLD noise on the basis of echo time (TE) dependence. The preprocessing, multi-echo independent components analysis (ME-ICA), has proven effective in denoising BOLD signal of motion and physiological artifacts in resting-state fMRI (Kundu et al., 2013, 2012). Data were preprocessed with ME-ICA version 2.5 (https://afni.nimh.nih.gov/pub/dist/src/pkundu/meica.py). Anatomical images were first skull stripped using the default parameters in FSL BET. ME-ICA processing was then run with the following options: -e 13.6, 29.79, 46.59; -b 12; –no_skullstrip; –space = Qwarp_meanE + tlrc. Here, the Qwarp_meanE + tlrc file represented a site-specific, MNI-space template of 30 younger and 30 older non-linearly registered adults. This template was created in AFNI using @toMNI_Qwarpar. Finally, ME-ICA denoised time series were smoothed with a 6 mm FWHM kernel in SPM8.

In order to assess the whole brain signal quality of the ME-ICA processed images, we calculated the images' temporal signal to noise ratio (tSNR), a measure of signal strength at the voxel level, calculated as the mean signal intensity of a voxel across the timeseries divided by its standard deviation. tSNR was calculated on the smoothed optimal combination with the ME-ICA denoising. Derived tSNR spatial maps were averaged across all subjects, thresholded at 100, and plotted in Supplemental Fig. 1. Following Kundu et al. (2013), tSNR was considered only within the overlap of a grey matter and functional mask. The results show good whole brain coverage, consistent with prior reports of ME-ICA (e.g. DuPre et al., 2016).

In order to identify the default network, we performed Group ICA using Group ICA fMRI Toolbox (GIFT; http://mialab.mrn.org/software/) on the resting-state data for all 183 participants. ICA is a fully data-driven approach that separates a dataset into components by maximizing their independence using high-order statistics. More specifically, GIFT is a MATLAB toolbox that extends this approach to the group level through 3 steps: compressing the data using Principal Components Analysis, computing group-level ICA, and back reconstructing individual subject ICA maps based on the aggregate map across subjects. We elected to estimate an 8-component solution and visually identified the default network from the components. To render the whole brain network image for the default network, we conducted a one-sample *t*-test on the back-reconstructed images of each participant. This test allowed us to 1) confirm we successfully identified the default network and 2) identify the regions most robustly expressed across groups. Many regions of the brain covaried with these core default network structures but did not reach statistical criteria for this test. Next, we compared the default network covariance patterns between younger and older adult groups. To do so, we conducted a two-sample *t*-test between the back-reconstructed images. It is important to note that the full default network images were compared between groups, and these images include regions that covaried with the core structures identified in the simple *t*-test in addition to sub-threshold regions. Group differences are not necessarily observed in regions identified by the simple *t*-test, and can extend to other regions of the brain as well. The two-sample *t*-test examines statistically robust higher and lower covariance patterns of brain activity with the canonical regions of the default network. This approach has been applied previously to determine both decreases in connectivity within the identified network, and increases in connectivity with brain structures outside of the identified canonical network (c.f. Spreng et al., 2017). Whole brain network difference maps were assessed for significance at $p < .001$ (uncorrected) with 20 or more contiguous voxels. Connectivity weights were extracted from a region of interest revealed in the Older > Younger contrast with a 10 mm diameter sphere centered on the peak left lateral PFC region MNI coordinate $x = -41.5$, $y = 34$, $z = 12.5$ with MarsBar in SPM8.

2.3. Autobiographical interview

The AI was conducted following the procedures as specified in the original paper (Levine et al., 2002). Older adult participants provided a detailed description of five personally significant events: one from early childhood (to age 11), one from the teenage years (ages 11–18), one from early adulthood (ages 18–30), one from middle adulthood (ages 30–55) and one from the past year. Younger adults provided three descriptions of a significant personal event: one from early childhood, one from the teenage years, and one from early adulthood. Composites of event scores drawn from an equal number (earliest and latest) yielded the same results. We report data from the entire sample to provide the most reliable estimates of recollection.

All participants were instructed to recall an event that occurred at a specific time and place. Recall for each event was probed at three levels: free recall, general probe (comprehension of instructions and general questions to elicit event details), and specific probe (targeted questions to elicit event details). Autobiographical memories were assessed cumulatively across the free recall and general probe conditions. All autobiographical interviews were recorded and transcribed. Transcriptions were checked for accuracy and anonymized, and autobiographical event word count for free recall and general probe were computed in Microsoft Word. Autobiographical memories were scored blind to the study hypotheses. Although scorers were not explicitly informed about participant group membership, autobiographical content typically informed the rater as to the general age of the participant. All scorers underwent extensive training on event identification and scoring of internal and external details consistent with the training protocol provided by Dr. Brian Levine. As described in the original report (Levine et al., 2002), transcribed autobiographical memory interviews were segmented into discrete informational units. Scorers labeled these units as ‘internal’ (episodic) if they pertained to the target event, were specific to time and place, and conveyed a sense of episodic re-experiencing. Details were labeled “external” if they consisted of factual or semantic information, extended to events that did not require recollection of a specific time and place, or were details unrelated to the main event. We assessed data from the main internal and external detail composites.

2.4. Additional cognitive assessments

All participants completed the NIH Toolbox of Cognition to derive fluid intelligence composite scores (Weintraub et al., 2014). These scores were used as covariates in the core tests of the DECHA. One older adult participant's data on the NIH Cognition Toolbox was not recorded and is excluded by list-wise deletion in the relevant analyses. See Table 1.

2.5. Reliability

Confidence intervals (CI) for correlations (r) and partial correlations (pr) were calculated from the bootstrap with 1000 resampling iterations.

3. Results

3.1. Neuroimaging

We identified the default network (Fig. 1A, Supplemental Fig. 1A) with an independent components analysis (ICA) of resting-state fMRI across a sample of 80 older and 103 younger adults. Next we compared the default network neuroimages (in a two samples *t*-test) between

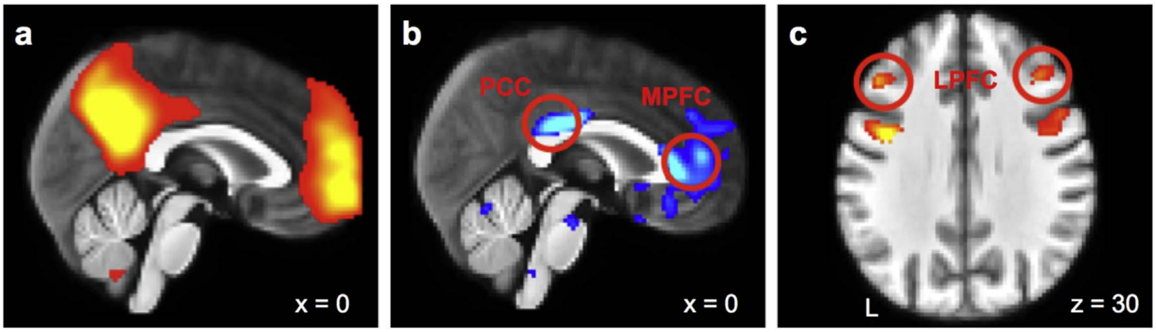

Fig. 1. The default network identified with independent components analysis and age related differences projected on the study specific template. (A) Default network across the entire sample. (B) Lower default network connectivity in older adults in posterior cingulate cortex (PCC) and medial prefrontal cortex (MPFC). (C) Greater default network connectivity in older adults, including lateral prefrontal cortex (LPFC).

older and younger adult groups. Consistent with previous reports (Damoiseaux, 2017), connectivity within the default network was reduced in older adults (See Fig. 1B, Supplemental Fig. 2B). We next examined increases in functional connectivity with the default network, predicting greater LPFC connectivity in older adults. Compared to the young, older adults had greater functional connectivity between the default network and LPFC (Fig. 1C; Supplemental Fig. 2C). Peak coordinates for the age-related differences in default network connectivity are in Supplemental Data Table S1. This observation of age-related default to executive (i.e., LPFC) coupling at rest is consistent with previous task activation studies (Rieck et al., 2017; Turner and Spreng, 2015). These results demonstrate that this pattern of network interactivity is reliably measureable at rest, and is not attributable to age-related differences associated with specific task demands. Rather, the pattern of default – executive coupling observed here reflects a persistent pattern of functional brain connectivity prevalent in older adulthood. Next, we assessed the behavioral relevance of default – executive coupling.

Fluid intelligence is known to decline with age (e.g. Park and Reuter-Lorenz, 2009), and the current sample also displayed significantly lower fluid intelligence scores in older versus younger adults (t(180) = 4.74, p < .001; Cohen's d = .71). We assessed whether the strength of default – LPFC coupling was negatively associated with fluid cognition across the entire sample, controlling for age, gender and education. We found a reliable non-zero correlation approaching significance (pr(177) = −.12, p = .051, single-tail, 95% CI: −.26 to −.0002; See Supplemental Data Fig. S3), consistent with previous findings (Rieck et al., 2017). A closer examination of the correlation with fluid IQ within groups, controlling for gender and education, suggested that younger adults may primarily drive this effect. In older adults, the association between default – LPFC coupling and fluid IQ was not significant (pr(75) = .03, p = .80, 95% CI: −.15 to .22). In younger adults, the association between default – LPFC coupling was significant (pr(99) = −.20, p < .05, 95% CI: −.37 to −.04). However, the default – executive coupling by age interaction for fluid IQ was not significant, indicating the magnitude of the association was not significantly different between the two groups (standardized beta = .19; t = 1.33, p = .19). From 1000 bootstrap samples, the 95% confidence intervals for the beta-coefficient of the interaction crossed zero, suggesting there was no reliable association (beta = 16.03, SE = 10.39, 95% CI: −4.38 to 37.35). In a related study, medial PFC to lateral PFC connectivity was correlated with working memory capacity in younger, but not older adults (Keller et al., 2015). The present findings suggest that the relationship between direct estimates of default – LPFC coupling and cognitive control abilities across the lifespan will be an important area of future research.

3.2. Autobiographical interview

During the AI (Levine et al., 2002) we asked participants to recall a series of specific life events from different life epochs. Their responses were transcribed and scored using a rigorous protocol to quantify episodic and semantic details in the recollection. Each memory was scored by two independent raters. Inter-rater reliability was .90 for internal details and .93 for external details. Mean number of internal and external event details per event were then averaged between raters. The mean number of details recalled per event for the young and old replicated prior observations (Levine et al., 2002). In a repeated measures 2 × 2 ANOVA, there was a significant age x detail interaction (F(1181) = 55.57, p < .001, partial eta squared = .24). Older adult memories had significantly more external details than the young (t(181) = −3.96, p < .001; Cohen's d = .59) and significantly fewer internal details (t(181) = 3.97, p < .001; Cohen's d = .58). Longer narratives of event descriptions resulted in more details overall, evidenced by a significant correlation between total details and word count (r(181) = .95, p < .001, 95% CI: .94–.97). For this reason, we standardized the total number of internal and external detail scores by word count to arrive upon internal and external detail density scores in our full sample of 183 younger and older adults. Consistent with the original report (Levine et al., 2002), we observed a significant age × detail density interaction (F(1181) = 97.24, p < .001, partial eta squared = .35). Older adult memories had significantly more semantic detail density than the young (t(181) = −9.61, p < .001; Cohen's d = 1.42) and significantly less episodic detail density (t(181) = 7.81, p < .001; Cohen's d = 1.78). It should be noted that the younger adult group had a truncated range of variance in external detail density scores (Levine's test for equality of variance F = 6.94, p < .01). Combined with unequal group sample sizes, differences in variance between groups may impact the effect of group differences and is a limitation of the current study. Independent sample's *t*-tests remained significant without the assumption of equality of variance across groups (t(179.02) = −9.18, p < .001). Subsequent analyses included non-parametric bootstrap resampling and an assessment of 95% confidence intervals of the effects with consistent results, thus mitigating this concern.

3.3. DECHA analyses

As a direct test of the DECHA model we correlated semantic density scores with estimates of default – executive (LPFC) coupling at rest. Controlling for gender, education and fluid intelligence, default – executive coupling was significantly correlated with semantic density in older adults (pr(74) = .26, p < .05, 95% CI: .06–.45), but not young (pr (98) = .02, p = .85, 95% CI: −.23 to .16). Additionally, the default – executive coupling by age interaction was significant, indicating a significant difference in slope between the two groups (standardized beta = .34; t = 2.90, p < .005; See Fig. 2). Due to concerns about an inequality of the variance for semantic density scores between groups and unequal sample sizes, this regression analysis was subject to 1000 bootstraps in order to determine, non-parametrically, the reliability of the coupling by age interaction. The 95% confidence intervals for the beta-coefficient of the interaction did not cross zero (beta = .014, SE = .005, 95% CI: .005–.023), suggesting the effect was reliably non-zero. These results demonstrate that the strength of default – executive coupling was associated with more semanticized recollection in older, but not younger adults. Critically, this relationship held when controlling for fluid intelligence, suggesting that this pattern of functional connectivity is specifically associated with semanticized recollection, and not simply an artifact of changing fluid cognitive abilities in older

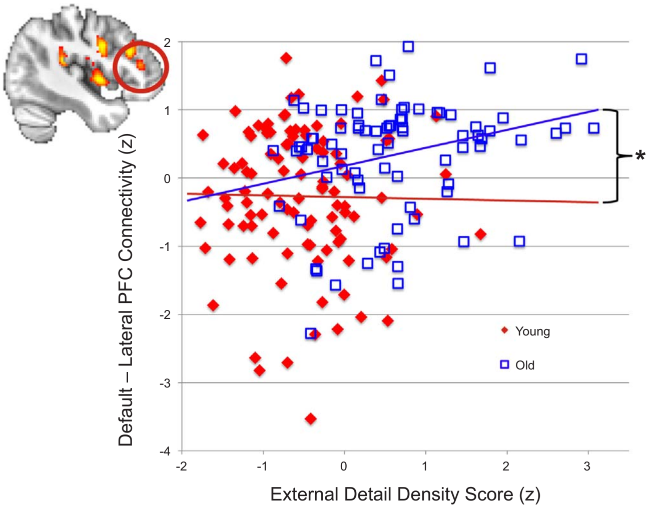

Fig. 2. External detail density scores, a measure of semantic autobiographical recollection, is significantly correlated with default network – lateral prefrontal cortex (PFC) coupling at rest in older but not young adults. * Designates a significant difference in the magnitude of the association between the two groups.

adults.

The relationship with semantic density and default – executive coupling was only reliable in older adults and did not hold across the entire sample when controlling for age (as well as gender, education and fluid IQ; pr(176) = .10, p = .17, 95% CI: −.03 to .22). Further, we investigated the specificity of this finding by examining other regions of dorsolateral PFC (DLPFC) that were functionally coupled with the default network (right DLPFC and caudal left DLPFC – see Supplemental Material). The relationship with semantic autobiographical recall held only for the more rostral left LPFC region of interest.

4. Discussion

Here we investigated whether a hallmark of cognitive aging, the transition from controlled to more crystalized cognition, was associated with increased functional coupling between the default network and executive control regions of the LPFC, providing a direct test of the Default – Executive Coupling Hypothesis of Aging (Turner and Spreng, 2015). Specifically, we investigated whether default – executive coupling measured at rest, in the absence of task-specific demands, would predict a shift from controlled, episodic retrieval to more semantic recollection on an autobiographical memory test. We adopted an individual differences approach to examine this association between autobiographical recollection and network dynamics in a large cohort of younger and older adults. As noted by Hebscher et al. (2017), sufficiently-powered individual difference studies are critically necessary to reliably detect brain and behavior relationships given the variability typically observed in studies of autobiographical memory.

Our findings provided clear support for the DECHA model. Default to executive coupling during rest was stronger for younger than older adults in LPFC, consistent with previous reports showing similar age-related patterns of network interactivity during goal-directed tasks (Rieck et al., 2017; Sambataro et al., 2010; Spreng and Schacter, 2012; Turner and Spreng, 2015) and at rest (Ng et al., 2016). Similar findings of default to LPFC coupling have been observed at rest in the context of reduced anti-correlation (Keller et al., 2015; Spreng et al., 2016) and network connectivity dedifferentiation, involving more positive connectivity between default and LPFC structures, with advancing age (Chan et al., 2014; Geerligs et al., 2015; Grady et al., 2016). Critically, the strength of this coupling predicted the density of semantic details recalled during the AI task in older adults, providing direct support for the DECHA.

The relationship with semantic density and default – executive coupling was observed in older but not younger adults, and did not hold across the entire sample when controlling for age. This finding contrasts with that of Rieck et al. (2017) who observed a relationship between task-driven modulation of default and executive network brain regions and fluid intelligence across the adult lifespan. However, an examination of within group associations suggests that the younger adults largely drove the effect observed here, consistent with prior observations (Keller et al., 2015).

Extrapolating beyond the current data, we predict that the association between semantic density and default – executive coupling is not an effect of individual differences per se, but emerges in middle age and is reliable only in older adults. We propose that this age interaction may be attributable to a relative lack of life experience and accrued knowledge in younger adults, who tend to rely on fluid abilities rather than crystalized world knowledge during cognitive task performance (Li et al., 2013). Interestingly, starting in middle age (35–54 years of age) there is less suppression of the default network (Rieck et al., 2017). This is consistent with the idea that, by this point in the lifespan, knowledge and general life experience is more actively shaping ongoing cognition. However, the current study is limited in only examining younger and older adult cohorts. An open area for future investigation will be to sample these changes across all decades of life. Consistent with the work of Rieck et al. (2017), this would provide important insights into the temporal unfolding of default to executive coupling, and concomitant cognitive changes, across the adult lifespan.

Our observations that autobiographical recollection is increasingly semanticized and dependent on default network structures in later life are consistent with several other findings reported in this special issue. In their longitudinal investigation of autobiographical memory in younger adults, Bonnici and Maguire (2017) report that a core node of the default network, ventromedial PFC, is implicated in consolidation of autobiographical memories over a period of as little as two years. While speculative, we suggest that this consolidation process associated with ventromedial PFC function, may result in increasingly semanticized and possibly schema-based representations of one's personal past when extended across decades. This notion is consistent with the findings of Irish et al. (2017) who reported more semantic, or gist-based, mnemonic representations during autobiographical recall in a sample of Alzheimer's disease patients over one year. Interestingly, the semanticization of autobiographical memory was associated with preserved cortical thickness in lateral and anterior temporal lobe regions, both nodes of the default network. These findings suggest that autobiographical memory becomes increasingly semanticized over the adult lifespan, and this process is likely associated with the integrity and functioning of default network brain regions. Our DECHA model extends this idea, suggesting that engagement of semanticized autobiographical representations in the service of goal-directed thought or action is supported by increased default – executive coupling in older adulthood.

Our findings suggest that by virtue of a longer life, older adults are able to access a larger store of personal experiences and world knowledge than their younger counterparts. However, the access to and quality of personal recollection changes with age. Control processes necessary to re-experience life events or retrieve specific details decline, while access to general facts and knowledge about oneself and the world remains relatively preserved. Here we argue that enhanced default – executive coupling is a candidate neural mechanism promoting this increasingly semanticized recollective experience in older adulthood. While we specifically studied DECHA through the lens of autobiographical memory, we expect that these changes in neural network interactivity serve as a key mechanism of the broader shift in the architecture of cognition with advancing age (Craik and Bialystok, 2006; Park and Reuter-Lorenz, 2009). Understanding how functional brain changes may influence or ultimately predict the rate of change from controlled to crystalized cognition more broadly will be a critical next step as this shift likely has profound implications for real world functioning in older adulthood. As the influence of past knowledge and experience grows, searching and sifting through stored representations may slow processing speed or alter decision-making ability, particularly in novel contexts. These changes are considered to be hallmarks of cognitive aging (Ramscar et al., 2014). It may also be the case that increasing reliance on stored knowledge may be adaptive in specific contexts where access to accumulated life experience may convey decision-making advantages. Indeed, this has been recently demonstrated in the domain of economic decision-making where increasing reliance on crystalized knowledge offset declines in fluid intellectual abilities for older adults (Li et al., 2013). Similarly, older adults have been shown to outperform younger adults on complex decision-making tasks when access to crystalized knowledge is adaptive, particularly in real-world environments (Blanco et al., 2016).

From this perspective, understanding how functional brain changes shape, or are shaped by, a shifting cognitive architecture across the adult lifespan will become increasingly important for understanding the trajectory of cognitive and real world functional changes that occur with advancing age. Traditional accounts of age-related cognitive decline have, for the most part, failed to consider this shifting architecture, where a lifetime of accumulated knowledge and experience can be accessed to guide adaptive goal-directed behavior, particularly in more ecologically-valid contexts, outside of the constraints of the laboratory. The findings reported here identify default – executive coupling as a candidate neural mechanism associated with this shift from controlled to crystalized cognition in later life. While our work here does not speak directly to the functional consequences of these network changes, there is mounting evidence that DECHA may signal preserved capacity for adaptive, real-world decision-making and problem-solving in later life

Author contributions

R. Nathan Spreng: Study concept and design, data analysis, wrote the paper.

Gary R. Turner: Study concept and design, wrote the paper.

Amber W. Lockrow: Behavioral data collection and scoring, neuroimaging data collection, processing and analysis.

Elizabeth DuPre: Neuroimaging data processing.

Roni Setton: Behavioral data scoring.

Karen A.P. Spreng: Behavioral data scoring and training, wrote the paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2017.06.009.

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