



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 crystallized 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 crystallized 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 crystallized 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 crystallized 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 crystallized 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 crystallized 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 measurable 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 crystallized 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., crystallized) 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
<i>Autobiographical Memory</i>				
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_Qwarp. 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).

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