

Creative aging: functional brain networks associated with divergent thinking in older and younger adults

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Abstract:

Creative thinking is associated with connectivity between the default and executive control networks in the young brain. In aging, this pattern of functional coupling has been observed across multiple tasks. We have described this as the Default-Executive Coupling Hypothesis of Aging and suggest that this connectivity pattern may also be associated with creativity in older adulthood. However, age differences in brain networks implicated in creativity have yet to be investigated. The overarching goal of the present study was to examine age-related changes to functional brain networks associated with creativity. Specifically, we explored functional connectivity patterns among default and executive control brain regions associated with creative thoughts in older and younger adults. In a cross-sectional design, young (mean age = 21 y; n = 30) and older (mean age = 70 y; n = 25) participants completed a divergent thinking task during fMRI, which was examined using region of interest functional connectivity analyses. Consistent with predictions, analyses demonstrated that default and executive networks are more functionally coupled during creative thinking for older than younger adults. Critically, despite similar performance on an in-scanner creativity task, increased network efficiency was associated with creative ability for older adults only. These findings provide novel evidence of default-executive coupling as a putative mechanism associated with creative ability in later life.

Keywords: Aging | creativity | divergent thinking | fMRI | functional connectivity | default-executive coupling | DECHA

Article:

1. Introduction

Creative cognition is a broadly defined ability that is presumed to require generation and flexible combination of concepts to form novel and useful ideas (Guilford, 1950). Divergent thinking is perhaps the most common operationalization of creative cognition (Guilford, 1950). Divergent thinking is most commonly measured by the alternate uses task, which involves producing novel uses for common objects such as a brick. These tasks are well established in the literature and

have the unique advantage of having predictive ability. Past work has shown that creative ability as measured by divergent thinking in school-aged children is predictive of success later in life. Children with higher divergent thinking ability continue to have more successful careers in arts and sciences later in life (Plucker, 1999; Torrance, 1988). Furthermore, creativity performance has been positively associated with academic success and conflict resolution abilities (Furnham and Bachtiar, 2008).

Taking into account its importance in life and predictive ability, characterization of creativity across the lifespan is an emerging area of research. This work has primarily focused on divergent thinking and has resulted in mixed findings. Early work has shown that aging is marked with both a reduced number of creative responses and the originality of responses (Alpaugh and Birren, 1977) and that this does not occur until middle adulthood (Jaquish and Ripple, 1984; Reese et al., 2001). More recently, it has been shown that creativity is maintained into older adulthood and does not follow a trajectory of decline as proposed by earlier work (Addis et al., 2016; Foos and Boone, 2008; Palmiero et al., 2014, Roskos-Ewoldson et al., 2008). It has been hypothesized that creative ability is preserved in older adults as a consequence of preserved crystallized intelligence (Palmiero et al., 2014), and reported differences could be due to differences in other cognitive abilities, such as working memory (Roskos-Ewoldson et al., 2008) and processing speed (Foos and Boone, 2008).

Acknowledging that creative-thinking abilities are important predictors of real-world functioning, efforts to understand the neural basis of creativity have also grown in recent years. These investigations of creativity using both whole-brain multivariate approaches (Beaty et al., 2015) and a priori region of interest (ROI) based investigations (Beaty et al., 2018, Vartanian et al., 2018) have demonstrated that creativity is associated with interactions between key default and executive control regions. Here, we build from these earlier findings in young adults to investigate changes in these networks between younger and older adults.

Although the vast majority of empirical work investigating the neurocognitive basis of creative cognition has focused on young adults, there is no work to date investigating the neural basis of creativity in aging. Functional neural networks and their interactions change with age (Damoiseaux, 2017). Overall, the most consistent evidence from cross-sectional investigations is that older adults show reduced functional connectivity within the default (Dennis and Thompson, 2014) and executive control networks (Damoiseaux, 2017), and increased between-network connectivity (Geerligs et al., 2015). Although the implications of these network changes for cognitive aging have been partially explored, few task paradigms have involved access to prior knowledge, where greater default-executive interactivity may be advantageous for older adults. Here, we explore this possibility within the realm of creative cognition, where access to prior knowledge is known to support creative ability (Madore et al., 2016).

We recently proposed a novel neural network hypothesis of cognitive aging, positing that greater, and less flexible, coupling of default and executive control networks is associated with declines in cognitive control and gains in semanticized cognition, two hallmarks of cognitive aging. The Default-Executive Coupling Hypothesis of Aging (DECHA; Turner and Spreng, 2015; Spreng and Turner, 2019) suggests that reduced modulation of the lateral prefrontal cortex and attenuated suppression of default network are functionally coupled in aging. This shift

toward greater coupling between default and executive regions may reflect greater reliance on crystallized cognitive abilities, or the semanticization of cognition, in the context of declining fluid or cognitive control abilities (Turner and Spreng, 2015, Spreng et al., 2018, Spreng and Turner, 2019). If default-executive coupling is associated with creative cognition in young and is a hallmark of neurocognitive aging in older adulthood, this raises an intriguing possibility that default-executive coupling, while associated with declining cognitive control, can be adaptive in cognitive domains where associative abilities (e.g., creative thought) are congruent with task goals. In this study, we explore this possibility directly.

Given the overlap in patterns of functional connectivity between the divergent thinking network in young (Beaty et al., 2015, Beaty et al., 2018) and DECHA in older adults (Turner and Spreng, 2015), we focused our analyses on examining the activity and interactivity between default and executive control networks during creative cognition, assayed by a divergent thinking task. Based on previous work, we predicted that all participants, young and old, would show greater default-executive coupling during creative (divergent) thinking. Then, we investigated whether the strength of default-executive coupling differed with age. We reasoned that if this pattern of network coupling is associated with creativity in young adults and is both greater and less flexible for older adults (Turner and Spreng, 2015), default-executive coupling would be greater for older adults than young adults during the divergent thinking task. Finally, we were interested in examining the association between network coupling, as measured by graph theory metrics of functional network integration, during divergent thinking and performance on the in-scanner divergent thinking task. Based on our DECHA model, we predicted that greater levels of default-executive coupling would be predictive of higher creative ability, and consistent with DECHA, this association would be stronger for older versus younger adults. If these hypotheses are supported, this study will provide the first evidence for altered network coupling associated with creative thought in older adults. Furthermore, these findings would support the DECHA, suggesting that functional interactions between default and executive control regions can support goal-directed cognitive performance when activation of prior knowledge is congruent with task goals.

2. Materials and methods

2.1. Participants

The original sample consisted of 30 young adults and 30 older adults recruited at the University of North Carolina at Greensboro. Participants received course credit or cash payment for their involvement in the study. Five older adults were excluded from the final analysis. Three were excluded due to noncompliance with the task instructions, and 2 others were excluded due to brain anomalies, resulting in a final sample of 25 older adults (13 females; mean age: 69.56 years, age range: 63–75) and 30 young adults (19 females; mean age: 21.17 years, age range: 18–34). Of note, females were overrepresented in the final samples for both age groups and slightly more so in the young adult sample. However, previous research has failed to find evidence for sex effects in creativity (Reese et al., 2001), suggesting that this difference should not impact the interpretability or generalizability of the findings. All participants were right-handed with normal or corrected-to-normal vision and no reported history of central nervous system affecting drugs or neurological disease. All participants completed the Mini-Mental State

Exam (MMSE) and had scores above 25 to be eligible for the present study. All participants provided written informed consent. The study was performed in accordance with the guidelines and regulations of University of North Carolina Greensboro Institutional Review Board, who approved the study methods.

2.2. Procedure

Participants completed a divergent thinking task during fMRI scanning. This task paradigm has been described previously (Beaty et al., 2015, Beaty et al., 2018), and the younger adult sample reported here was included in these earlier reports. An alternate use task served as the divergent thinking condition (*Create*), and an object characteristics task (*Object*) provided the control condition. The alternate use task required participants to generate creative uses for everyday objects (e.g., a brick); the object characteristics task required participants to generate typical properties of everyday objects. These two tasks provide an optimal contrast for isolating brain activity related to the creative manipulation of objects during divergent thinking while controlling for activity related to the mental visualization of objects (Fink et al., 2009, Fink et al., 2010). We contrasted these two experimental conditions in our analyses and referred to these as *Create* > *Object*. This contrast examines whether and how functional connectivity differs between divergent thinking (i.e., *Create*) and a control task (*Object*), which was closely matched on factors of noninterest (e.g., visualization). Participants received thorough training on both tasks and completed several practice trials before scanning.

The task paradigm consisted of a jittered fixation cross (4–6 seconds), a cue indicating the upcoming condition (“create” or “object”; 3 seconds), an idea-generation period presenting an object in text (e.g., “umbrella”; 12 seconds), and a response period requiring participants to vocalize their response into an MRI-compatible microphone (5 seconds); an experimenter logged responses for subsequent coding (Beaty et al., 2017, Beaty et al., 2018, Benedek et al., 2014, Fink et al., 2015). Participants were encouraged to continue to think of possible responses until the end of the idea-generation period to maintain active engagement with the tasks and to vocalize their most original response in the *Create* condition or the most characteristic object feature in the *Object* condition (Beaty et al., 2015, Beaty et al., 2018). A total of 46 trials were administered in an event-related design. For each participant, experimental stimuli were randomly assigned to either condition (alternate uses or object characteristics). All trials were included in the subsequent analysis (Beaty et al., 2015, Beaty et al., 2018). Fig. 1 provides a visual representation of the task paradigm.

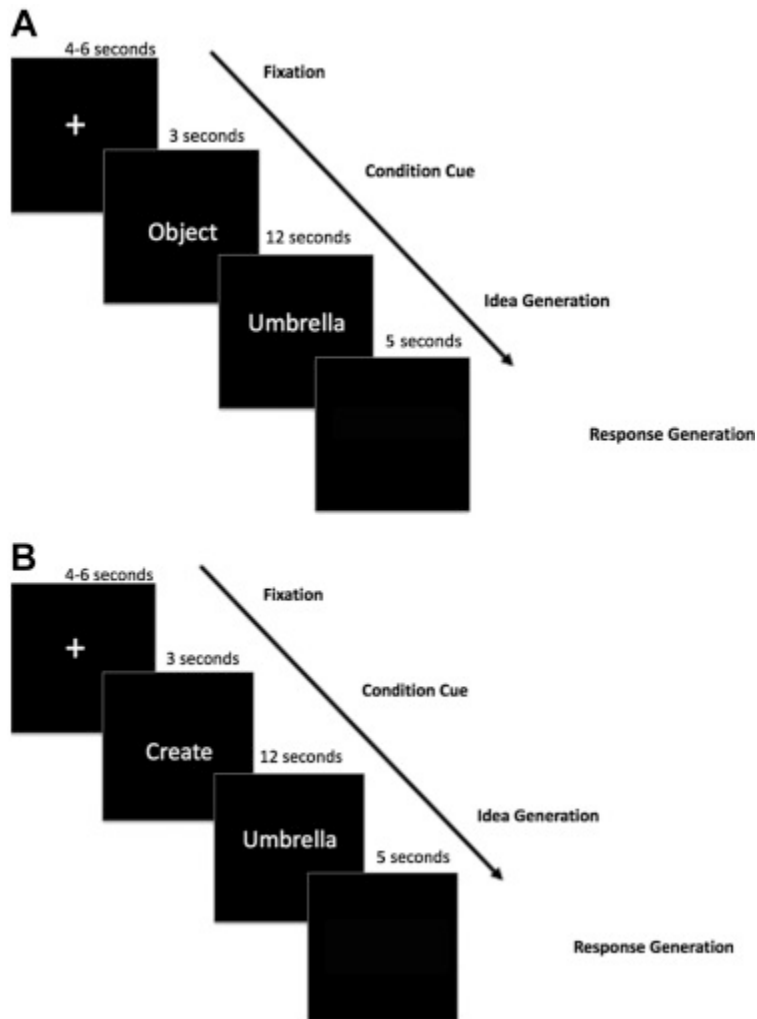


Figure 1. Visual representation of the task paradigm used in the study with a 4- to 6-second fixation cross, followed by condition cue (Panel A: Create; Panel B: Object). After the condition cue, participants were provided with the name of the object for which they had 12 seconds to think of creative and novel uses (Create condition) or everyday common uses (Object condition). After the idea-generation period, they were asked to provide a verbal response (response-generation period = 5 seconds) for their most creative use for the object.

Responses provided by the participants in the response period were rated by three independent raters using the subjective scoring method (Benedek et al., 2013, Christensen et al., 1957, Silvia, 2008), an approach grounded in the consensual assessment technique of creativity assessment (Amabile, 1982). The three raters were trained to score responses for creative quality, using a 1 (not at all creative) to 4 (very creative) scale. This rating score was averaged across raters to yield a single rating for each participant. This rating is referred to as '*creativity rating*' in subsequent analyses and discussion.

2.3. fMRI data acquisition and preprocessing

Participants completed the tasks in a single fMRI run. Whole-brain imaging was performed on a 3T Siemens Magnetom MRI system (Siemens Medical Systems, Erlangen, Germany) using a 16-

channel head coil. A structural magnetization prepared rapid acquisition gradient echo scan was acquired following a standard acquisition protocol (repetition time = 2350 ms, echo time = 2.26 ms, field of view = 256×256 , slice thickness = 1 mm, voxel size = 1 mm isotropic) as reported in previous work (Beaty et al., 2015, Beaty et al., 2018). Blood oxygen level dependent sensitive T2*-weighted functional images were acquired using a single-shot gradient-echo echo-planar imaging pulse sequence (repetition time = 2000 ms, echo time = 30 ms, flip angle = 78° , 32 axial slices, $3.5 \times 3.5 \times 4.0$ mm, distance factor 0%, field of view = 192×192 mm, interleaved slice ordering) and corrected online for head motion. Total time for the task portion of the scan was approximately 19 minutes, with an average of 580 volumes collected per participant. The first 2 volumes were discarded to allow for T1 equilibration effects. Head motion was restricted using firm padding that surrounded the head. Visual stimuli were presented using E-Prime and viewed through a mirror attached to the head coil. After functional imaging, a high-resolution T1 scan was acquired for anatomic normalization.

Imaging data were slice-time corrected and realigned using the Statistical Parametric Mapping 12 package (Wellcome Institute of Cognitive Neurology, London). In addition, the Artifact Detection Toolbox was used to identify motion outlier values in the fMRI time series. A global signal threshold of $z = 9$ and a motion displacement threshold of 2 mm were used to scrub outlying time points. A scrubbing approach has been shown to effectively minimize motion-related artifacts in seed-based correlation analyses (Power et al., 2011, Power et al., 2012). This was used in addition to the 6 motion parameters (3 translational and 3 rotational) obtained during motion realignment. Functional volumes were coregistered and resliced to a voxel size of 2 mm^3 , normalized to the Montreal Neurological Institute template brain, and smoothed with an 8 mm^3 isotropic Gaussian kernel.

2.4. Functional connectivity analyses

Then, functional connectivity between default and executive regions was examined using the CONN toolbox (Whitfield-Gabrieli and Neito-Castanon, 2012) in MATLAB. For each participant, CONN implemented CompCor, a method for identifying principal components associated with segmented white matter and cerebrospinal fluid (Behzadi et al., 2007). These components were entered as confounds along with realignment parameters in a first-level analysis. We used this approach in lieu of global signal regression, given previous reports of spurious correlations which may be generated by removal of the global signal (Murphy and Fox, 2017). ROIs for the frontoparietal, default, and salience (cingulo-opercular, Dosenbach et al., 2007) networks were defined using the network parcellation scheme by Gordon et al. (2014). In total, we used 105 ROIs (40, salience network; 41, default network; 24, frontoparietal network).

2.5. Analytic approach

Past investigations have shown that an interactive network of default and executive control regions is associated with creative cognition (e.g., Beaty et al., 2016, Ellamil et al., 2012, Vartanian et al., 2018). These networks are also affected as a consequence of aging and show greater coupling with each other (Damoiseaux, 2017). Given this a priori rationale, we were specifically interested in isolating functional connectivity within default-executive regions that are associated with creative cognition using an in-scanner divergent thinking task. To do so,

we examined functional connectivity among ROIs falling within default and executive networks (frontoparietal and salience networks). We then examined age interactions in the pattern of observed network connectivity for all participants. Finally, we examined associations between network coupling during divergent thinking and objective ratings of creativity during the divergent thinking task.

2.5.1. Functional connectivity during divergent thinking task performance

First, we looked at functional connectivity between our a priori nodes across all participants for the Create > Object contrast. Statistically, this was modeled with a weighted general linear model, using individual participant functional connectivity maps for all specified nodes for Create > Object. Functional connectivity between all possible ROI pairs was tested using individual level *t*-tests, between each seed and target ROI pair. All results reported are corrected for multiple comparisons using an alpha level of 0.05 at the seed level. Using this statistical approach, we next report group level ROI-to-ROI connectivity findings for young and older adults for Create > Object.

2.5.2. Age differences in functional connectivity during divergent thinking

To examine age-related differences in creative thought, we conducted between-group analyses. Statistically, we used a second-level weighted general linear model with group as a between-subject variable and examined differences via a contrast in functional connectivity between the two conditions, Create > Object. To control for differences in gray matter volume due to age-related atrophy, we included individual gray matter volume as a regressor. Between-group comparisons looking at differences in ROI-to-ROI functional connectivity were tested using a *t*-test between each seed ROI-to-ROI pair. All results reported are corrected for multiple comparisons using an alpha level of 0.05 at the seed level. Positive findings reflect greater ROI-to-ROI connectivity for the Create condition in older adults (OLD [Create > Object] > YOUNG [Create > Object]). Negative results reflect greater ROI-to-ROI connectivity for the Create condition in young adults (YOUNG [Create > Object] > OLD [Create > Object]).

2.5.3. Age differences in associations between functional connectivity and creative ability

We explored whether measures of connectivity among nodes of the default, frontoparietal, and salience networks predicted individual differences in creative ability as measured by divergent thinking task performance. Previous work has shown that functional networks become increasingly integrated as a function of age (Damoiseaux, 2017), which can be reflected in coupling between networks. Given our a priori hypothesis that default-executive coupling is associated with creative cognition, we used graph theory measures of functional integration to examine this relationship. Functional integration in the brain is the ability to combine information from distributed brain regions and is measured by global efficiency and path length. Global efficiency reflects effective information transfer within a network of nodes (i.e., ROIs) and edges (i.e., correlations or “paths” between nodes). It is mathematically expressed as the inverse of the average shortest path length in a graph *G* to all other nodes in the graph. For our purposes, global efficiency provided a marker of information flow across the three networks of interest and has previously been shown to be correlated with creative ability in young adults

(Beatty et al., 2015). To investigate whether brain network organization predicts creative ability, we examined the relationship between global efficiency and the independent ratings of responses generated during the ‘Create’ condition. Given the categorical nature of the creativity ratings, we used Spearman rank correlations. Global efficiency values were extracted for the 105 default, frontoparietal and salience network nodes based on the Create > Object subject-level contrast, using the CONN toolbox. Spearman rank-order correlations were conducted for young and older adults to examine the relationship between global efficiency and creative ratings and then compared between groups.

3. Results

3.1. Behavioral results

3.1.1. Neurocognitive

To assess fluid intelligence, we used the series completion task from Cattell's Culture Fair Intelligence Test (Cattell and Cattell, 1961/2008). To assess crystallized intelligence, we used two tests of vocabulary knowledge from the Educational Testing Services Kit of Factor-Referenced Cognitive Tasks (Ekstrom et al., 1976), the Advanced Vocabulary Test II (note that these data were not available for three young and two older participants). Consistent with previous reports in typical aging cohorts (Park et al., 2001, Verhaeghen, 2003, Verhaeghen and Cerella, 2002), the performance of older adults was lower than that of young on fluid intelligence ($M[\text{young}] = 8.07$, standard deviation [SD] = 1.41; $M[\text{old}] = 5.74$, SD = 1.14; $t(48) = 6.38$; $p < 0.001$) and higher on crystallized intelligence (advanced vocabulary: $M[\text{young}] = 9.67$ [SD = 2.50], $M[\text{old}] = 13.17$ [SD = 2.66], $t(48) = -4.81$, $p < 0.001$; extended vocabulary: $M[\text{young}] = 13.11$ [SD = 2.71], $M[\text{old}] = 17.48$ [SD = 3.50], $t(48) = -4.97$, $p < 0.001$).

3.1.2. Divergent thinking

Three independent raters provided creativity ratings for each response generated by all participants during trials for the ‘Create’ condition. There was no significant difference in creativity ratings for responses generated by older adults during the ‘Create’ condition ($M = 2.9$, $SD = 0.18$) and young adults ($M = 3.08$, $SD = 0.20$, $t(40) = 1.16$, $p = 0.25$).

3.2. Functional connectivity during divergent thinking task performance

For all participants, young and old, during the Create condition, nodes of the salience and default networks were functionally connected. Specifically, this was observed between (1) the left posterior insula and frontal pole and (2) the left medial prefrontal cortex and posterior cingulate cortex. In contrast, connectivity associated with the Object condition was limited to two nodes of the salience network: left postcentral gyrus and right cingulate gyrus. These findings are detailed in Table 1, where results are organized by within-network and between-network interactions (Fig. 2).

Table 1. ROI-to-ROI connectivity for the default network (DN), salience network (SN), and frontoparietal network (FPN) across all participants with a Create > Object contrast, corresponding to results in Fig. 2. Each row denotes significant connections between network node and other network nodes and their network affiliation as defined by Gordon et al. (2014)

Region	Network	Hem	Node	MNI coordinates				<i>p</i>
				X	Y	Z	T	
Create								
Posterior insula	SN	L	71	-38.7	-16	-5.3		
Frontal pole	DN	L	114	-27.5	53.6	0	4.83	0.034
PCC	DN	L	1	-11.2	-52.4	36.5		
dmPFC	DN	L	25	-5.6	42.2	35.1	4.49	0.034
Object								
Postcentral gyrus	SN	L	105	-58.8	-23.9	31		
Cingulate gyrus	SN	R	185	8.6	4.2	40.1	-4.77	0.034

Key: dmPFC, dorsomedial prefrontal cortex; DN, default network; Hem, hemisphere; L, left; MNI, Montreal Neurological Institute; PCC, posterior cingulate cortex; R, right; ROI, region of interest; SN, salience network.

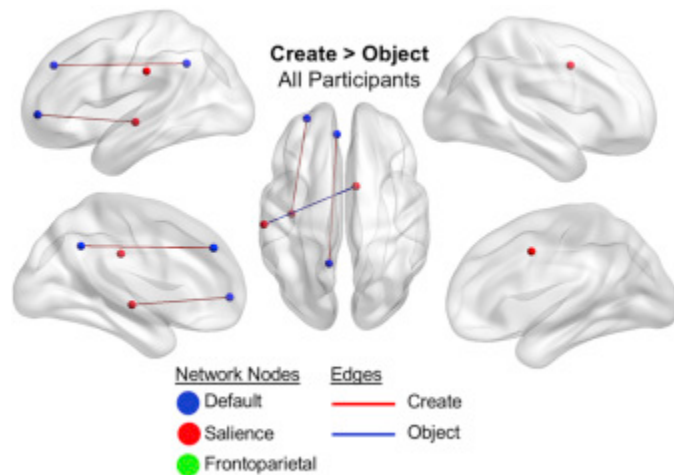


Figure 2. ROI-to-ROI results for a Create > Object contrast for all participants presented in a glass brain. Color-coded nodes include regions from the default network, salience network, and frontoparietal network. The color of the edges (connections between nodes) indicates the direction of the contrast. Red edges indicate ROI-to-ROI connectivity between nodes during the Create condition, whereas blue edges indicate ROI-to-ROI connectivity during the Object condition across all participants. These results correspond to findings detailed in Table 1. ROI, region of interest.

3.3. Age differences in functional connectivity during divergent thinking

A within-subject condition-based contrast (Create > Object) was used at the first level to generate within-subject ROI-to-ROI functional connectivity maps. At the first level, no negative ROI-to-ROI connectivity values survived a threshold of $p = 0.05$, with false discovery rate corrected at the seed level. Hence, between-group differences in connectivity evaluated at the second level reflect positive connectivity between nodes for young and older adults. At the second level, a between-subject contrast was conducted to examine group differences in ROI-to-ROI functional connectivity that corresponded with Create > Object. We also controlled for any differences in gray matter volume by including it as a regressor. Hence, positive findings reflect

greater ROI-to-ROI connectivity for the Create condition in older adults. On the other hand, negative results reflect greater ROI-to-ROI connectivity for the Create condition in young adults. Young adults showed greater positive connectivity during divergent thinking than older adults between default and salience network nodes (blue edges, Fig. 3A). Specifically, this was noted between left postcentral gyrus (salience network) and right superior frontal gyrus (default network).

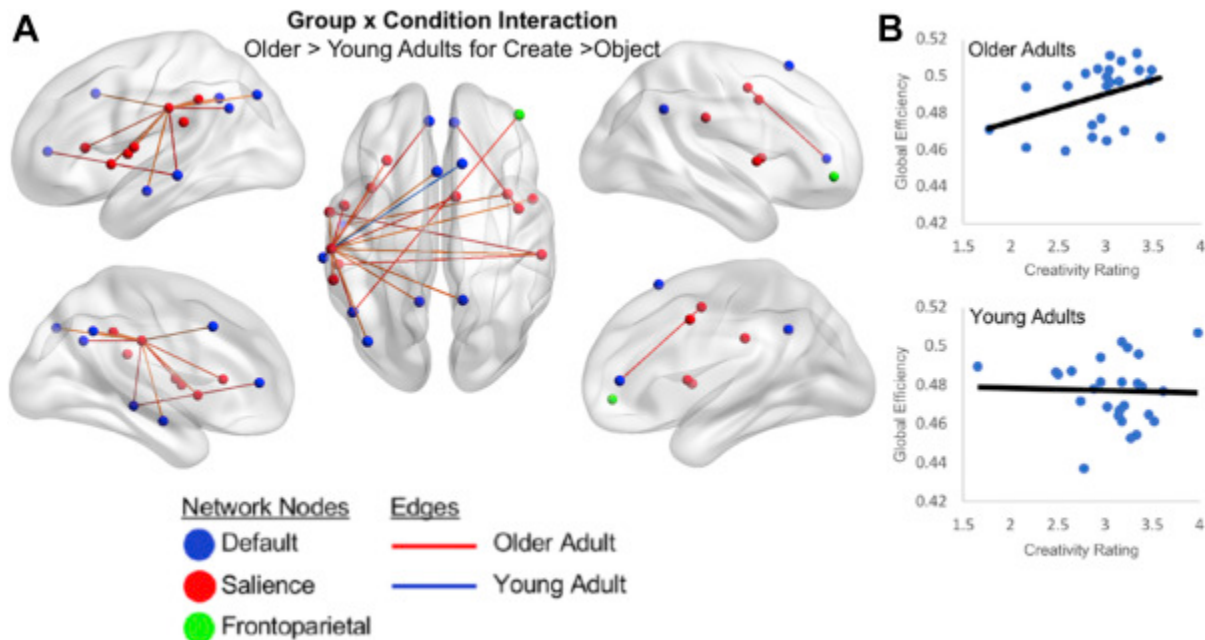


Figure 3. (A) Age-condition interaction of ROI-to-ROI connectivity between nodes from the default network, salience network, and frontoparietal network presented in a glass brain. Nodes are color coded by network affiliation. A within-subject condition contrast was conducted at the first level using a Create > Object contrast. Then, a between-group analysis was conducted to determine ROI-to-ROI functional connectivity differences between young and older adults. Red edges indicate ROI-to-ROI connectivity between nodes during the Create condition which is greater in older adults. Blue edges indicate ROI-to-ROI connectivity between nodes during the Create condition which is greater in young adults. These results correspond to findings detailed in Table 2. (B) Scatter plots depicting the relationship between creativity ratings and global efficiency of the divergent thinking network in Panel A in older and young adults. Older adults show a significant correlation between creativity ratings and global efficiency, with a significant difference in slope between groups. ROI, region of interest.

Older adults showed greater positive functional connectivity during divergent thinking, both within and between networks (red edges, Fig. 3A).

Within-network positive functional connectivity within the salience network was observed between left postcentral gyrus, left supramarginal gyrus, left anterior insula, left rolandic operculum, left precentral gyrus, right middle anterior cingulate cortex, and right postcentral gyrus. Within-network positive functional connectivity within the default network was observed between left middle temporal gyrus and left ventromedial prefrontal cortex.

Older adults also showed greater between-network functional connectivity. This included positive functional connectivity between key nodes of the default and executive control network (left angular gyrus and, right inferior frontal gyri and left post central gyrus) and default and salience network between (1) left precentral gyrus and right ventromedial prefrontal cortex; (2) left postcentral gyrus and, left medial superior prefrontal cortex, bilateral posterior cingulate cortex, left angular gyrus, and left middle temporal gyrus; (3) left inferior temporal gyrus and right anterior insula and left postcentral gyrus. These findings are detailed in Table 2, where results are organized by within-network and between-network interactions.

Table 2. ROI-to-ROI connectivity findings using Gordon et al. (2014) nodes for the default network (DN), salience network (SN), and frontoparietal network (FPN), corresponding to results shown in Fig. 3. ROI-to-ROI functional connectivity maps were first contrasted at the within-subject level using a Create > Object contrast. Then, between-subject analyses were conducted using an Old > Young contrast. Positive findings correspond to significant ROI-to-ROI connectivity for older adults during the Create condition, whereas negative findings correspond to significant ROI-to-ROI connectivity for young adults during the Create condition. Each row denotes significant connections between network node and other network nodes and their network affiliation as defined by Gordon et al. (2014)

Region	Network	Hem	Node	MNI coordinates				<i>p</i>
				X	Y	Z	T	
Young adults								
Between-network connectivity								
<i>SN-DN</i>								
Postcentral gyrus	SN	L	105	-58.8	-23.9	31		
SFG	DN	R	165	11.9	21.9	59.9	-2.74	0.04
Older adults								
Within-network connectivity								
<i>SN-SN</i>								
Postcentral gyrus	SN	L	105	-58.8	-23.9	31		
SMG	SN	L	63	-57.7	-40.6	35.8	2.89	0.04
Anterior insula	SN	L	82	-37.3	8.9	-0.9	2.99	0.04
Anterior insula	SN	L	84	-28.8	23.7	8.4	3.31	0.03
Rolandic operculum	SN	L	101	-59.8	-4.1	8.8	2.85	0.04
Precentral gyrus	SN	L	111	-51.8	-0.6	5	3.72	0.017
mACC	SN	R	185	8.6	0.2	40.1	3.45	0.03
Postcentral gyrus	SN	R	223	54.9	-27	29.6	2.78	0.04
Postcentral gyrus	SN	R	274	50.1	3	3.9	2.82	0.04
Postcentral gyrus	SN	R	223	54.9	-27	29.6		
Rolandic operculum	SN	L	101	-59.8	-4.1	8.8	4.15	0.013
Postcentral gyrus	SN	L	103	-55.1	-32.3	23	3.51	0.04
<i>DN-DN</i>								
MTG	DN	L	126	63.2	-28.7	-7.2		
vmPFC	DN	L	152	-6	44.9	6.3	3.51	0.04
Between-network connectivity								
<i>DN-FPN</i>								
AG	DN	L	6	-11.7	26.7	57		
IFG	FPN	R	240	42.8	48.3	-5.1	3.52	0.04
<i>DN-SN</i>								
Precentral gyrus	SN	R	198	42.5	-2.3	47.2		
vmPFC	DN	R	184	7.7	44.1	5.5	3.66	0.04
Postcentral gyrus	SN	L	105	-58.8	-23.9	31		
PCC	DN	L	1	-11.2	-52.4	36.5	3.61	0.04

Region	Network	Hem	Node	MNI coordinates				<i>p</i>
				X	Y	Z	T	
AG	DN	L	6	-47.2	-58	30.8	4.26	0.004
PCC	DN	L	26	-1.7	-17.7	39.1	2.78	0.04
AG	DN	L	94	-39.3	-73.9	38.3	2.84	0.04
MTG	DN	L	126	-63.2	-28.7	-7.2	4.36	0.004
PCC	DN	R	162	12.3	-51.6	34.5	2.94	0.04
ITG	DN	L	127	-53.1	-11.4	-16		
Anterior insula	SN	R	246	36.5	5.7	6	2.97	0.04
Postcentral gyrus	SN	L	105	-58.8	-23.9	31	2.77	0.04

Key: AG, angular gyrus; dmPFC, dorsomedial prefrontal cortex; DN, default network; Hem, hemisphere; IFG, inferior frontal gyrus; ITG, inferior temporal gyrus; mACC, middle anterior cingulate cortex; MNI, montreal neurological institute; MTG, middle temporal gyrus; PCC, posterior cingulate cortex; PFC, prefrontal cortex; ROI, region of interest; SFG, superior frontal gyrus; SMG, supramarginal gyrus; SN, salience network; vmPFC, ventromedial prefrontal cortex.

3.4. Age differences in associations between functional connectivity and creative ability

Finally, we were interested in graph theoretical metrics of the default-executive regions that demonstrated greater ROI-to-ROI functional connectivity for older and young adults, during divergent thinking. Spearman rank-order correlations were used to determine the relationship between network global efficiency observed during the individual level Create > Object contrast and creativity ratings for ideas generated during the Create condition.

Consistent with predictions, for older adults, global efficiency values for this network were positively correlated with creativity ratings ($r_s(23) = 0.46, p = 0.02, 95\%$ confidence interval: 0.06–0.77) (Fig. 3B). This correlation was not significant in young adults ($r_s(24) = -0.13, p = 0.54, 95\%$ confidence interval: -0.54 to 0.28) (Fig. 3B). The correlation between global efficiency and creativity ratings in older adults was significantly greater than that observed in young adults ($z = 2.11, p = 0.03$).

4. Discussion

The present study determined functional connectivity interactions of the default and executive networks associated with divergent thinking in young and older adults. We first demonstrated that both young and older adults show task-driven coupling between regions of the default and executive control networks during creative cognition, consistent with recent work implicating components of these networks in divergent thinking (Chen et al., 2018; Gonen-Yaacovi et al., 2013; Wu et al., 2015, Vartanian et al., 2018; Beaty et al., 2015, Beaty et al., 2018). Then, we demonstrated that although both age groups performed similarly on the task, network interactions differed for young and old adults during the Create task condition. Specifically, older adults showed greater connectivity than younger adults between default and executive control networks, consistent with predictions. Finally, we reported that the global efficiency of these networks, a measure of network integration, was positively correlated with independent creativity ratings on the divergent thinking task for older adults and was significantly different from that of younger adults. Taken together, these findings suggest that coupling between default and executive networks, associated with divergent thinking ability in young adults (e.g., Ellamil et al., 2012, Green et al., 2015, Pinho et al., 2014, Vartanian et al., 2018), is enhanced in older

adults, and more efficient crosstalk between these networks may serve as a putative neural marker of creative cognition in later life.

We observed functional connectivity between default and executive regions during divergent thinking in older adults when compared with younger adults. Divergent thinking-related nodes consisted of default network regions (superior frontal gyrus, anterior cingulate cortex, posterior cingulate cortex, angular gyrus, middle temporal gyrus) and executive control regions (inferior and middle frontal gyri, precentral gyrus, postcentral gyrus, and inferior temporal gyrus). We also observed functional connectivity between key nodes of the salience network (e.g., precentral gyrus and anterior insula). Our findings extend previous work conducted with younger adults using both resting-state (Beaty et al., 2014, Vartanian et al., 2018) and task-based studies of creativity (Beaty et al., 2015, Beaty et al., 2018) showing greater connectivity between core default regions (precuneus, posterior cingulate cortex), executive regions (inferior frontal gyri), and salience network (insula).

Models of creative cognition propose a two-stage creative process that includes both generative and evaluative components. Creativity begins with crudely formed ideas and associations (the generation stage), followed by the exploration of ideas through evaluation and testing (the evaluation stage) (Basadur et al., 1982, Finke et al., 1992). Brain-based models of creativity propose that the default network is critical for generation of candidate ideas retrieved from long-term memory. Executive control networks, including the salience and frontoparietal networks, are subsequently engaged to evaluate these ideas in the latter stages of creative cognition (Beaty et al., 2016). Our findings are consistent with this model and implicate two candidate control processes in creative cognition in older adulthood. First, the pattern of increased functional connectivity between default network brain regions and the right inferior frontal gyrus, implicated in inhibitory processing (Rae et al., 2014), suggests that greater inhibitory control may be required at the generative stage to enable older adults to escape the constraints of overlearned associations to set the stage for their reconfiguration in the latter evaluation stage, as has been shown in younger adults (Beaty et al., 2014, Vartanian et al., 2018).

Second, default network coupling with left lateralized nodes, including middle temporal gyrus and salience network regions, implicated in semantic control processing (Jefferies, 2013, Noonan et al., 2013), suggests that greater semantic control is necessary to retrieve weak semantic associations (Krieger-Redwood et al., 2016) and ultimately evaluate and reconfigure these as necessary in the service of creative cognition. Furthermore, the semantic control network is spatially adjacent to both default and executive systems (Davey et al., 2016, Jackson et al., 2016, Ralph et al., 2017) and is thus well positioned to engage control processes necessary to retrieve and reshape semanticized knowledge. Taken together, our findings strongly support the default-executive coupling hypothesis as a candidate-neural mechanism necessary to both suppress overlearned and enhance weaker semantic associations to support the emergence of a creative thought. However, it is important to note that previous findings in young adults, derived from both whole-brain and ROI-based approaches (e.g., Beaty et al., 2015), as well as our neural network model, led us to propose strong a priori hypotheses associated with default-executive interactivity. Although these hypotheses were supported by our findings, we cannot rule out contributions of other network interactivity patterns to the maintenance of creative abilities in older adulthood.

As proposed by the DECHA, older adults rely to a greater extent on stored representational knowledge structures mediated by the default network. In the DECHA framework, stored representations assume an increasingly central role in goal-directed cognition (Turner and Spreng, 2015). Previous work has shown that the strength of default-executive coupling at rest in older adults predicted more semanticized autobiographical recall in older adults (Spreng et al., 2018), suggestive of less reliance on controlled recollective processes and greater engagement of semantic representations. Although a broader, individual difference analysis of neurocognitive contributions to creativity is beyond the scope of the study, it is worth noting that this interpretation is consistent with our finding that older adults had lower fluid and higher crystallized intelligence than their younger counterparts. In the context of creative thought in older adults, default network engagement may facilitate enhanced retrieval of prior knowledge representations to support divergent thinking in the context of declining cognitive control abilities in later life. Beaty et al (2016) proposed that creative thought involves similar cognitive and neural mechanisms as goal-directed tasks and that interplay between the default network and executive control regions subserves the subcomponents of goal-directed cognition. Specifically, the default network may be important for the generation of creative ideas, leveraging prior knowledge or when decisions are required to be made based on information represented in memory (Konishi et al., 2015, Murphy et al., 2018). Executive regions, in turn, are necessary to constrain or shape these ideas via top-down monitoring to align with the goals of the task. This may also require top-down exertion of semantic control to allow reshaping of knowledge from memory to fit the current task goals (Jefferies, 2013; Ralph et al., 2017).

Overall, our results suggest that older adults are able to benefit from the consequences of a shifting neural architecture in the context of creative thinking. Past work has reliably demonstrated that large-scale functional networks become decreasingly segregated and “merge” over time (Chan et al., 2014). This network dedifferentiation, involving more positive connectivity between default and executive regions, has been reported 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). The DECHA proposes that this changing neural architecture reflects greater reliance on internally stored representations and knowledge, acquired by virtue of a longer life, as compared to young adults. In our study, we demonstrate that cognitively healthy older adults are able to leverage their knowledge base to support divergent thinking and generate creative responses at a level equivalent to that of younger adults. This may be a domain-specific exemplar of the semanticization of cognition in older adulthood and, specifically, on how accessing prior knowledge representations can support cognitive performance on tasks where these representations are consistent with task goals (Spreng et al., 2018).

5. Conclusions

These findings suggest that functional coupling of default and executive control regions supports creative cognition in older adulthood. Despite equivalent behavioral performance with young adults, functional coupling between default and executive control regions was associated with creative cognition in older adults. Also, the overall level of functional integration between the default and executive networks, as measured by global efficiency, was significantly related to creative ability in older adults, when compared to young adults. This indicates that older adults

are engaging in greater default-executive coupling, which is positively associated with creative cognition. This pattern of functional coupling suggests that prior knowledge, accessed through default network regions, may contribute more to creativity in older versus younger adults. Given the paucity of investigations characterizing the neural basis of creative ability in later stages of life, future research will be necessary to replicate and extend these findings to elucidate the neural substrates of creativity in aging. Creative pursuits are implicated in numerous facets of successful aging including physiological, social, spiritual, and cognitive functioning (Duhamel, 2016). Given the importance of creativity to preserved independence and a sense of agency and purpose in later life, better understanding as to how brain changes promote or impede creative thought will be an important avenue for future research. In this context, future research investigating the neural basis of creative thoughts in later life offers an exciting opportunity to explore the cognitive benefits associated with the changing architecture of cognition and brain function in older adulthood (Spreng and Turner, 2019).

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References

- Addis, D.R., Pan, L., Musicaro, R., Schacter, D.L., 2016. Divergent thinking and constructing episodic simulations. *Memory* 24, 89-97.
- Alpaugh, P.K., Birren, J.E., 1977. Variables affecting creative contributions across the adult life span. *Hum. Develop.* 20, 240-248.
- Amabile, T.M., 1982. Children's artistic creativity: detrimental effects of competition in a field setting. *Personal. Social Psychol. Bull.* 8, 573-578.
- Basadur, M., Graen, G.B., Green, S.G., 1982. Training in creative problem solving: effects on ideation and problem finding and solving in an industrial research organization. *Organ. Behav. Hum. Perform.* 30, 41-70.
- Beaty, R.E., Benedek, M., Wilkins, R.W., Jauk, E., Fink, A., Silvia, P.J., Neubauer, A.C., 2014. Creativity and the default network: a functional connectivity analysis of the creative brain at rest. *Neuropsychologia* 64, 92-98.
- Beaty, R.E., Benedek, M., Kaufman, S.B., Silvia, P.J., 2015. Default and executive network coupling supports creative idea production. *Sci. Rep.* 5, 10964.
- Beaty, R.E., Benedek, M., Silvia, P.J., Schacter, D.L., 2016. Creative cognition and brain network dynamics. *Trends Cogn. Sci.* 20, 87-95.

Beaty, R.E., Silvia, P.J., Benedek, M., 2017. Brain networks underlying novel metaphor production. *Brain Cogn.* 111, 163-170.

Beaty, R.E., Kenett, Y.N., Christensen, A.P., Rosenberg, M.D., Benedek, M., Chen, Q., Silvia, P.J., 2018. Robust prediction of individual creative ability from brain functional connectivity. *Proc. Natl. Acad. Sci. U. S. A.* 115, 1087-1092.

Behzadi, Y., Restom, K., Liau, J., Liu, T.T., 2007. A component based noise correction method (CompCor) for BOLD and perfusion based fMRI. *Neuroimage* 37, 90-101.

Benedek, M., Mühlmann, C., Jauk, E., Neubauer, A.C., 2013. Assessment of divergent thinking by means of the subjective top-scoring method: effects of the number of top-ideas and time-on-task on reliability and validity. *Psychol. Aesthet. Creat. Arts* 7, 341.

Benedek, M., Jauk, E., Fink, A., Koschutnig, K., Reishofer, G., Ebner, F., Neubauer, A.C., 2014. To create or to recall? Neural mechanisms underlying the generation of creative new ideas. *NeuroImage* 88, 125-133.

Cattell, R.B., Cattell, A.K.S., 1961/2008. *Measuring Intelligence with the Culture Fair Tests*. Hogrefe, Oxford, UK.

Chan, M.Y., Park, D.C., Savalia, N.K., Petersen, S.E., Wig, G.S., 2014. Decreased segregation of brain systems across the healthy adult lifespan. *Proc. Natl. Acad. Sci. U. S. A.* 111, E4997-E5006.

Chen, Q., Beaty, R.E., Wei, D., Yang, J., Sun, J., Liu, W., Yang, W., Zhang, Q., Qiu, J., 2018. Longitudinal alterations of frontoparietal and frontotemporal networks predict future creative cognitive ability. *Cereb. Cortex* 28, 103-115.

Christensen, P.R., Guilford, J.P., Wilson, R.C., 1957. Relations of creative responses to working time and instructions. *J. Exp. Psychol.* 53, 82.

Damoiseaux, J.S., 2017. Effects of aging on functional and structural brain connectivity. *NeuroImage* 160, 32-40.

Davey, J., Thompson, H.E., Hallam, G., Karapanagiotidis, T., Murphy, C., De Caso, I., Jefferies, E., 2016. Exploring the role of the posterior middle temporal gyrus in semantic cognition: integration of anterior temporal lobe with executive processes. *NeuroImage* 137, 165-177.

Dennis, E.L., Thompson, P.M., 2014. Functional brain connectivity using fMRI in aging and Alzheimer's disease. *Neuropsychol. Rev.* 24, 49-62.

Dosenbach, N.U., Fair, D.A., Miezin, F.M., Cohen, A.L., Wenger, K.K., Dosenbach, R.A., Schlaggar, B.L., 2007. Distinct brain networks for adaptive and stable task control in humans. *Proc. Natl. Acad. Sci. U. S. A.* 104, 11073-11078.

Duhamel, K.V., 2016. Creativity and the Golden Years: Biopsychosocial and Cultural Influences for Living a Successful Life.

Ekstrom, R.B., French, J.W., Harman, H.H., Dermen, D., 1976. Manual for Kit of Factor-referenced Cognitive Tests. Educational Testing Service, Princeton, NJ.

Ellamil, M., Dobson, C., Beeman, M., Christoff, K., 2012. Evaluative and generative modes of thought during the creative process. *Neuroimage* 59, 1783-1794.

Fink, A., Grabner, R.H., Benedek, M., Reishofer, G., Hauswirth, V., Fally, M., Neubauer, A.C., 2009. The creative brain: investigation of brain activity during creative problem solving by means of EEG and fMRI. *Hum. Brain Mapp.* 30, 734-748.

Fink, A., Grabner, R.H., Gebauer, D., Reishofer, G., Koschutnig, K., Ebner, F., 2010. Enhancing creativity by means of cognitive stimulation: evidence from an fMRI study. *Neuroimage* 52, 1687-1695.

Fink, A., Benedek, M., Koschutnig, K., Pirker, E., Berger, E., Meister, S., Weiss, E.M., 2015. Training of verbal creativity modulates brain activity in regions associated with language and memory-related demands. *Hum. Brain Mapp.* 36, 4104-4115.

Finke, R.A., Ward, T.B., Smith, S.M., 1992. *Creative Cognition: Theory, Research, and Applications*. The MIT Press, Cambridge, MA, USA.

Foos, P.W., Boone, D., 2008. Adult age differences in divergent thinking: It's just a matter of time. *Educ. Gerontol.* 34, 587-594.

Furnham, A., Bachtiar, V., 2008. Personality and intelligence as predictors of creativity. *Pers. Individual Diff.* 45, 613-617.

Geerligs, L., Renken, R.J., Saliassi, E., Maurits, N.M., Lorist, M.M., 2015. A brain-wide study of age-related changes in functional connectivity. *Cereb. Cortex* 25, 1987-1999.

Gonen-Yaacovi, G., De Souza, L.C., Levy, R., Urbanski, M., Josse, G., Volle, E., 2013. Rostral and caudal prefrontal contribution to creativity: a meta-analysis of functional imaging data. *Front. Hum. Neurosci.* 7, 465.

Gordon, E.M., Laumann, T.O., Adeyemo, B., Huckins, J.F., Kelley, W.M., Petersen, S.E., 2014. Generation and evaluation of a cortical area parcellation from resting-state correlations. *Cereb. Cortex* 26, 288-303.

Green, A.E., Cohen, M.S., Raab, H.A., Yedibalian, C.G., Gray, J.R., 2015. Frontopolar activity and connectivity support dynamic conscious augmentation of creative state. *Hum. Brain Mapp.* 36, 923-934.

Guilford, J.P., 1950. Creativity. *Am. Psychol.* 5, 444-454.

Jackson, R.L., Hoffman, P., Pobric, G., Ralph, M.A.L., 2016. The semantic network at work and rest: differential connectivity of anterior temporal lobe subregions. *J. Neurosci.* 36, 1490-1501.

Jaquish, G.A., Ripple, R.E., 1984. Adolescent divergent thinking: a cross-cultural perspective. *J. Cross Cultural Psychol.* 15, 95-104.

Jefferies, E., 2013. The neural basis of semantic cognition: converging evidence from neuropsychology, neuroimaging and TMS. *Cortex* 49, 611-625.

Konishi, M., McLaren, D.G., Engen, H., Smallwood, J., 2015. Shaped by the past: the default mode network supports cognition that is independent of immediate perceptual input. *PLoS One* 10, e0132209.

Krieger-Redwood, K., Jefferies, E., Karapanagiotidis, T., Seymour, R., Nunes, A., Ang, J.W.A., Smallwood, J., 2016. Down but not out in posterior cingulate cortex: deactivation yet functional coupling with prefrontal cortex during demanding semantic cognition. *Neuroimage* 141, 366-377.

Madore, K.P., Jing, H.G., Schacter, D.L., 2016. Divergent creative thinking in young and older adults: extending the effects of an episodic specificity induction. *Mem. Cognit.* 44, 974-988.

Murphy, K., Fox, M.D., 2017. Towards a consensus regarding global signal regression for resting state functional connectivity MRI. *Neuroimage* 154, 169-173.

Murphy, C., Jefferies, E., Rueschemeyer, S.A., Sormaz, M., Wang, H.T., Margulies, D.S., Smallwood, J., 2018. Distant from input: evidence of regions within the default mode network supporting perceptually-decoupled and conceptually-guided cognition. *Neuroimage* 171, 393-401.

Ng, K.K., Lo, J.C., Lim, J.K., Chee, M.W., Zhou, J., 2016. Reduced functional segregation between the default mode network and the executive control network in healthy older adults: a longitudinal study. *Neuroimage* 133, 321-330.

Noonan, K.A., Jefferies, E., Visser, M., Lambon Ralph, M.A., 2013. Going beyond inferior prefrontal involvement in semantic control: evidence for the additional contribution of dorsal angular gyrus and posterior middle temporal cortex. *J. Cogn. Neurosci.* 25, 1824-1850.

Palmiero, M., Di Giacomo, D., Passafiume, D., 2014. Divergent thinking and age-related changes. *Creativity Res. J.* 26, 456-460.

Park, D.C., Polk, T.A., Mikels, J.A., Taylor, S.F., Marshuetz, C., 2001. Cerebral aging: integration of brain and behavioral models of cognitive function. *Dialogues Clin. Neurosci.* 3, 151-165.

Pinho, A.L., de Manzano, Ö., Fransson, P., Eriksson, H., Ullén, F., 2014. Connecting to create: expertise in musical improvisation is associated with increased functional connectivity between premotor and prefrontal areas. *J. Neurosci.* 34, 6156-6163.

Plucker, J.A., 1999. Is the proof in the pudding? Reanalyses of Torrance's (1958 to present) longitudinal data. *Creativity Res. J.* 12, 103-114.

Power, J.D., Cohen, A.L., Nelson, S.M., Wig, G.S., Barnes, K.A., Church, J.A., Petersen, S.E., 2011. Functional network organization of the human brain. *Neuron* 72, 665e678.

Power, J.D., Barnes, K.A., Snyder, A.Z., Schlaggar, B.L., Petersen, S.E., 2012. Spurious but systematic correlations in functional connectivity MRI networks arise from subject motion. *Neuroimage* 59, 2142-2154.

Rae, C.L., Hughes, L.E., Weaver, C., Anderson, M.C., Rowe, J.B., 2014. Selection and stopping in voluntary action: a meta-analysis and combined fMRI study. *Neuroimage* 86, 381-391.

Ralph, M.A.L., Jefferies, E., Patterson, K., Rogers, T.T., 2017. The neural and computational bases of semantic cognition. *Nat. Rev. Neurosci.* 18, 42-55.

Reese, H.W., Lee, L.J., Cohen, S.H., Puckett Jr., J.M., 2001. Effects of intellectual variables, age, and gender on divergent thinking in adulthood. *Int. J. Behav. Dev.* 25, 491-500.

Rieck, J.R., Rodrigue, K.M., Boylan, M.A., Kennedy, K.M., 2017. Age-related reduction of BOLD modulation to cognitive difficulty predicts poorer task accuracy and poorer fluid reasoning ability. *Neuroimage* 147, 262-271.

Roskos-Ewoldson, B., Black, S.R., McCown, S.M., 2008. Age-related changes in creative thinking. *J. Creat. Behav.* 42, 33-59.

Sambataro, F., Murty, V.P., Callicott, J.H., Tan, H.Y., Das, S., Weinberger, D.R., Mattay, V.S., 2010. Age-related alterations in default mode network: impact on working memory performance. *Neurobiol. Aging* 31, 839-852.

Silvia, P.J., 2008. Discernment and creativity: how well can people identify their most creative ideas? *Psychol. Aesthet. Creat. Arts* 2, 139.

Spreng, R.N., Schacter, D.L., 2012. Default network modulation and large-scale network interactivity in healthy young and old adults. *Cereb. Cortex* 22, 2610-2621.

Spreng, R.N., Turner, G.R., 2019. The shifting architecture of cognition and brain function in older adulthood. *Perspect. Psychol. Sci.*

Spreng, R.N., Lockrow, A.W., DuPre, E., Setton, R., Spreng, K.A., Turner, G.R., 2018. Semanticized autobiographical memory and the default-executive coupling hypothesis of aging. *Neuropsychologia* 110, 37-43.

Torrance, E.P., 1988. The nature of creativity as manifest in its testing. In: Sternberg, R.J. (Ed.), *The nature of creativity: contemporary psychological perspectives*. Cambridge University Press, New York, NY, USA, pp. 43-75.

Turner, G.R., Spreng, R.N., 2015. Prefrontal engagement and reduced default network suppression co-occur and are dynamically coupled in older adults: the default-executive coupling hypothesis of aging. *J. Cogn. Neurosci.* 27, 2462-2476.

Vartanian, O., Beatty, E.L., Smith, I., Blackler, K., Lam, Q., Forbes, S., 2018. One-way traffic: the inferior frontal gyrus controls brain activation in the middle temporal gyrus and inferior parietal lobule during divergent thinking. *Neuropsychologia* 118 (Pt A), 68-78.

Verhaeghen, P., 2003. Aging and vocabulary scores: a meta-analysis. *Psychol. Aging* 18, 332-339.

Verhaeghen, P., Cerella, J., 2002. Aging, executive control, and attention: a review of meta-analyses. *Neurosci. Biobehav Rev.* 26, 849-857.

Whitfield-Gabrieli, S., Nieto-Castanon, A., 2012. Conn: a functional connectivity toolbox for correlated and anticorrelated brain networks. *Brain Connect.* 2, 125-141.

Wu, X., Yang, W., Tong, D., Sun, J., Chen, Q., Wei, D., Zhang, Q., Zhang, M., Qiu, J., 2015. A meta-analysis of neuroimaging studies on divergent thinking using activation likelihood estimation. *Hum. Brain Mapp.* 36, 2703-2718.