

CREATIVE AGING: FUNCTIONAL NEURAL NETWORKS ASSOCIATED WITH
CREATIVITY IN AGING

AREEBA ADNAN

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Abstract

Creativity is the ability to generate novel associations and has been linked to better problem-solving and real-world functional abilities. Creative ability has been implicated in successful aging including psychological, social, spiritual and, cognitive functioning (Duhamel, 2016). Creative thinking is associated with connectivity between default and executive control regions in the young brain. In aging, this pattern of functional coupling is observed across multiple tasks and associated with better performance on tasks that closely mirror real-world functioning, where prior knowledge is congruent with task goals. This has been described as the Default-Executive Coupling Hypothesis of Aging (Turner & Spreng, 2015), and proposes that this changing neural architecture reflects greater reliance on internally stored representations and knowledge. This shift towards greater semanticized cognition in later stages of life reflected in changes in network connectivity and interactivity may also support creative cognition into older adulthood. However, age-differences in brain networks of creativity have yet to be directly investigated. This dissertation explored age-related functional connectivity patterns of creative thought among default and executive control networks using task-based and intrinsic functional connectivity methods. In study one, old and young participants completed a divergent thinking task measuring creative thinking, while undergoing fMRI scanning. 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 global network efficiency of default-executive nodes was associated with creative ability for older adults only. These findings provide novel evidence of default-executive coupling as a putative mechanism supporting creative ability in later life. Next, we investigated whether this pattern of default-executive coupling supporting creative thinking is

reflected in the intrinsic architecture of the aging brain. Younger and older adults underwent fMRI scanning at rest and completed a divergent thinking task to assess creative ability outside the scanner. Results indicated that both younger and older adults have equivalent performance on offline measures of creativity. However, relative to the younger adults, older adults showed a pattern of greater between-network intrinsic functional connectivity among default-executive networks associated with creative ability. Results from both study one and two provide evidence for a greater reliance of the aging brain on default-executive coupling to support creative cognition. In study three, we investigated whether creativity is associated with fluid or crystallized intelligence in young and older adults, as further, albeit preliminary, evidence in support of a ‘semanticization of cognition’ hypothesis of creative cognition in later life. Results showed that fluid intelligence was reliable predictor of creativity across both young and older adults. Contrary to the semanticization hypothesis, crystallized intelligence was not a significant predictor of creativity in older adults. However, this may reflect the limited sample size for an individual difference analysis and the narrow assessment of crystalized knowledge. Taken together, the dissertation findings presented here extend previous research in aging and creative thinking by demonstrating that creativity is preserved in normal aging yet relies on a different functional network architecture than has been reported in young. These functional brain changes may reflect a cognitive shift towards greater reliance on semantic knowledge that has important implications for understanding and predicting functional capacity in later life. Future investigations of creative ability in aging may provide a novel lens through which we can better understand the implications of creative thought in aspects of successful aging including maintenance of an agentic self-view, independence and a positive personal self-view that is key for mental health (Duhamel, 2016; Runco, 2004).

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CHAPTER ONE

Introduction

Defining Creativity

Creativity is a quintessential and arguably unique human characteristic. It conjures forms of expression most commonly found in art galleries, architectural feats, concert halls, and science laboratories, but also in the small wonders of our everyday lives. Creative cognition is essential for economic and political advancement, and serves as the foundation for artistic, scientific, and technological innovations. Creative ability is a complex, multidimensional construct that is typically defined in terms of its end product, or the generation of novel and useful outcomes (Stein 1953; Sternberg and Lubart 1996; Runco and Jaeger 2012). Indeed, common conceptions of creativity often invoke the idea of ‘creative talents’, producing artistic outputs in the performing arts. Creativity is increasingly considered to hold vaulted status in the sciences, commerce, and in the millennial era of technological development.

Consistent with its oft-ascribed stature as a highpoint of human endeavor, creativity has been associated with real world success across multiple functional domains. Creative ability has been shown to predict success in conflict situations (De Dreu, Nijstad, & van Knippenberg, 2008) as well as academic performance (Furnham & Bachtiar, 2008) and appears to be an adaptive trait for success across multiple aspects of functioning in everyday life including self-expression, adaptability, problem solving, and health (Runco, 2004). A longitudinal study of creative ability in school-aged children, for example, has found that top performers in divergent thinking continued on to lead successful careers in both the arts and sciences (Plucker, 1999; Torrance, 1988).

Most research investigating associations between creative cognition and human achievement, including those referenced above, have stepped away from the idea of creativity as a domain specific capacity (e.g. in the arts or sciences). Instead, creativity is considered to be a more domain general ability, typically operationalized as divergent thinking ability. Similarly, emerging research investigating the cognitive and neural bases of creativity almost universally assess creative cognitive ability as performance on a divergent thinking task. In keeping with this tradition, throughout the dissertation, the terms creativity, creative cognition, and creative ability are used interchangeably and operationalized here as performance on divergent thinking tasks. Next, we describe measures of divergent thinking and provide evidence for this approach as an assay of creative cognition.

Divergent thinking was first introduced as a construct to measure creativity by Guilford (1950) and advanced using ecologically valid modes of assessment, specifically open-ended tasks requiring novel idea generation. During these tasks, individuals generate ideas in response to verbal or figural prompts (Wallach and Kogan, 1965; Michael and Wright, 1989). In a typical verbal task (e.g. Alternate Uses Task), people are asked to generate unusual uses for common objects (Alternate Uses Task; e.g. bricks, knives, and newspapers), exemplars of common objects (Instances Task; e.g. objects that are loud, strong or round) or consequences of hypothetical events (Situations Task; e.g. what would happen if people went blind or no longer needed sleep). In a typical nonverbal task, people are asked to provide creative solutions to completing a provided stimulus (Incomplete Figures Task) and creative ways to use stimuli to create a figure (Circles and Squares Task and Creative Design Task).

Divergent thinking tasks are perhaps most analogous to fluency tasks which require individuals to produce as many exemplars as possible given a phonemic (the letter A), semantic

(grocery items) or other categorical cue. Both divergent thinking and fluency tasks require generative ability, or an endogenous drive to produce responses that are subsequently quantified as a metric of task performance and ultimately serve as a measure of cognitive ability. Unlike fluency tasks, divergent thinking tasks capture both the quantity and quality of the responses. Response quality on a divergent thinking task is typically analyzed along several dimensions including *originality* (i.e. how novel or rare the response is), *spontaneous flexibility* (the number of conceptual shifts between responses), *adaptive flexibility* (changing of strategies to produce responses), *ideational fluency* (i.e. speed of response production) and the ability to *produce transformations* (changing or modifying an object from its original state) (Guilford, 1967). Evidence supporting the ecological validity of divergent thinking as an assay of creativity has been demonstrated in recent work showing that divergent thinking predicts both the quantity of self-reported creative achievement (Jauk, Benedeck and Neubauer, 2014) as well as the quality of expert-rated creative performances on jazz improvisation ability (Beaty, Smeekens, Silvia, Hodges and Kane, 2013).

Dual Process Models of Creativity

Paralleling the dual definition of creativity i.e. the ability to produce ideas that are both novel and useful (Amabile and Tighe, 1985), research investigating the cognitive architecture of creativity has led to a dual process hypothesis, suggesting that creative cognition unfolds over generative and evaluative phases. The *generation stage* begins with crudely formed ideas and associations. This formative stage is then followed by an evaluative phase wherein ideas are tested for novelty and utility (Basadur et al., 1982; Fink et al., 1992). Theoretical accounts of creative cognition, specifically the production of novel ideas through the generative and evaluative stages, assume that novel ideas rely on meaningful variations or recombinations of

available knowledge (Koestler, 1964). Highly novel and creative ideas are conceptualized as a recombination of unrelated concepts (Mednick, 1962).

The *associative theory* is one of the most influential models of creative cognition (Mednick, 1962). This theory suggests that differences in individual levels of creativity can be explained by variations in the structural organization of concepts within semantic networks. Mednick described the process of creative thinking as “the forming of associative elements into new combinations which either meet specific requirements or are in some way useful” (1962, p.221). Mednick observed that whereas most people have rather steep associative hierarchies (i.e., a given stimulus evokes only highly related items in memory), creative people have flat associative hierarchies (i.e., a given stimulus evokes not just highly related but also remotely related items). Associative elements in this context are defined as those existing in an individual’s cognitive schema and encompass semantic and episodic memory processes. According to the associative theory, memory plays a significant role in both domain general (e.g. divergent thinking) and domain specific (e.g. performing arts) creative abilities, as both require engaging acquired knowledge to construct novel and useful solutions to open-ended problems. Recent behavioural evidence is consistent with this idea. Associative memory processes (Benedek et al., 2012; Silvia et al., 2013) including both semantic (Abraham & Bubic, 2015; Leon et al., 2014) as well as episodic memory (Addis, Musicaro & Schacter, 2016; Madore, Addis & Schacter, 2015) have been associated with creative cognition. Following the dual process hypothesis, memory and associative processes play an important role in *creative idea generation*.

However, evidence suggests that creativity engages additional cognitive processes beyond the domain of memory. Despite the importance of memory in facilitating creativity, substantial

evidence also suggests that it can also be a limiting factor in idea production by imposing functional fixedness (Duckner, 1945; Osman, 2008; Chrysikou and Weisberg, 2005; Ward et al., 2005). For example, deficits on a commonly reported divergent thinking task, the Alternate Uses Task, have been attributed to an inability to move beyond salient conceptual knowledge (Beaty and Silvia, 2012; Chrysikou et al., 2016; Gilhooly et al., 2007). Executive control may help to overcome the rigidity imposed by anchoring creative cognition to mnemonic representations. Control processes such as response inhibition (Benedek et al., 2012), controlled memory retrieval (Benedek et al., 2012; Silvia et al., 2013) and conceptual category switching (Finke et al., 1992; Nusbaum & Silvia, 2012) have been associated with better performance on tasks of creative cognition, presumably by enabling creative thought processes to monitor, evaluate and ultimately overcome the gravity, or ideational inflexibility, imposed by prior knowledge. Specifically, executive control is seen to be necessary to support mental simulations necessary to continually evaluate and ultimately reconfigure existing knowledge representations to produce truly novel or original outputs (Benedek et al., 2017). Within the dual process model of creativity, executive control processes appear to support creativity by facilitating the second stage of creativity, *creative idea evaluation*. Taken together, both associative and executive control processes interact to facilitate both the generative and evaluative phases of creative cognition.

Other models of creativity have proposed a similar dual-process approach. Basadur et al. (1982) proposed the notion of ideation-evaluation cycles. The authors distinguished between three major stages in the creative thinking process — problem finding, problem solving, and solution implementation — and suggested that ideation and evaluation are involved at each stage in varying degrees according to the domain. For instance, domains that emphasize problem finding have a high ratio of ideation to evaluation, whereas domains that emphasize solution

implementation show the opposite pattern. They propose that dispositional differences in the tendency to ideate vs. evaluate lead to differences in the domain best suited to an individual.

Similarly, Finke, Ward and Smith's (1992) 'Genoplore' model proposes that creative thinking may be divided into two overarching stages: Idea generation and exploration. These are further subdivided into discrete sub-stages with multiple operations occurring at each stage. For instance, generation can involve retrieval of items from memory, formation of associations between items, and synthesis and transformation of the resultant 'preinventive' structures. Exploration can involve identifying the attributes of these pre-inventive structures and considering their potential function in different contexts. Evidence for this model comes from findings suggesting that as people generate ideas, they appear to utilize exemplars from the same or a related domain. They then endow the new idea with many of the attributes of the previous exemplar. Another recent dual process theory of creative thinking, proposed by Nijstad, De Dreu, Rietzschel and Baas (2010), suggested that creativity can arise through two pathways: a flexibility pathway and a persistence pathway. Greater cognitive flexibility is viewed as generating more categories of ideas, as well as more frequent shifting between them, leading to greater originality. The persistence pathway represents the possibility of achieving creativity through effortful exploration of only a few categories or perspectives. This systematic search will lead to creative idea generation, after the readily-available solutions have been exhausted.

In summary, a common thread between these multiple theories of creativity is the presence of multiple stages or steps in the creative process. Completion of these stages likely involves multiple aspects of cognitive functioning including both associative or mnemonic abilities as well as executive control processes.

Neural Mechanisms of Creative Cognition

The involvement of memory and executive control processes in creativity is further supported by recent neuroimaging studies investigating the neural basis of creative cognition. Research in younger adults suggests that generation processes are associated with engagement of a functionally connected assembly of brain regions known as the default network which has been implicated in associative or elaborative processing (Beaty et al., 2018). The default network is composed of a set of midline, inferior parietal, lateral temporal, and prefrontal brain regions. This network was originally seen to be engaged in the absence of externally directed tasks (Gusnard and Raichle, 2001; Shulman et al., 1997), prompting its early label as a ‘task negative’ network. More recently, the default network is considered to be active and necessary to support a range of internally directed, or self-generated cognitive processes that typically involve associative or elaborative processing (Andrew-Hanna et al., 2014).

The network is also important for cognitive processes that rely on internal representational knowledge of oneself and the world, including future thinking (Schacter et al., 2012), perspective taking (Buckner et al., 2007), mental simulation (Andrews-Hanna et al., 2014; Zabelina and Andrews-Hanna, 2016), navigation, and theory of mind (Spreng et al., 2009). In the context of creativity, the default network has been investigated during divergent thinking tasks using both structural and functional neuroimaging methods (Fink et al., 2013, Jauk et al., 2015; Jung et al., 2010; Takeuchi et al., 2010; Benedek et al., 2014; Fink et al., 2014; Takeuchi et al., 2011). Specifically, the posterior cingulate cortex (Fransson et al., 2008) and the inferior parietal lobule (Abraham et al., 2012, Benedek et al., 2014, Fink et al., 2009, Fink et al., 2010) have been implicated in divergent thinking ability. Further, creative idea generation appears to engage a left-lateralized brain network, closely overlapping the default network, comprising of the inferior

parietal lobe, medial prefrontal cortex and posterior cingulate cortex (Abraham et al., 2012; Beaty et al., 2017; Gonen-Yaacovi et al., 2013; Fink et al., 2009).

Similarly, and consistent with the dual process accounts of creativity, neuroimaging studies have also associated activity in brain regions implicated in executive control with creative cognitive ability, specifically those in the fronto-parietal network (FPN). The dorsolateral prefrontal cortex has been implicated in studies of domain general creative cognition (Chen et al., 2017; Gonen-Yaacovi et al., 2013; Wu et al., 2015) as well as domain specific artistic abilities (Beaty, 2015; Pinho et al., 2014,2016). Further, the left inferior frontal gyrus has also been implicated in creative cognition (Gonen-Yaacovi et al., Vartanian et al., 2014). This region is typically activated during cognitive tasks that require controlled retrieval and monitoring processes, particularly when task demands require target response selection amongst competing alternatives (Zhang et al., 2004). Evaluative or monitoring processes are essential for the evaluative stages of creative cognition in the dual stage models reviewed above (e.g. Mednik, 1962).

A putative role for default and executive control regions in idea generation and evaluation suggests that these brain regions interact to support creative cognition. Consistent with this idea, a number of studies have now shown that default and executive control networks do indeed functionally interact to support performance across a range of creative cognition tasks including divergent thinking (Beaty et al., 2015; Mayseless et al., 2015), creative drawing (Ellamil et al., 2012), poetry generation (Liu et al., 2012) and musical improvisation (Pinho et al., 2016). Further, this pattern of network interactivity is observed both during task as well as at rest, suggesting the task-free, or intrinsic, network architecture of the brain may be a marker of creative ability (Beaty et al., 2014; 2018).

Finally, with respect to the neural network architecture underlying creative cognitive ability, a third, functional network, spatially interposed between default and frontal brain regions, has also been implicated in creative cognition. The salience network is considered to be a sub-component, along with the FPN, in the dual-component model of executive control (Dosenbach et al., 2007). In the context of creativity or divergent thinking ability, the salience network is thought to be important for facilitating the transition from the generation to evaluation phases of creative cognition, mediated by the default and executive control networks respectively (Beaty et al., 2015). In this interacting network account, the right anterior insula, a salience network node, is postulated to couple with the default network (specifically the posterior cingulate cortex) to facilitate idea generation, as well as the left dorsolateral prefrontal cortex to facilitate idea evaluation (Beaty et al., 2016).¹

Together, these investigations into the neural correlates of creative thought suggest default and executive control networks (FPN and salience) interact to support creative cognition. Reflecting this idea, a recent neural network model of creative thought suggests that functional coupling among default and executive control networks is a core neural substrate for creative thought (Beaty et al., 2015). Further, the extent of network interactivity appears to be modulated by the demand for cognitive control during creative task performance. Consistent with this idea, verbal creativity tasks requiring generation of semantically distant verbs (i.e., responses that are more remotely associated with target nouns) are associated with co-activation of control regions and the medial prefrontal cortex, a hub of the default network (Green et al., 2015).

Further evidence for cooperation between default and executive control regions to support creative processes comes from both domain-general (e.g. divergent thinking discussed

¹ While the executive control network within this literature largely overlaps with the fronto-parietal network (Vincent et al., 2008), throughout the dissertation, I will refer to the broader executive control network as being comprised of both fronto-parietal and salience networks.

earlier; Beaty et al., 2015; 2016) and domain specific studies of creativity. In domain-general forms of creativity, the creative quality of divergent thinking responses predicted increased functional coupling of the ventral anterior cingulate and the left angular gyrus, regions involved in cognitive control and self-generated thought, respectively (Beaty et al., 2015). The temporal pattern of connectivity between these networks, unfolding throughout the creative process, also appears to be an important neural substrate supporting distinct stages of creative thought. Coupling between default and salience networks occurs at the early generative stage of divergent thinking while this pattern of functional coupling shifts to default and executive control networks at the later evaluative stage of creativity (Beaty et al., 2015). Thus, different neural substrates implicated in executive control (i.e. salience network and FPN) exhibit varying patterns of connectivity with the default network based on the stage of creative thought.

Within the context of domain-specific creative abilities, such as musical improvisation, default and control networks also show increased functional coupling (Pinho et al., 2015). Improvising requires executive control processes to guide internally generated ideas while holding task goals online, necessary to support ongoing generation of creative thought as improvisation proceeds (Pinho et al., 2015). Default and executive control networks, specifically the posterior cingulate and dorsolateral prefrontal cortex, also exhibit coupling during the evaluation of visual ideas (Ellamil et al., 2012). Art students were asked to sketch ideas for a book cover and then evaluate their ideas while undergoing fMRI scanning. Idea generation was associated with widespread activity of default regions, whereas idea evaluation was associated with both default (e.g., medial prefrontal cortex and posterior cingulate cortex) and control network activity (e.g., dorsolateral prefrontal cortex and anterior cingulate cortex).

Taken together, these findings suggest that both default and executive control networks

are engaged and interact in the service of creative cognition. Interestingly, these neural network results closely align with dual component cognitive accounts of creativity involving both associative (mediated by default network regions) and evaluative processes (mediated by executive control regions). These data have significantly advanced our understanding of the neural network architecture associated with creative cognition. However, most of the work in this area has involved younger adults. Few studies have investigated how this neural substrate may be altered over the adult life course. The following sections of the Introduction now turn to a review of creativity in older adulthood and identify current research gaps that are the focus of the dissertation.

Aging and Creative Cognition

There is reason to suspect that both the cognitive and neural mechanisms supporting creativity may change from younger to older adulthood. It is now well established that aging is accompanied with declines in cognitive control processes (Park et al., 2001), which have been implicated in creative cognition in young (e.g. Addis et al., 2016). In contrast, more crystallized abilities including consolidated prior knowledge representations, or semantics, also implicated in creativity in young (e.g. Abraham & Bubic, 2015; Leon et al., 2014) are relatively preserved into old age (Verhaeghen, 2003; Park et al., 2001). This suggests that in typical aging, the architecture of cognition shifts from controlled to increasingly semanticized cognition (Spreng and Turner, in revision). Similarly, brain networks implicated in creative cognition also show normal age-related changes. Specifically, brain networks become increasingly dedifferentiated with reduced within-network and increased between-network connections (e.g. Chan et al., 2014; Geerligs et al., 2014). While there is strong evidence that both the cognitive and neural mechanisms implicated in creative cognition are altered with typical aging, surprisingly few

studies have investigated the impact of these changes on creativity in older adulthood. The behavioural evidence for age-related changes in creativity is briefly reviewed below.

Early work exploring changes in creativity with age was primarily founded upon two cognitive models (Levy and Langer, 1999). The *peak and decline model* (Lindauer, 1998) argued that creativity is a discrete ability that follows a course of growth into early adulthood followed by a period of decline beginning by the fourth or fifth decade of life. Several studies have provided support for this line of thinking, demonstrating that creativity, as measured by divergent thinking tasks, does indeed show decline beginning around middle adulthood (Alpaugh & Birren, 1977; Guilford, 1967; Palmiero et al., 2015; Jaquish and Ripple, 1981). A second *lifespan developmental model* (Sasser-Coen, 1993) suggests that it is not creativity per se that declines with age, but rather that creativity declines as a consequence of changing cognitive abilities. Support for this idea has emerged from several recent studies where visual working memory (Roskos-Ewoldsen et al., 2008) and processing speed (Foos and Boone, 2008, Leon et al., 2014) demands on the divergent thinking tasks were adjusted to be equivalent for both age-cohorts. This manipulation virtually eliminated age differences on the creative tasks. Evidence for age differences in creative cognition was also reported in an episodic study involving episodic induction (Madore et al., 2015). Older and younger participants were trained to mentally simulate past experiences, a technique which has been shown to enhance episodic memory performance (Madore & Schacter, 2014). This simulation training improved generative ability on a divergent thinking task, demonstrating the importance of episodic memory for creative cognition. While the magnitude of gains was not directly tested across age cohorts, these findings suggest that declining episodic memory ability in older age should have a relatively larger impact on creative ability in older adulthood. This line of investigation raises the intriguing possibility

that creativity relies on different cognitive capacities, and associated neural mechanisms, in older versus younger adults.

Age-related Brain Changes and Creative Cognition

There is mounting evidence for age-related changes within the specific brain networks implicated in creative cognition (default, fronto-parietal, and salience networks). The default network shows decreased within-network connectivity and reduced suppression during externally-directed tasks (Andrews-Hanna et al., 2014; Damoiseaux, 2017 for reviews). These changes occur in the context of increased functional coupling of the default network with other functional networks including executive control networks (Grady et al., 2014). Executive control networks also show decline in within-network and corresponding increases in between-network connectivity (Geerligs et al., 2012; 2014; Madhyastha and Grabowski, 2014; Sala-Llonch et al., 2012). Similar findings have been observed for the salience network with age-related decreases in within-network (Onoda et al., 2012; Geerligs et al., 2014) and greater between-network coupling (Siman-Tov et al., 2017).

These studies demonstrate that normal aging is associated with altered connectivity patterns in brain networks implicated in creative cognition (Beaty et al., 2016; 2018). While this generalized pattern of network dedifferentiation (i.e. increased between-network connectivity) has been typically associated with cognitive decline in later life, greater functional coupling between default and executive networks is associated with increased creativity in young adults (Beaty et al., 2015). This leads to the intriguing possibility that greater network coupling in older adulthood may support specific cognitive abilities, such as creativity, in later life. An emerging model of neurocognitive aging, the Default-Executive Coupling Hypothesis of Aging (DECHA, Turner and Spreng, 2015) provides preliminary support for this idea. We explore the DECHA in

more detail in the following section.

Default-Executive Coupling Hypothesis of Aging

A recent hypothesis has attempted to reconcile two of the most widely reported findings in neurocognitive aging: increased recruitment of prefrontal brain regions and reduced suppression of the default network (Turner and Spreng, 2015). The DECHA predicts that reduced modulation of lateral prefrontal activity and reduced default network suppression are functionally coupled and this pattern of altered brain activity represents a neural network marker of neurocognitive aging. Support for this idea comes from studies demonstrating that for older versus younger adults, increased recruitment of lateral prefrontal regions co-occurs with reduced default network suppression as cognitive control demands increase (see Turner and Spreng, 2015). These findings are interpreted as reflecting greater access to stored representational knowledge, mediated by default network regions and to support goal-directed task performance, mediated by executive control brain regions. Turner and Spreng (2015) hypothesize that successful suppression of default network regions with age, could in fact be detrimental for older adults when task demands are congruent with default-network function, including mnemonic demands to access prior knowledge and experiences.

As discussed above, interactivity between default and executive control networks (FPN and salience network) has been shown to be important for creativity in younger adults. In older adults, functional networks show greater coupling during rest (Geerligs et al., 2014; Spreng, Stevens, Viviano & Schacter, 2016) and during task (Turner and Spreng, 2015; Spreng, Stevens, Viviano & Schacter, 2016); however, the DECHA argues that this coupling may be beneficial when default network structures can be recruited to access stored representational knowledge to support task performance (Spreng et al., 2018). This connectivity pattern may support older adult

performance on tasks when access to prior knowledge, subserved by the default network, is congruent with task goals. Support for this idea in the context of creative cognition is hinted at by the episodic simulation research wherein engaging episodic memory processes, associated with default network functioning, led to higher levels of creativity in older adults (Madore et al., 2016). In this dissertation, we integrate prior research suggesting that greater coupling of default and executive networks is associated with creative cognition in young, and the DECHA model of neurocognitive aging to explore the network neuroscience of creativity in older adulthood.

Current Dissertation

The central research objective of the dissertation is to investigate differences in both task-driven and resting state neural networks associated with creative cognition in young and older adulthood. Investigations into the neural correlates of creativity in young adults show that functional connectivity between default and executive control systems is associated with creative ability (Beaty et al., 2015). Critically these networks show increased coupling with age (Damoiseaux, 2017) and this pattern may support performance on tasks when access to prior knowledge is congruent with task goals (Spreng et al., 2018). This leads to the prediction that greater default-executive coupling may support creative cognition in later life. However, there are no published investigations of the neural network basis of creative cognition in older adulthood. To address this gap, the current dissertation has two primary research aims and hypotheses.

The first aim is to investigate age-differences in functional brain networks implicated in creative thinking ability. To address this aim, older and younger adults completed a divergent thinking task, an assay of creative thought, while undergoing fMRI scanning. Functional connectivity patterns within and among three functional brain networks, implicated in creative

thought in young, were investigated and contrasted between young and typically-aging older adults. Previous evidence of age-related dedifferentiation of functional networks as well as the DECHA leads to two hypotheses: (i) greater default-executive control network connectivity during divergent thinking will be observed in older versus younger adults and (ii) this pattern of greater network coupling in older adults will be associated with better task performance.

The second aim of the dissertation is to examine whether intrinsic functional connectivity patterns (i.e. measured at rest) within and among these target brain networks predict creative ability, and how these brain-behaviour associations differ between older and younger adults. Here, in a separate cohort of younger and older adults, patterns of intrinsic functional connectivity were associated with performance on an offline measure of divergent thinking obtained outside of the scanner. As intrinsic functional connectivity between default and executive control networks has been associated with creative cognition in young, the core hypothesis for this aim is that intrinsic coupling of default and executive regions would be more robustly associated with creative cognition in older versus younger adults.

A third preliminary aim is to investigate the putative cognitive substrates of divergent thinking ability in younger and older adults. Given the equivocal nature of the evidence for age-differences in creativity, here data collected from aims one and two is leveraged to conduct a preliminary investigation of age-differences in the cognitive profiles of creative thought in younger and older adulthood. In addition to aiding with our interpretation of the findings from aims one and two, this preliminary aim will lay the groundwork for larger, individual difference investigations into the cognitive substrates of creative thought.

Overall, the studies included in the dissertation will provide the first investigations of age-differences in the neural network architecture of creative cognition. While there has been

little consensus in the field with respect to changes in creative cognition across the adult lifespan, recent evidence suggests that creativity may in fact be relatively preserved in later life. A novel model of neurocognitive aging, the DECHA, identifies a candidate neural network mechanism underlying the maintenance of creative cognition into older adulthood, however this possibility has yet to be investigated. Given the importance of creativity to real world problem-solving and the maintenance of functional independence, of critical importance in later life, characterizing the neural basis of creative cognition may provide new insights and open novel avenues of inquiry into the neural and cognitive determinants of successful aging.

CHAPTER TWO

Study One: Functional Brain Networks Associated with Divergent Thinking in Older and Younger Adults

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). Further, creativity performance has been positively associated with academic success as well as conflict resolution abilities (Furnham & Bachtar, 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; Lee and Puckett, 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 (Roscos-Ewoldson, Black and McCown, 2008; Palmiero, et al 2014; Addis, et al,

2016; Foos and Boone, 2008). It has been hypothesized that creative ability is preserved in older adults as consequence of preserved crystallized intelligence (Palmiero, Giacomo and Passafium, 2014) and reported differences could be due to differences in other cognitive abilities, such as working memory (Roscos-Ewoldson, Black and McCown, 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* 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 to investigate changes in these networks between younger and older adults.

While 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) as well as increased between-network connectivity (e.g. Geerligs et al., 2015). While 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 DECHA (Turner & Spreng, 2015) suggests that reduced modulation of the lateral prefrontal cortex (PFC) and attenuated suppression of default network are functionally coupled in aging. This shift towards 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 & Spreng, 2015; Spreng et al., 2018; Spreng & Turner, *in revision*). 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. Here we explore this possibility directly.

Given the overlap in patterns of functional connectivity between the divergent thinking network in young (Beaty, 2015; 2018) and DECHA in older adults (Turner & Spreng, 2015), we focused our analyses on examining activity and interactivity within 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. Next, 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 & Spreng, 2015), default-executive coupling would be greater for older adults than young adults during the divergent thinking task. Lastly, 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. Further, 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.

Methods

Participants.

The original sample consisted of 30 young adults and 30 older adults recruited at University of North Carolina at Greensboro (UNCG). 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 two others 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 over represented 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 CNS-affecting drugs or neurological disease. All participants completed the Mini Mental State Exam (MMSE)

and had scores above 25 to be eligible for the current study. All participants provided written informed consent. The study was performed in accordance with the guidelines and regulations of UNCG's Institutional Review Board, who approved the study methods.

Procedure.

Participants completed a divergent thinking task during fMRI scanning. This task paradigm has been described previously (Beaty et al., 2015; 2018) and the younger adult sample reported here was included in these earlier reports. An alternate uses task served as the divergent thinking condition (*Create*) and an object characteristics task (*Object*), provided the control condition. The alternate uses 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 (see also Fink et al., 2009; 2010). We contrasted these two experimental conditions in our analyses and refer 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 non-interest (e.g. visualization). Participants received thorough training on both tasks and completed several practice trials prior to scanning.

The task paradigm consisted of a jittered fixation cross (four to six seconds), a cue indicating the upcoming condition ("create" or "object"; three 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 (five seconds); an experimenter logged responses for subsequent coding (Beaty et al., 2017, 2018; Benedek, Beaty

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, 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, 2018). Figure 2.1 provides a visual representation of the task paradigm.

Responses provided by the participants in the response period were rated by three independent raters blind to participants age, using the subjective scoring method (Benedek, Mühlmann, Jauk, & Neubauer, 2013; Christensen, Guilford, & Wilson, 1957; Silvia et al., 2008), an approach grounded in the consensual assessment technique of creativity assessment (Amabile, 1982). This approach has been popular for several decades in the study of creative products. It requires independent raters who are not necessarily experts in creativity, to rate products for creativity. This rating is based on the rater's tacit, personal meaning of creativity. Prior work has shown that raters have high consistency and agreement (Amabile, 1982; Baer, Kaufman, & Gentile, 2004; Kaufman, Gentile, & Baer, 2005; Kaufman, Lee, Baer, & Lee, 2007). The consensual assessment technique has worked in a wide range of contexts and samples, indicating that the subjective scores have sufficient validity (see Amabile, 1996).

The three raters were trained to score responses for creative quality, using a 1 (not at all creative) to 4 (very creative) scale. Training was provided in an independent session with the author of this dissertation, where raters practiced rating dummy responses in a group setting.

Ratings for examinee responses were then provided in a subsequent group session, with the writer present.

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. The interrater reliability between the three raters across all participants was $ICC = 0.52, 0.55, 0.61$. This level of moderate inter-rater reliability is consistent with previous reports and aligns with the overall literature employing this scoring method (Benedek et al., 2013)

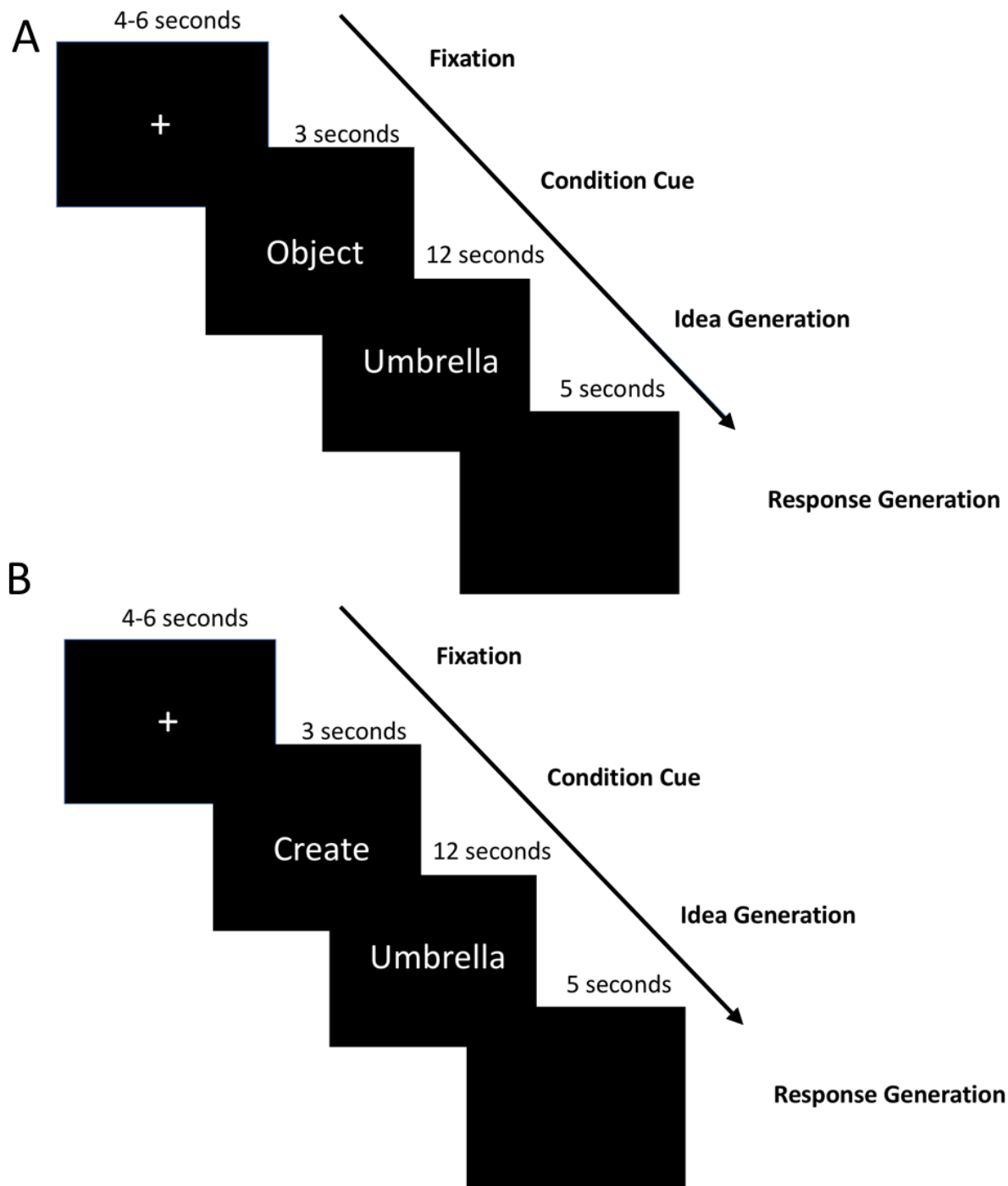


Figure 2.1. Visual representation of task paradigm used in study with a 4-6 second fixation cross, followed by condition cue (Panel A – *Object*; Panel B – *Create*). Following the condition cue, participants were provided with the name of the object for which they had 12 seconds to think of creative and novel uses (*Create* condition) or everyday common uses (*Object* condition). Following the idea generation period, they were asked to provide a verbal response (response generation period – 3 seconds) for their most creative use for the object.

fMRI data acquisition and connectivity pre-processing.

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 MP-RAGE was acquired following a standard acquisition protocol (TR=2350 ms, TE=2.26 ms, FOV=256x256, slice thickness=1mm, voxel size=1mm isotropic) as reported in previous work (Beaty et al., 2015, 2018). BOLD-sensitive T2*-weighted functional images were acquired using a single shot gradient-echo EPI pulse sequence (TR=2000ms, TE=30ms, flip angle=78°, 32 axial slices, 3.5×3.5×4.0mm, distance factor 0%, FoV=192×192mm, interleaved slice ordering) and corrected online for head motion. An average of 580 volumes were collected per participants and the first two 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. Following 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 (SPM) 12 package (Wellcome Institute of Cognitive Neurology, London). Additionally, the ARTifact Detection Toolbox (ART) 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 two mm was 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, 2012). This was used in addition to the six motion parameters (three translational and three rotational) obtained during motion realignment. For each participant, principal components associated with segmented white matter signal and cerebrospinal fluid signal (Behzadi et al.,

2007) were identified. 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).

Finally, functional volumes were co-registered and resliced to a voxel size of two mm³, normalized to the MNI template brain (Montreal Neurological Institute), and smoothed with an eight mm FWHM Gaussian kernel.

Network functional connectivity matrices.

Region of interest (ROI) nodes for the fronto-parietal, default, and salience (cingulo-opercular) networks were pre-defined using the network parcellation scheme by Gordon and colleagues (2014). The parcellation was derived using resting state data and has 333 ROI's, providing sufficient resolution to capture individual differences prominent in aging (Fornito et al., 2010), and to avoid compromising sensitivity and blurring regional boundaries when networks are decomposed into simpler parcellations (Power et al., 2011). Supplementary Figure 1 in Appendix A shows the overlay between the Gordon et al (2014) parcellation and another prominent parcellation by Yeo and colleagues (2011). For our purposes, we used 105 ROI's corresponding with default (41 nodes) and executive control networks (40 – salience network; 24 FPN).

The CONN toolbox (<http://www.nitrc.org/projects/conn>; Whitfield-Gabrieli & Neito-Castanon, 2012) was used to examine ROI-to-ROI functional connectivity. Mean percent signal change within each of the 105 ROI's was averaged within-condition and a cross correlation matrix was created for each ROI. Resulting Pearson-correlation coefficients for each ROI, within

condition, were then converted to a z score, using Fisher's transformation and are referred to as *functional connectivity* in analyses (*detailed below in Analytic Approach*).

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 greatly 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 ROI's falling within default and executive networks (fronto-parietal and salience networks). We next 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.

Functional connectivity during divergent thinking task performance.

First, we looked at functional connectivity between our apriori nodes **within each group**, for the *Create > Object* contrast. Statistically, we looked at the simple main effect of condition, using a weighted general linear model, with individual participant functional connectivity maps, defined by bivariate correlations (as per functional connectivity matrices) for all specified ROI's for *Create > Object*. Functional connectivity between all possible ROI pairs was tested using individual level t-tests, between each seed and target ROI pair, for this contrast. All results reported are corrected for multiple comparisons using an alpha level of 0.05, at the seed level.

Using this statistical approach, we report group level ROI-to-ROI connectivity findings for young and older adults for *Create > Object*.

Age differences in functional connectivity during divergent thinking.

Next, to examine age related differences in creative thought, we conducted **between group analyses**. Statistically, we used a second level general linear weighted model with group as a between-subject variable and examined group 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 was 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*]).

Age differences in associations between functional connectivity and creative ability.

We explored whether measures of connectivity among nodes of the default, fronto-parietal 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 apriori 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 (Beaty 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 creative ratings, we used Spearman rank correlations. Global efficiency values were extracted for the 105 default, FPN 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, then compared the correlations between groups.

Results

Behavioural Results

Neurocognitive.

To assess fluid intelligence, we used the series completion task from Cattell's Culture Fair Intelligence Test (Cattell & Cattell, 1961/2008). To assess crystallized intelligence, we administered two tests of vocabulary knowledge from the Educational Testing Services Kit of Factor-Referenced Cognitive Tasks: 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 (e.g. Park et al., 2001; Verhaeghen et al., 2002; Verhaeghen, 2003),

older adults performed lower than young on fluid intelligence [$M(\text{young})=8.07$, $SD=1.41$, $M(\text{old})=5.74$, $SD=1.14$, $t(48)=6.38$, $p < .001$] and higher on crystalized intelligence [Advanced Vocab: $M(\text{young})=9.67$, $SD=2.50$; $M(\text{old})=13.17$, $SD=2.66$, $t(48)= -4.81$, $p < .001$; Extended Vocab: $M(\text{young})=13.11$, $SD=2.71$; $M(\text{old})=17.48$, $SD=3.50$, $t(48)= -4.97$, $p < .001$]

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 ($M = 3.08$, $SD = 0.20$), $t(40) = 1.16$, $p = 0.25$.

Functional Connectivity during Divergent Thinking Task Performance

Young Adults.

Here, we looked at the simple main effect of group and associated ROI-to-ROI connectivity using a *Create > Object* contrast for young adults. During the *Create* condition, young adults showed greater positive functional connectivity between (1) the right cingulate gyrus (salience network) and the right middle frontal gyrus (FPN); (2) right superior frontal gyrus (default network) and the left anterior insula (salience network). In contrast, during the *Object* condition, young adults showed greater positive functional connectivity between nodes of the salience network, specifically between the left postcentral gyrus and, right cingulate gyrus and right supramarginal gyrus. These findings are visually depicted in Figure 2.2 and detailed in Table 2.1.

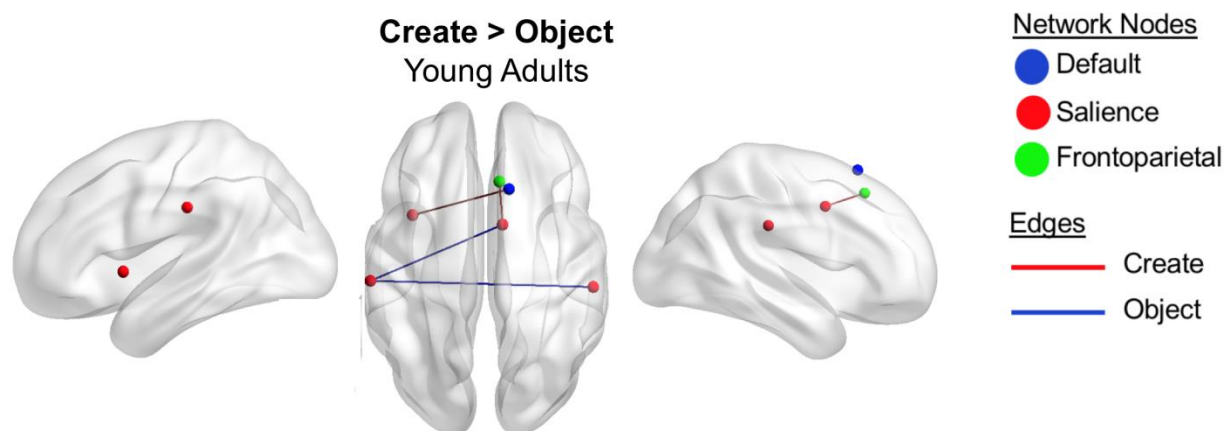


Figure 2.2. ROI-to-ROI results for a *Create* > *Object* contrast for young adults. Colour coded nodes include regions from the default network (DN), fronto-parietal network (FPN), and salience network (SN). The colour of the edges (connections between nodes) indicates the direction of the contrast. Red edges indicate ROI-to-ROI connectivity between nodes during the *Create* condition while blue edges indicate ROI-to-ROI connectivity during the *Object* condition in young adults. These results correspond to findings detailed in *Table 2.1*.

Table 2.1

ROI-to-ROI connectivity findings using Gordon et al., (2014) nodes for the default network (DN), salience network (SN) and fronto-parietal network (FPN) for young adults with a Create>Object Contrast, corresponding to results in Figure 2.2. Each row denotes significant connections between-network node and other network nodes and their network affiliation as defined by Gordon and colleagues (2014).

	<i>Network</i>	<i>Hem</i>	<i>Node</i>	<i>MNI Coordinates</i>			<i>T</i>	<i>p</i>	<i>Beta</i>
				<i>X</i>	<i>Y</i>	<i>Z</i>			
<i>Create</i>									
<i>Between-network Connectivity</i>									
<i>SN-FPN</i>									
Cingulate Gyrus	SN	R	185	8.6	4.2	40.1			
MFG	FPN	R	182	7	25.7	47.3	6.21	0.001	0.19
<i>DN-SN</i>									
SFG	DN	R	165	11.9	21.9	59.9			
Anterior Insula	SN	L	82	-37.3	8.9	-0.9	5.99	0.002	0.18
<i>Object</i>									
<i>Within-Network Connectivity</i>									
<i>SN-SN</i>									
Postcentral Gyrus	SN	L	105	-58.8	-23.9	31			
Cingulate Gyrus	SN	R	185	8.6	4.2	40.1	-5.82	0.003	0.16
Supramarginal Gyrus	SN	R	223	54.9	-27	29.6	-5.76	0.003	0.17

Note: DN – Default Network; FPN – Fronto-parietal network; Hem – Hemisphere; L – Left; MFG – Middle Frontal Gyrus; MNI – Montreal Neurological Institute; R – Right; SFG – Superior Frontal Gyrus; SN – Salience Network.

Older Adults.

Here, we looked at the simple main effect of group and associated ROI-to-ROI connectivity using a *Create>Object* contrast for older adults.

During the *Create* condition, older adults had significant positive functional connectivity both within-network and between-network. Specifically, there was significant positive functional connectivity between nodes of the default network including between (1) left medial superior PFC and right ventromedial prefrontal cortex (vmPFC) and, (2) left middle temporal gyrus and left vmPFC.

Older adults also had significant positive functional connectivity between-networks which corresponded to between default and executive coupling (default network and FPN, default network and salience network), as well as coupling between executive subnetworks (FPN and salience network). The default network and FPN were connected via the following significant positive connections: (1) right vmPFC and, left intraparietal sulcus and right inferior frontal gyrus; (2) right middle temporal gyrus and left middle frontal gyrus. The default and salience networks were connected via the following significant positive connections: (1) right superior temporal gyrus and, left precentral gyrus, left superior insula, left anterior insula (2) left post central gyrus and, left middle temporal gyrus and left angular gyrus and (3) left angular gyrus and left posterior insula.

During the *Object* condition, older adults had significant positive functional connectivity between-networks. Specifically, this was noted between the (1) default network and salience network and, between (2) FPN and salience network. The default and salience networks were connected by positive functional connectivity between the right medial superior frontal gyrus and

left postcentral gyrus. The FPN and salience network were connected by positive functional connectivity between the right superior frontal gyrus and left precentral gyrus. These findings are visually displayed in Figure 2.3 and detailed in Table 2.2.

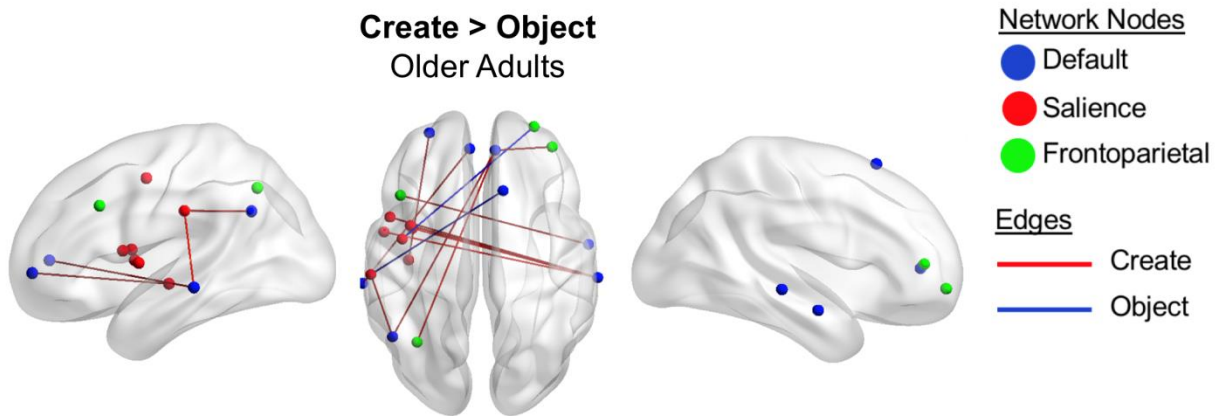


Figure 2.3. ROI-to-ROI results for a *Create* > *Object* contrast for older adults. Colour coded nodes include regions from the default network (DN), fronto-parietal network (FPN) and salience network (SN). The colours of the edges (connections between nodes) indicate the direction of the contrast. Red edges indicate ROI-to-ROI connectivity between nodes during the *Create* condition while blue edges indicate ROI-to-ROI connectivity during the *Object* condition in young adults. These results correspond to findings detailed in *Table 2.2*.

Table 2.2

ROI-to-ROI connectivity findings using Gordon et al., (2014) nodes for the default network (DN), salience network (SN) and fronto-parietal network (FPN) for older adults with a Create>Object Contrast, corresponding to results in Figure 2.3. Each row denotes significant connections between-network node and other network nodes and their network affiliation as defined by Gordon and colleagues (2014).

		<i>Network</i>	<i>Hem</i>	<i>Node</i>	<i>MNI Coordinates</i>			<i>T</i>	<i>p</i>	<i>Beta</i>
					<i>X</i>	<i>Y</i>	<i>Z</i>			
<i>Create</i>										
<i>Within-Network Connectivity</i>										
<i>DN-DN</i>										
AG		DN	L	6	-47.2	-58	30.8			
	vmPFC	DN	R	184	7.7	44.1	5.5	3.88	0.03	0.18
MTG		DN	L	126	-63.2	-28.7	-7.2			
	vmPFC	DN	L	152	-6	44.9	6.3	3.82	0.04	0.16
<i>Between-network Connectivity</i>										
<i>DN-FPN</i>										
vmPFC		DN	R	184	7.7	44.1	5.5			
	IPS	FPN	L	96	-34.1	61	42.4	3.66	0.005	0.18
	IFG	FPN	R	168	38.1	45.9	7.7	4.46	0.008	0.18
MTG		DN	R	290	57.5	-7.4	-16.4			
	MFG	FPN	L	108	-43	19.4	33.5	4.56	0.013	0.16
<i>DN-SN</i>										
STG		DN	R	225	62.5	-25.6	-5.5			
	Precentral Gyrus	SN	L	112	-48.6	7.5	11.1	4.21	0.03	0.13
	Superior Insula	SN	L	76	-37.7	2.9	11.7	3.87	0.03	0.11
	Precentral Gyrus	SN	L	111	-51.8	-0.6	5	3.53	0.03	0.13

	Anterior Insula	SN	L	81	-36.6	1.4	6.4	3.33	0.03	0.13
Medial SFG		DN	L	114	-27.5	53.6	0			
	Posterior Insula	SN	L	71	-38.7	-16	-5.3	5.17	0.003	0.19
Postcentral Gyrus		SN	L	105	-58.8	-23.9	31			
	MTG	DN	L	126	-63.2	-28.7	-7.2	2.88	0.03	0.16
	AG	DN	L	6	-47.2	-58	30.8	3.88	0.03	0.16
Object Between-network Connectivity DN-SN										
Medial SFG		DN	R	165	11.9	21.9	59.9			
	Postcentral Gyrus	SN	L	105	-58.8	-23.9	31	-4.37	0.02	0.16
FPN-SN										
SFG		FPN	R	277	28.4	57	-5.1			
	Precentral Gyrus	SN	L	40	-42.1	-4.5	47.3	-3.76	0.03	0.16

Note: AG – Angular Gyrus; DN – Default Network; FPN – Fronto-parietal network; Hem – Hemisphere; IFG – Inferior Frontal Gyrus; IPS – Intra Parietal Sulcus; MFG – Middle Frontal Gyrus; L – Left; MNI – Montreal Neurological Institute; MTG – Middle Temporal Gyrus; R – Right; SFG – Superior Frontal Gyrus; STG – Superior Temporal Gyrus; SN – Salience Network; vmPFC – Ventromedial Prefrontal Cortex

All participants.

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 Figure 2.4 and Table 2.3, where results are organized by within-network and between-network interactions.

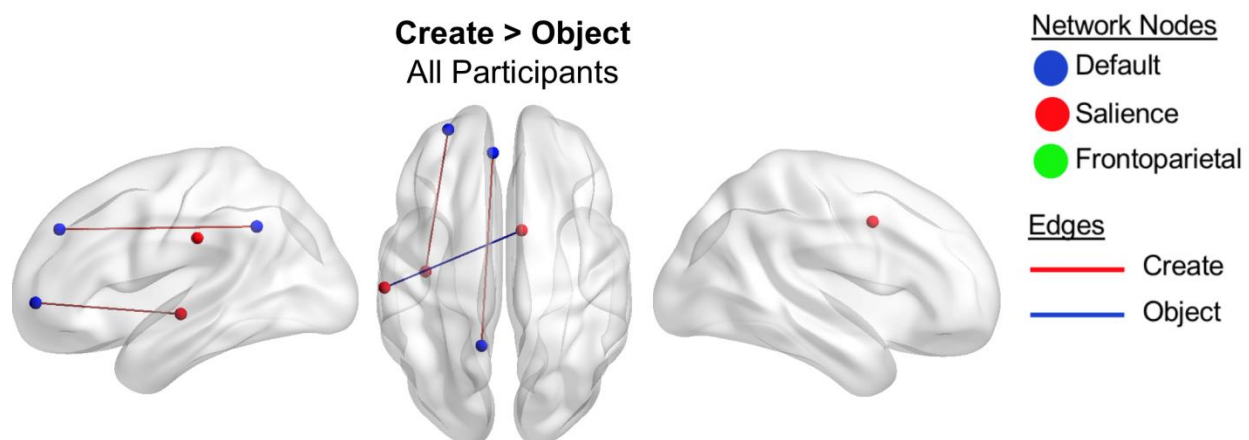


Figure 2.4. ROI-to-ROI results for a *Create* > *Object* contrast for all participants. Colour coded nodes include regions from the default network (DN), fronto-parietal network (FPN) and salience network (SN). The colour of the edges (connections between nodes) indicate the direction of the contrast. Red edges indicate ROI-to-ROI connectivity between nodes during the *Create* condition while blue edges indicate ROI-to-ROI connectivity during the *Object* condition in all participants. These results correspond to findings detailed in Table 2.3.

Table 2.3

ROI-to-ROI connectivity findings using Gordon et al., (2014) nodes for the default network (DN), salience network (SN) and fronto-parietal network (FPN) for all participants with a Create>Object Contrast, corresponding to results in Figure 2.4. Each row denotes significant connections between-network node and other network nodes and their network affiliation.

<i>Network</i>		<i>Hem</i>	<i>Node</i>	<i>MNI Coordinates</i>			<i>T</i>	<i>p</i>	
				<i>X</i>	<i>Y</i>	<i>Z</i>			
<i>Create</i> <i>Within Network Connectivity</i> <i>DN-DN</i>									
PCC		DN	L	1	-11.2	-52.4	36.5		
	dmPFC	DN	L	25	-5.6	42.2	35.1	4.49	0.034
<i>DN-SN</i>									
Frontal Pole		DN	L	114	-27.5	53.6	0	4.83	0.034
	Insula	SN	L	71	-38.7	-16	-5.3		
<i>Object</i> <i>Within Network Connectivity</i> <i>SN-SN</i>									
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

Note: dmPFC – dorsomedial Prefrontal Cortex; DN – Default Network; FPN – Fronto-parietal network; Hem – Hemisphere; L – Left; MNI – Montreal Neurological Institute; PCC – Posterior Cingulate Cortex; R - Right; SN – Salience Network.

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 $p = 0.05$, FDR corrected at the seed level (see Table 2.1 and Table 2.2). Hence, between-group differences in connectivity evaluated at the second level, reflect positive connectivity between nodes for young and older adults respectively. 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, compared to older adults, between default and salience network nodes (Figure 2.5A). Specifically, this was noted between left post central gyrus (salience network) and right superior frontal gyrus (default network).

Older adults showed greater positive functional connectivity during divergent thinking both within and between-networks (warm colours, Figure 2.5.A).

Within-network positive functional connectivity within the salience network was observed between (1) left post central gyrus and, left supramarginal gyrus, left anterior insula, left rolandic operculum, left precentral gyrus, right middle anterior cingulate cortex and right post central gyrus. Within-network positive functional connectivity within the default network was observed between left middle temporal gyrus and left vmPFC.

Older adults also showed greater between-network functional connectivity. First, older adults had greater between-network coupling between default and both executive control networks; FPN and SN. Specifically, the left angular gyrus had significant positive functional connectivity with the right inferior frontal gyrus and left post central gyrus. There was additional between-network positive functional connectivity between key nodes of the default and salience network specifically, between (1) between left precentral gyrus and right vmPFC; (2) left post central gyrus and, bilateral posterior cingulate cortex, left angular gyrus and left middle temporal gyrus and (3) left inferior temporal gyrus and, right anterior insula and left post central gyrus. These findings are visually depicted in Figure 2.5 and also detailed in Table 2.4, where results are organized by within-network and between-network interactions.

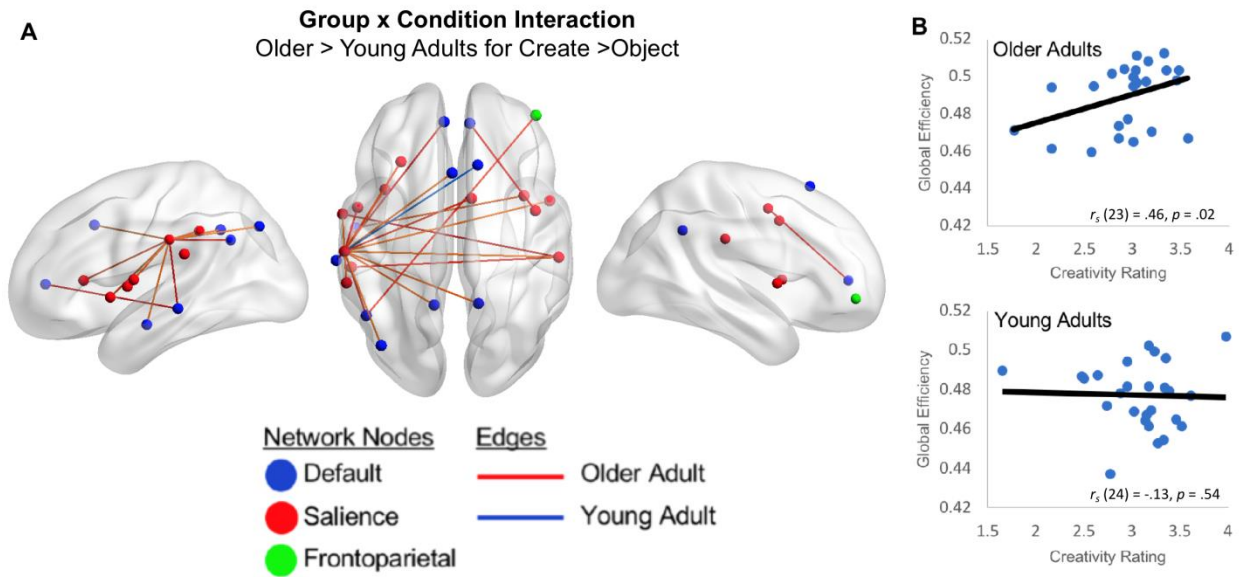


Figure 2.5. (Panel A) Age by Condition Interaction of ROI-to-ROI connectivity between nodes from the default network (DN), fronto-parietal network (FPN) and salience network (SN). Nodes are colour coded by network affiliation. A within-subject condition contrast was conducted at the first level using a *Create* > *Object* contrast. Next, a between-groups analysis was conducted to look at ROI-to-ROI functional connectivity differences between young and older adults. Red edges indicate ROI-to-ROI connectivity between nodes for *Create* > *Object* contrast in older adults. Blue edges indicate ROI-to-ROI connectivity between nodes during the *Create* > *Object* contrast in young adults. (Panel B) Scatter plots depicting the correlation between creativity ratings and global efficiency of the divergent thinking network in young and older adults.

Table 2.4

ROI-to-ROI connectivity findings using Gordon et al., (2014) nodes for the default network (DN), salience network (SN) and fronto-parietal network (FPN), corresponding to results shown in Figure 2.5. ROI-to-ROI functional connectivity maps were first contrasted at the within-subject level using a Create>Object contrast. Next, between-subject analyses were conducted using an Old > Young contrast. Positive findings correspond to significant ROI-to-ROI connectivity for older adults for the Create > Object contrast, while negative findings correspond to significant ROI-to-ROI Connectivity for young adults during the Create > Object contrast. Each row denotes significant connections between-network node and other network nodes and their network affiliation.

	<i>Network</i>	<i>Hem</i>	<i>Node</i>	<i>MNI Coordinates</i>			<i>T</i>	<i>p</i>
				<i>X</i>	<i>Y</i>	<i>Z</i>		
Young Adults <i>Between-network Connectivity</i> <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
Older Adults <i>Within-Network Connectivity</i> <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	4.2	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									
	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
Older Adults <i>Between-network Connectivity</i> <i>DN-FPN-SN</i>									
AG		DN	L	6	-47.2	-58	30.8		
	IFG	FPN	R	240	42.8	48.3	-5.1	3.52	0.04
	Postcentral Gyrus	SN	L	105	-58.8	-23.9	31	4.26	0.004
<i>SN-DN</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
	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
Young Adults <i>Between-network Connectivity</i> SN-DN									
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 <i>Within-Network Connectivity</i> SN-SN									
	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	4.2	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	L	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	
Older Adults <i>Between-network Connectivity</i> <i>DN-FPN</i>									
AG	DN	L	6	-47.2	-58	30.8			
IFG	FPN	R	240	42.8	48.3	-5.1	3.52	0.04	
<i>SN-DN</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	
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

Note: AG – Angular Gyrus; dmPFC – dorsomedial Prefrontal Cortex; DN – Default Network; FPN – Fronto-parietal 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; SFG – Superior Frontal Gyrus; SMG – Supramarginal Gyrus; SN – Salience Network; vmPFC – ventromedial Prefrontal Cortex.

Age Differences in Associations Between Functional Connectivity and Creative Ability

Lastly, 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 ($r_s(23) = .46, p = .02, 95\% \text{ CI: } 0.06 - 0.77$) (Figure. 2.5B). This correlation was not significant in young adults ($r_s(24) = -.13, p = .54, 95\% \text{ CI: } -0.54 - 0.28$) (Figure. 2.5B). The correlation between global efficiency and creativity ratings in older adults was significantly greater than that observed in young adults ($z = 2.11, p = 0.03$).

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., 2017; Gonen-Yaacovi et al., 2013; Wu et al., 2015; Vartanian et al., 2014; Beaty et al., 2015, 2018). Next, 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 positive connectivity, when compared to young 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 than young adults. Taken together, these findings suggest that positive coupling between default and executive networks, associated with divergent thinking ability in young (e.g. Vartanian et al., 2018; Pinho et al., 2015; Elamil et al., 2012; Green et al., 2015), 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 positive functional connectivity between default and executive regions during divergent thinking in older adults, when compared to young adults. Divergent thinking-related nodes consisted of default network regions (vmPFC, posterior cingulate cortex, angular gyrus, middle temporal gyrus) and executive control regions (inferior frontal gyrus, precentral gyrus, postcentral gyrus, and inferior temporal gyrus). We also observed positive 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 (Vartanian et al., 2018; Beaty et al., 2014) and task based studies of creativity (Beaty et al., 2015; 2018) showing greater connectivity between core default regions (precuneus, posterior cingulate cortex), FPN 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 fronto-parietal 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), suggest 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 young (Beaty et al., 2014; Vartanian et al., 2018).

Second, default network coupling with left lateralized nodes, including middle temporal gyrus as well salience network regions, implicated in semantic control processing (Jefferies, 2013; Noonan et al., 2011), suggests that greater semantic control is necessary to retrieve weak semantic associations (Kreiger-Redwood et al., 2016) and ultimately evaluate and reconfigure these as necessary in the service of creative cognition. Further, 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 creative thought. However, it is important to note that previous findings in young, 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. While 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. While 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 and colleagues (2016) propose that creative thought involves similar cognitive and neural mechanisms as goal-directed tasks and that interplay between the default network and executive control regions subserve the sub-components 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 the reshaping of knowledge from memory to fit the current task goals (Jeffries, 2013; Lambon-Ralph et al., 2016).

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 & Schacter, 2012; Turner & 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, how accessing prior knowledge representations can support cognitive performance on tasks where these representations are consistent with task goals (Spreng et al., 2018).

Conclusions

These findings suggest that functional coupling of default and executive control regions support creative cognition in older adulthood. Despite equivalent behavioural performance with young adults, functional coupling between default and executive control regions was associated with creative cognition in older adults. We also show that the overall level of functional integration between the default and executive networks, as measured by global efficiency, was significantly related to creative ability, 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, work to generate a brain-based account of creative ability would serve to advance the development of interventions to foster creative cognition, towards the goal of sustaining functional capacity and independence in older adulthood.

While speculative, the finding that default-executive coupling is associated with creativity in older adulthood may hold translational potential as an avenue for future intervention research. Functional neuroimaging is increasingly used to inform neurorehabilitation research, with evidence from several sources suggesting that neural biomarkers can inform the design of more effective training programs (Adnan et al., 2017; Chen et al., 2011; Gallen et al., 2016). Training in creative thought presents a novel approach to shape default-executive coupling, which may in turn be leveraged to support cognitive function when prior knowledge is congruent with task goals. Although translational implications are outside the scope of the current investigation, we suggest that future research investigating the neural basis of creative thought 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 & Turner, *in revision*).

CHAPTER THREE

Study Two - Intrinsic Default – Executive Coupling of the Creative Aging Brain

Introduction

Creativity is commonly defined as the ability to produce something novel and useful (Stein, 1953). Creativity is critical for social and economic development, but also for almost all areas of daily living (Duhamel, 2016). Creativity has been measured using divergent thinking measures, since it was operationalized as a construct by Guilford (1950). Creativity is a predictor of academic and career success (Plucker, 1999; Torrance, 1988) and is positively associated with problem solving abilities (Furnham and Bachtiar, 2008). Positive associations between creativity and functional independence have been observed in older adulthood (Duhamel et al., 2016). Early work examining divergent thinking, a common measure of creativity, in older adulthood suggested a progressive decline in creative cognition commencing in middle age (Alpaugh and Birren, 1977; Jaquish and Ripple, 1984; Reese et al., 2001). However, this pattern of decline may also be explained by age-related declines in fluid cognitive abilities such working memory (Roskos-Ewoldson, Black and McCown, 2008) or processing speed (Foos and Boone, 2008) rather than reduced creative ability *per se*.

More recent findings have failed to identify an age-related decline in creativity (Roskos-Ewoldson et al., 2008; Palmeiro et al., 2014; Addis et al., 2016; Foos and Boone, 2008; Madore, Jing & Schacter, 2016). These studies observe similar levels of creativity between younger and older adults but speculate that the cognitive substrates of creativity may change with age. One hypothesis suggests that creative cognition becomes increasingly reliant on semantics or crystalized knowledge which is relatively preserved into older age (Palmeiro, Giacomo and Passafium, 2014). Consistent with this idea, older adult performance on a divergent

thinking task benefited from a pre-task episodic simulation exercise involving recollection of a personal past event (Madore et al., 2016). The authors interpreted this as reliance on mnemonic processes to support creativity in older adults.

In recent years the field of creativity neuroscience has focused on the neural substrates of creative cognition. The vast majority of reports have employed functional MRI methods to record brain activity in younger adult subjects during performance on measures of divergent thinking (Abraham, Beudt, Ott, & von Cramon, 2012; Cousijn et al., 2014; Fink, Grabner, Benedek, & Neubauer, 2006; Fink et al., 2009; Fink et al., 2010; Kleibeuker, Koolschijn, et al., 2013; Kleibeuker et al., 2017). The pattern of task-based brain activity associated with creative cognition in these studies closely overlaps two canonical functional brain networks, the default network and the fronto-parietal network (FPN).

The default network, including in part the inferior parietal lobe, posterior cingulate cortex and middle temporal gyrus, has been consistently implicated in divergent thinking (Gonen-Yaacovi, 2013), particularly in the early, generative phases of task performance (Beaty et al., 2015;2016). Regions of the FPN, including the right dorsolateral prefrontal cortex are hypothesized to be important for exerting cognitive control during the latter, idea evaluation phase (Wu et al., 2015; Chen et al., 2015, 2017; Beaty et al., 2015; Benedek et al., 2014). While executive control and default networks can demonstrate an antagonistic relationship during cognitive control tasks, recent work suggests that they positively couple during control tasks when access to prior knowledge is congruent with task goals (Spreng and Schacter, 2012; Spreng et al., 2014). Recent investigations of functional connectivity in young adults performing various creative tasks and domains reveal a pattern of default-executive coupling that was positively associated with task performance (Zabelina and Andrews-Hanna, 2016; Jung et al., 2013; Beaty

et al., 2016; Christoff et al., 2016; Green et al., 2015; Mayseless et al., 2015). While speculative, this pattern of functional coupling is consistent with behavioral evidence suggesting that access to prior knowledge, mediated by default network brain regions, can support creative cognition (Madore et al., 2015; 2016).

The salience network has also been shown to couple with the default and executive control networks during creative cognitive tasks (Beaty et al., 2015). The salience network has been implicated in the detection of behaviorally relevant stimuli and redirecting attentional resources to salient stimuli in one's external or internal milieu (Uddin, 2015). Two nodes of the salience network, the dorsal anterior cingulate cortex and anterior insula, are important for creative cognition. Interestingly, both FPN and salience network nodes are interconnected and have been postulated to form a broader executive control network (Dosenbach et al., 2007). During divergent thinking tasks, the default network shows dynamic coupling with the executive control network (salience and FPN) at different phases of creative thought (Beaty et al., 2015). In the early, generative phase coupling is increased between the default and salience networks. In the latter, evaluative phase of the task, default network coupling shifts from salience to FPN regions (Beaty et al., 2015). Recent work from our group observed a similar pattern of default-executive control coupling that was greater for older versus younger adults, despite equivalent performance on the divergent thinking task (Adnan et al., 2019). Here we extend beyond task activation paradigms to examine the relationship between creativity and the intrinsic functional architecture of the brain in older and younger adults.

Patterns of functional connectivity observed in the brain during the resting state may be shaped by the repeated entrainment of functional connections associated with cognitive processing (Aziz-Zadeh et al., 2013; Dietrich and Kanso, 2010; Stevens and Spreng, 2014; Wei

et al., 2014; Zhao et al., 2014). Resting state functional connectivity (RSFC) measures have been associated with numerous cognitive abilities and are increasingly investigated as putative neural markers for cognitive functioning in health and disease (Fox and Raichle, 2007). Consistent with this idea, creative thought has been associated with greater static and dynamic connectivity among hubs of the default and executive networks at rest (Sun et al., 2018; Zhu et al., 2017; Beaty et al., 2014; Beaty et al., 2018a). This connectivity pattern has also been positively associated with creative cognition outside the scanner (Beaty et al., 2018a). A similar pattern of network coupling has also been associated with the personality trait of ‘openness’, reflecting individual differences in one’s tendency to engage in imaginative and creative processes (Beaty et al., 2018b).

Our recent task-based findings suggest that greater coupling between default and executive control systems may support creative thought in older adulthood (Adnan et al., 2019). As discussed above, the pattern of functional connectivity we observed is consistent with a recent report suggesting that older adults show greater reliance on mnemonic processes, associated with default network functioning, during creative task performance (e.g. Madore et al., 2016). Similarly, engagement of executive control regions has been shown to be modulated by the level of complexity in creativity tasks (Beaty et al., 2015). As older adults are known to over-recruit executive control brain regions at lower levels of task demand (Reuter-Lorenz and Cappell et al., 2008), it follows that these patterns of greater default and executive network activity during creative cognition may be functionally coupled. This idea is consistent with the default-executive coupling hypothesis of aging (DECHA, Turner and Spreng, 2015). The DECHA suggests that functional connectivity between these two networks is a core feature of neurocognitive aging and may support cognitive performance when access to prior knowledge is

congruent with task goals (Spreng and Schacter, 2012; Spreng et al., 2018; Turner and Spreng, 2015). Enhanced default-executive coupling observed during a divergent thinking task would be consistent with the idea that access to prior knowledge may support creative thought in older adults (Madore et al., 2016; Palmeiro et al., 2014).

Whether this pattern of altered functional connectivity represents a task-specific alteration in brain networks implicated in creative thought or reflects a more enduring shift in the intrinsic connectivity of the brain in later life has yet to be investigated. Here we use resting state functional connectivity (RSFC) MRI to investigate whether patterns of RSFC within and among brain network implicated in creative cognition predict creativity measured outside of the scanner, and whether observed brain and behavioral associations differ by age. Consistent with the DECHA model, we predict that intrinsic coupling between regions of the default and executive control networks will be associated with better performance on a divergent thinking task and that this association would be more robust in older versus younger adults.

Methods

Participants

Young and older adults were recruited from the community and completed a comprehensive cognitive test battery and magnetic resonance image (MRI) scanning as part of a larger ongoing multi-site study at York University and Cornell University. 32 older adults were included in the current study from York University while 12 older adults were included from Cornell University, giving a final sample of 44 older adults (mean age = 70.03 years, $SD = 4.75$; 21 females). 18 young adults were included from York University while 4 young adults were included from Cornell University, giving a final sample of 22 younger adults (mean age: 24.76, $SD = 3.36$; 15 females) that were included in the current study. Of note, females were over represented in the final samples for both age groups, and slightly more so in the younger adult sample. There was

no difference in creativity between men ($M = 2.79$, $SD = 0.55$) and women ($M = 2.68$, $SD = 0.4$), $F(1, 62) = 0.37$, $p = 0.55$, and between younger ($M = 2.81$, $SD = 0.38$) and older ($M = 2.59$, $SD = 0.53$) adults, $F(1, 62) = 3.3$, $p = 0.07$. Furthermore, 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. Participants received monetary compensation for their time (equivalent to \$50 CAD/USD for the MRI scan and \$10 CAD/USD per hour). To be eligible for the study, participants had to be: a) between the ages of 18-35 (Young) or over age 60 (Old); b) right-handed; and c) a fluent English speaker. Exclusion criteria included any MRI contraindications and/or a history of neurological, neuropsychiatric, or cardiovascular disease. All participants provided informed consent consistent with procedures approved by the Institutional Review Boards of York University and Cornell University. All participants were cognitively normal based on self-report on intake and cognitive screen (MMSE > 26).

Previous work has shown that both creative ability (Feist, 1998; McCrae, 1987; Silvia, Nusbaum, Berg, Martin, & O'Connor, 2009) and default network engagement (Beaty et al., 2018b) are predicted by the 'Big-Five' personality trait of 'openness'. All participants completed both the divergent thinking measures and a comprehensive personality inventory, the Big Five Aspect Scales (BFAS) (Goldberg, 1992). A two-tailed t-test revealed that there was a significant difference in self-reported openness to experience between young ($M = 3.52$, $SD = 0.26$) and older ($M = 3.81$, $SD = 0.24$), $t(64) = -2.19$, $p = 0.032$, Cohen's $d = 1.16$ adults. Furthermore, openness to experience was significantly correlated with creative ratings across all participants [$r(62) = 0.26$, $p = 0.03$], in older adults [$r(42) = 0.39$, $p = 0.008$] and in young adults [$r(20) = 0.44$, $p = 0.04$]. Given prior work associating creativity and openness, and recent investigations

showing that intrinsic networks associated with creativity also co-vary with openness to experience (Beaty et al., 2018) we used BFAS-O as a control variable in all subsequent analyses.

Offline measures of creative ability.

The divergent thinking task was completed by all participants outside of the scanner and consisted of three paper-pencil alternate uses tasks (Kaufman et al., 2008). The alternate uses tasks required participants to generate creative uses for three common objects: a box, a rope and a knife. Participants had three minutes to verbally articulate as many responses as possible, which were recorded by the test administrator. After each task, participants were presented with their list of responses and asked to rank them for creative quality. Ranking permits the use of a top-scoring method wherein the originality score is based on the creativity evaluation of a predefined number of top-ideas (Silvia et al., 2008). The top-scoring method addresses confounds of fluency and “represents people’s best efforts, in their own judgment, and it thus represents people’s best level of performance when they are instructed to do their best (p. 71).” In addition, the top-scoring method has a psychometric benefit of standardizing the number of responses across participants.

Participant-identified top-ideas were then scored by three trained raters who were blind to participant’s age group (Benedek, Mühlmann, Jauk, & Neubauer, 2013; Christensen, Guilford, & Wilson, 1957; Silvia et al., 2008). The three raters were trained to score responses for creative quality, using a 1 (not at all creative) to 4 (very creative) scale. We applied the Top 3 scoring procedure (Silvia et al., 2008; Benedek et al., 2014) involving selection of the three most creative responses indicated by participant rankings and averaged across the three raters' scores. Overall creativity ratings were obtained by averaging ratings for each of the three common objects.

There was a moderate level of convergence between ratings provided by raters for the three tasks. The interrater reliability between the three raters was $ICC = 0.62, 0.59, 0.61$ for the tasks “box”, “rope” and “knife”. This level of moderate inter-rater reliability is consistent with previous reports and aligns with the overall literature employing this scoring method (Benedek et al., 2013). We also computed interrater reliability for responses generated by young and older adults. There was moderate interrater reliability observed between raters for older adults, [$ICC = 0.51, 0.57, 0.53$] and for young adults [$ICC = 0.56, 0.61, 0.59$] for the tasks “box”, “rope” and “knife”. There was no significant difference in creative ability as measured by average ratings between young ($M = 2.79, SD = 0.3$) and older ($M = 2.59, SD = 0.14$) adults, $t(42) = 1.39, p = 0.17$, Cohen’s $d = 0.85$. Thus, older adults provided similarly creative ideas as their younger counterparts.

RSFC Analyses

Multi-echo fMRI data acquisition and preprocessing.

Imaging data for participants recruited at Cornell University were acquired using 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. Imaging data for participants recruited at York University were acquired using a Siemens 3T Magnetom Tim Trio MRI scanner. All scanning protocols were carefully matched across sites.

Anatomical scans from the Cornell MRI Facility were acquired with a T1-weighted volumetric MRI magnetization prepared rapid gradient echo (repetition time (TR)=2530ms; echo time (TE)=3.44ms; flip angle (FA)=7°; 1.0mm isotropic voxels, 176 slices). Anatomical scans were acquired during one 5m25s run with 2x acceleration with sensitivity encoding. Anatomical

scans from the York University MRI Facility were acquired with a T1- weighted volumetric MRI magnetization prepared rapid gradient echo (TR= 900ms; TE=2.52ms; TI=900ms; FA=9°; 1.0mm isotropic voxels, 192 slices). Anatomical scans were acquired during one 4m26s run with 2x acceleration with generalized auto calibrating partially parallel acquisition (GRAPPA) encoding with an iPAT acceleration factor of 2. Structural data was corrected for non-uniform intensities, affine-registered to Montreal-Neurological Institute (MNI) atlas and skull-stripped using FSL.

Multi-echo fMRI was developed as a data acquisition sequence to facilitate removal of noise components from resting fMRI datasets (Kundu et al., 2012, 2013; Power et al., 2018). This acquisition method can lead to a four-fold improvement in the temporal signal-to-noise ratio in resting-state fMRI (Kundu et al., 2015) and has been found to effectively remove distance dependent motion confounds in RSFC analyses (Power, et al., 2018). The method relies on the acquisition of multiple echoes, allowing direct measurement of T2* relaxation rates. Blood oxygen level dependent (BOLD) signal can then be distinguished from non-BOLD noise on the basis of TE dependence. The multiple echo-times are recombined and analyzed using independent components analysis to remove noise components (such as those originating from white matter, CSF, movement). This method has shown to be successful in denoising BOLD signal of motion and physiological artifacts (Kundu et al., 2013; Kundu et al., 2012). Participants completed one 10m 6s resting-state multi-echo BOLD functional scans with eyes open, blinking and breathing normally in the dimly lit scanner bay. At Cornell University, resting-state functional scans were acquired using a multi-echo echo planar imaging (ME-EPI) sequence with online reconstruction (TR=3000ms; TE's=13.7, 30, 47ms; FA=83°; matrix size=72x72; field of view (FOV)=210mm; 46 axial slices; 3.0mm isotropic voxels]. Resting-state functional scans

were acquired with 2.5x acceleration with sensitivity encoding. At York University, resting-state functional scans were acquired using a multi-echo echo planar imaging (ME-EPI) sequence with online reconstruction (TR=3000ms; TE's=14, 30, 46 ms; FA=83°; matrix size=64x64; FOV=216mm; 43 axial slices; 3.4x3.4x3mm voxels]. Resting-state functional scans were acquired with 3x acceleration with GRAPPA encoding. Data were preprocessed with multi-echo independent components analysis (ME-ICA) version 2.5 (<https://afni.nimh.nih.gov/pub/dist/src/pkundu/meica.py>) and aligned to MNI space. ME-ICA processing was then run with the following options: -e 13, 30, 46, -b 15s; -no_skullstrip; -space = Qwarp_meanE+tlrc. Qwarp_meanE+tlrc represented an averaged MNI-space template of our younger and older adults. As we were interested in functional brain networks, smoothing was not applied as this has been shown to artificially affect the similarity of networks across subjects (Alakörkkö et al., 2017). Data were not further filtered as ME-ICA has shown to be successful in denoising BOLD signal of artifacts (Kundu et al., 2013; Kundu et al., 2012). Components identified as both noise and signal were visually inspected for further quality control. Accepted components identified as signal were compiled in a single 4D file to be used for further connectivity analyses.

RSFC matrices.

ROI's for the fronto-parietal, default, and salience networks were defined using the network parcellation scheme by Gordon and colleagues (2014). In total, we used 105 ROI's (40 – salience network; 41 default network; 24 FPN).

The CONN toolbox (<http://www.nitrc.org/projects/conn>; Whitfield-Gabrieli & Neito-Castanon, 2012) was used to examine ROI-to-ROI functional connectivity. The mean time series of voxels within each of the 105 ROI's were averaged across the resting-state run, and correlated with the average time series of all other ROI's. Resulting Pearson-correlation coefficients were

then fisher-to-z transformed and are referred to as *functional connectivity* in analyses (*detailed below in Analytic Approach*). Given that this was a multi-site study, we included scanner location as a nuisance regressor in all analyses.

Analysis Approach.

Within-group RSFC associated with creative ability.

First, we used a within-group approach to examine creativity associated patterns of RSFC among our networks of interest in young and older adults, while controlling for openness to experience and scanner site. Here, we examined within group patterns of connectivity (young and older adults) independently, and offline measures of creativity were used as a second level regressor of interest in both analyses. Functional connectivity between all possible ROI pairs was tested using individual level t-tests, between each seed and target ROI pair. Results were corrected for multiple comparisons using a false discovery rate threshold of 0.05, at the ROI level. For both groups, positive findings reflect patterns of ROI-to-ROI connectivity that positively correlate with creative ability, while negative findings indicate negative correlations with creative ability.

Between-group RSFC associated with creative ability.

Second, to examine age-related differences in creativity, we adopted a between group analysis. Here we contrasted group level maps of ROI-to-ROI functional connectivity correlated with offline measures of creativity, while controlling for openness to experience. This contrast was specified as *Older Adults > Young Adults*. Results were corrected for multiple comparisons using a false discovery rate threshold of 0.05, at the seed level. For this analysis, warm colours reflect patterns of positive functional connectivity that correlate with creative ability in older

adults; cool colours indicate patterns of positive functional connectivity that correlate with creative ability in young adults.

Results

Within-Group Patterns of Functional Connectivity Associated with Creative Cognition

We examined the patterns of intrinsic functional connectivity that were significantly predictive of creative ability in older and young adults. We also examined the overlap in patterns of functional connectivity predictive of creativity in young and older adults. In these analyses, we controlled for the personality trait openness to experience and scanner site.

Young Adults.

Young adults showed a distributed pattern of between-network functional connectivity that positively predicted divergent thinking performance outside of the scanner. Between-network connectivity predictive of creativity comprised of significant connections between (1) salience and FPN (left inferior frontal gyrus and, left middle anterior cingulate cortex and left anterior insula); (2) key nodes of the FPN and default networks (e.g. vmPFC, PCC, medial superior PFC); (3) default and salience network nodes.

Young adults also showed patterns of within-network connectivity, specifically between nodes of the salience network (left rolandic operculum and left anterior insula) and nodes of the default network (e.g. left vmPFC and right medial PFC). These findings are detailed in Table 3.1 and Figure 3.1.

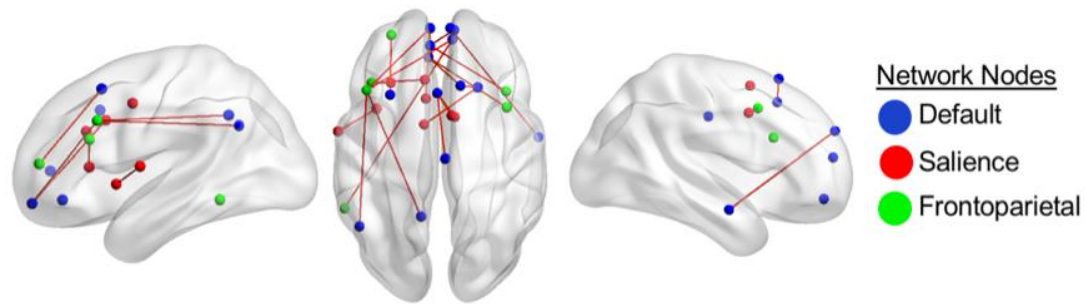


Figure 3.1. Resting state functional connectivity correlating with divergent thinking ability in young adults, after controlling for scanner site and personality (openness to experience). Color coded nodes include regions from the default network (DN), fronto-parietal network (FPN) and salience network (SN). The color of the edges denotes the direction of correlation between functional connectivity and divergent thinking ability. Only positive correlations between ROI-to-ROI functional connectivity and divergent thinking ability survived a seed-level FDR correction at an alpha level of 0.05. Results correspond to findings in Table 3.1.

Table 3.1

ROI-to-ROI connectivity positively correlating with divergent thinking ability in young adults, controlling for the personality trait, openness to experience and scanner site (corresponding to Figure 3.1).

		<i>Network</i>	<i>Hem</i>	<i>Node</i>	<i>MNI Coordinates</i>			<i>T</i>	<i>p</i>
					<i>X</i>	<i>Y</i>	<i>Z</i>		
Young Adults									
<i>Between Network Connectivity</i>									
<i>SN-FPN</i>									
IFG		FPN	L	109	-43	19.4	33.5		
	mACC	SN	L	28	-9	25.3	27.7	3.94	0.01
	Anterior Insula	SN	L	84	-28.8	23.7	8.4	3.37	0.03
<i>DN-FPN</i>									
vmPFC		DN	R	279	7.2	48.4	-10.1		
	ITG	FPN	L	9	-55.9	-47.7	-9.3	4.09	0.006
	MFG	FPN	L	108	-43	19.4	33.5	3.94	0.006
vMPFC		DN	L	117	-6.8	38.2	-9.4		
	DLPFC	FPN	R	328	38.9	9.6	42.7	3.41	0.04
IFG		FPN	R	276	38.6	18.8	25.5		
	vmPFC	DN	L	152	-6	44.9	6.3	3.91	0.013
MFG		FPN	L	108	-43	19.4	33.5		
	PCC	DN	L	1	-11.2	-52.4	36.5	4.27	0.004
	Medial Superior PFC	DN	L	6	-47.2	-58	30.8	4.21	0.004
	vmPFC	DN	L	116	-5.9	54.8	11.3	3.98	0.01
MFG		FPN	L	149	28.6	50.9	10.1		
	DLPFC	DN	L	156	-29.3	16.8	50.7	3.51	0.04
<i>DN-SN</i>									

Precentral Gyrus	SN		22	-9.4	-0.1	42.9			
medPFC	DN	R	200	21.9	21	46.2	3.49	0.04	
ACC	SN	L	27	-8.4	14.6	33.8			
vmPFC	DN	L	116	-5.9	54.8	-11.3	3.57	0.01	
PCC	DN	L	26	-1.7	-17.7	39.1			
SFG	SN	R	181	6.7	5	55.9	3.38	0.03	
mACC	DN	R	185	8.6	4.2	40.1	3.37	0.04	
PCC	DN	R	186	3	-19.6	37.9	3.61	0.03	
Within Network Connectivity									
<i>SN-SN</i>									
Rolandic Operculum	SN	L	101	-59.8	-4.1	8.8			
Anterior Insula	SN	L	82	-37.3	2.9	11.7	3.8	0.01	
<i>DN-DN</i>									
medPFC	DN	R	323	5.9	54.9	29.4			
MTG	DN	R	290	57.5	-7.4	-16.4	4.43	0.002	
vmPFC	DN	L	152	-6	44.9	6.3			
medPFC	DN	R	322	8.2	53.8	14	4.3	0.003 6	
vMPFC	DN	L	117	-6.8	38.2	-9.4			
DLPFC	DN	R	165	11.9	21.9	59.9	3.3	0.004	
medPFC	DN	R	200	21.9	21	46.2			
medFG	DN	R	165	11.9	21.9	59.9	3.81	0.01	

Note: AG – Angular Gyrus; DN - Default Network; DLPFC – Dorsolateral PFC; FPN - Fronto-parietal network; Hem = Hemisphere; IFG – Inferior Frontal Gyrus, ITG – Inferior Temporal Gyrus; L – Left; mACC – middle Anterior Cingulate Cortex; PCC – Posterior Cingulate Cortex; PFC – Prefrontal cortex; R – Right; SN - Salience Network; vmPFC – Ventromedial Prefrontal Cortex.

Older Adults.

For older adults, both within- and a more spatially distributed between- network connectivity profile was positively associated with creative task performance. Within-network connectivity was observed between (1) nodes of the salience network (insula, postcentral gyrus, frontal eye fields) and default network (right medial PFC and middle frontal gyrus); (2) nodes of the FPN (dorsolateral PFC, superior frontal gyrus, middle frontal gyrus, inferior parietal lobule) and default network (medial PFC, vmpFC, inferior temporal gyrus, posterior cingulate cortex). Widespread between-network connectivity was observed among (2) core nodes of default network (e.g. between angular gyrus and medial PFC). These findings are visually depicted in Figure 3.2 and detailed in Table 3.2.

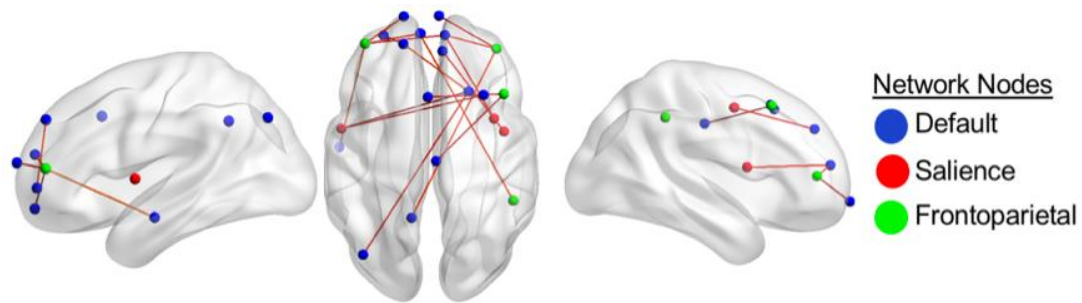


Figure 3.2. Resting state functional connectivity correlated with divergent thinking ability in older adults, after controlling for scanner site and personality (openness to experience). Color coded nodes include regions from the default network (DN), fronto-parietal network (FPN) and salience network (SN). The color of the edges denotes the direction of correlation between functional connectivity and divergent thinking ability. Only positive correlations between ROI-to-ROI functional connectivity and divergent thinking ability survived a seed-level FDR correction at an alpha level of 0.05. Results correspond to findings in Table 3.2.

Table 3.2

ROI-to-ROI connectivity positively correlating with divergent thinking ability in older adults, controlling for the personality trait, openness to experience, and scanner site (corresponding to Figure 3.2).

		<i>Network</i>	<i>Hem</i>	<i>Node</i>	<i>MNI Coordinates</i>			<i>T</i>	<i>p</i>
					<i>X</i>	<i>Y</i>	<i>Z</i>		
Older Adults									
<i>Between Network Connectivity</i>									
<i>DN-SN</i>									
medPFC	Superior Insula	DN	R	322	8.2	53.8		3.78	0.01
		SN	R	238	36.7	5.2	12.7		
medPFC	FEF	DN	R	325	6.8	44.5	34.8	3.74	0.02
		SN	R	198	42.5	-2.3	47.2		
Precentral Gyrus		SN	L	111	-51.8	-0.6	5		
	medPFC	DN	R	200	21.9	21	46.2	4.25	0.0035
	MFG	DN	R	326	30.6	18.9	48.7	4.1	0.0035
<i>FPN-DN</i>									
DLPFC	medPFC	FPN	L	7	-38.1	48.8	10.5	4.17	0.005
		DN	L	150	-6.5	54.7	18.1		
SFG		FPN	R	327	42.4	19.5	48.2	4.05	0.008
	PCC	DN	R	186	3	-19.6	37.9		
	PCC	DN	L	26	-1.7	-17.7	39.1	3.91	0.01
DLPFC	medPFC	FPN	L	7	-38.1	48.8	10.5	3.8	0.01
		DN	R	322	8.2	53.8	14		
MFG	medPFC	FPN	R	168	38.1	45.9	7.7	3.62	0.01
		DN	R	322	8.2	53.8	14		

DLPFC		FPN	L	7	-38.1	48.8	10.5		
	Frontal Pole	DN	L	151	-15.7	64.7	13.7	3.46	0.02
	vmPFC	DN	L	116	-5.9	54.8	-11.3	3.44	0.02
	ITG	DN	L	127	-53.1	-11.4	-16	2.98	0.04
MFG		FPN	R	168	38.1	45.9	7.7		
	vmPFC	DN	R	278	4.8	65.1	-7.1	4.08	0.007
	PCC	DN	R	1	-11.2	-52.4	36.5	3.36	0.03
medPFC		DN	L	150	-6.5	54.7	18.1		
	DLPFC	FPN	L	7	-38.1	48.8	10.5	3.66	0.03
	IPL	FPN	R	167	47.9	-42.5	41.5	3.4	0.03
<i>Within Network Connectivity</i>									
<i>DN-DN</i>									
AG		DN	L	94	-39.3	-73.9	38.3		
	medPFC	DN	R	200	21.9	21	46.2	3.52	0.04
		DN	L	145	-15.9	48.6	37.2		
	medPFC	DN	R	200	21.9	21	46.2	3.32	0.04
	medPFC	DN	L	114	-27.5	53.6	0	3.28	0.04

Note: FPN - Fronto-parietal Network; Hem – Hemisphere; IFG – Inferior Frontal Gyrus; L – Left; MNI – Montreal Neurological Institute DN – Default Network; mACC – middle Anterior Cingulate Cortex; medFG – medial Frontal Gyrus; medPFC – medial prefrontal cortex; MFG – Middle Frontal Gyrus; MTG – Middle Temporal Gyrus; PFC – Prefrontal Cortex; R – Right; SN – Salience Network SMG – Supramarginal Gyrus; SN – Salience Network; PCC – Posterior Cingulate Cortex; vmPFC – ventromedial prefrontal cortex

All Participants

Both younger and older adults have some overlap in patterns of intrinsic functional connectivity predictive of creativity. This was noted within-networks (within salience network) and between networks (between default and salience network nodes and between default and FPN nodes). There was also overlap in within-network connectivity between default network nodes. Table 3.3 and Figure 3.3 provide details for these nodes and associated connectivity results.

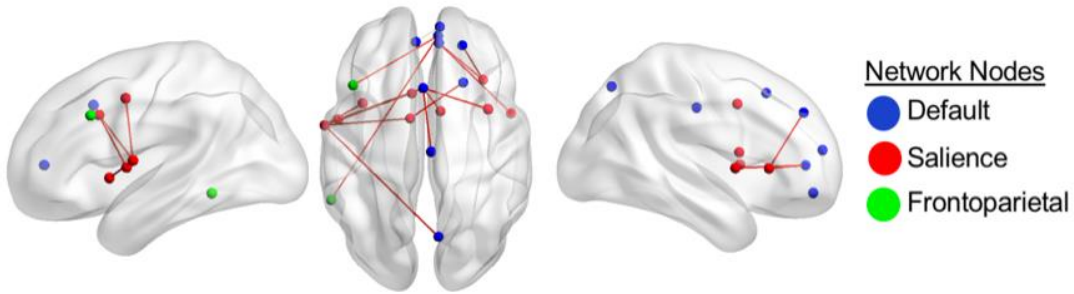


Figure 3.3. Overlap between resting state functional connectivity correlated with divergent thinking ability across young and older adults, after controlling for scanner site and personality (openness to experience). Color coded nodes include regions from the default network (DN), fronto-parietal network (FPN) and saliency network (SN). The color of the edges denotes the direction of correlation between functional connectivity and divergent thinking ability. Only positive correlations between ROI-to-ROI functional connectivity and divergent thinking ability survived a seed-level FDR correction at an alpha level of 0.05. Connections displayed are corrected a seed-level FDR correction at an alpha level of 0.05. Results correspond to findings in Table 3.3.

Table 3.3.

ROI-to-ROI connectivity positively correlated with divergent thinking ability and overlapping between young and older adults, after controlling for scanner site and personality (openness to experience) (corresponding to Figure 3.3).

	<i>Network</i>	<i>Hem</i>	<i>Node</i>	<i>MNI Coordinates</i>			<i>T</i>	<i>p</i>
				<i>X</i>	<i>Y</i>	<i>Z</i>		
<i>Between Network Connectivity</i>								
<i>DN-SN</i>								
Rolandic Operculum	SN	L	101	-59.8	-4.1	8.8		
AG	DN	R	257	7.4	-69.3	49.9	4	0.008
Insula	SN	L	248	33.7	22.6	3.7		
medPFC	DN	R	316	21.4	42.8	35.1	3.85	0.008
PCC	DN	L	26	-1.7	-17.7	39.1		
Superior Insula	SN	R	246	36.5	5.7	6	3.83	0.01
Precentral Gyrus	SN	L	111	-51.8	-0.6	5	3.58	0.03
Superior Insula	SN	R	238	36.7	5.2	12.7	3.54	0.04
vmPFC	DN	R	184	7.7	44.1	5.5		
Postcentral Gyrus	SN	R	274	50.1	3	3.9	3.7	0.02
Insula	SN	L	248	33.7	22.6	3.7	3.56	0.02
mACC	SN	L	22	-9.4	-0.1	42.9		
medPFC	DN	R	200	21.9	21	46.2	3.69	0.03
<i>DN-FPN</i>								
vmPFC	DN	R	279	7.2	48.4	-10.1		
ITG	FPN	L	9	-55.9	-47.7	-9.3	3.57	0.03
MFG	FPN	L	108	-43	19.4	33.5	3.46	0.03
<i>Between Network Connectivity</i>								
<i>DN-DN</i>								
vmPFC	DN	L	152	-6	44.9	6.3		

	medPFC	DN	R	322	8.2	53.8	14	2.53	0.04
PCC		DN	L	26	-1.7	-17.7	39.1		
	PCC	DN	R	186	3	-19.6	37.9	3.73	0.02
	mACC	DN	R	185	8.6	4.2	40.1	3.37	0.03
SN-SN									
Rolandic Operculum		SN	L	101	-59.8	-4.1	8.8		
	Anterior Insula	SN	L	82	-37.3	2.9	11.7	4.33	0.0033
	mACC	SN	L	22	-9.4	-0.1	42.9	3.62	0.03
	ACC	SN	L	27	-8.4	14.6	33.8	3.33	0.04

Note: FPN - Fronto-parietal Network; Hem – Hemisphere; IFG – Inferior Frontal Gyrus; L – Left; MNI – Montreal Neurological Institute DN – Default Network; mACC – middle Anterior Cingulate Cortex; medFG – medial Frontal Gyrus; medPFC – medial prefrontal cortex; MFG – Middle Frontal Gyrus; MTG – Middle Temporal Gyrus; PFC – Prefrontal Cortex; R – Right; SN – Salience Network SMG – Supramarginal Gyrus; SN – Salience Network; PCC – Posterior Cingulate Cortex; vmPFC – Ventromedial Prefrontal Cortex

Age Differences in Patterns of Functional Connectivity Associated with Creative Ability.

When the brain-behavior correlation maps for both age groups were directly contrasted, controlling for BFAS-O and scanner site, a pattern of greater within-network connectivity was associated with better divergent thinking performance for the younger cohort. Specifically, greater connectivity between default network nodes, including between (1) left vmPFC and, bilateral medial PFC, left inferior temporal gyrus, left frontal pole and left superior frontal gyrus (2) right middle temporal gyrus and right medial PFC and (3) right medial PFC and, left vmPFC and left medial PFC was associated with better divergent thinking ability for the younger participants. Young adults also had greater functional connectivity between (1) default and FPN nodes (e.g. between right vmPFC and left inferior temporal gyrus) and (2) default and salience network nodes (right posterior cingulate cortex and right anterior cingulate cortex) positively associated with divergent thinking ability

In older adults, greater between-network functional connectivity was associated with better divergent thinking ability. Greater between-network functional connectivity, associated with better outside scanner task performance, was also observed between all three networks. This was not observed in young adults, and included functional connectivity between right medial PFC, right intraparietal sulcus and left superior insula. There was also widespread functional connectivity between (1) default and FPN nodes in older adults that predicted creativity, including connections between (a) left middle temporal gyrus and right intraparietal sulcus; (2) FPN and salience networks nodes: (a) left middle frontal gyrus and right precentral gyrus; (b) left inferior parietal lobule and left precentral gyrus; (3) default and salience network nodes (e.g. right vmPFC and right superior insula).

There was also within network connectivity observed among (1) salience network nodes, between right superior insula and, right supramarginal gyrus, left middle frontal gyrus middle, left postcentral gyrus, left middle anterior cingulate cortex and right anterior cingulate cortex; (2) within the FPN, between right inferior frontal gyrus and, the left inferior temporal gyrus and left middle frontal gyrus; and (3) within the default network between right middle temporal gyrus and right medial PFC.

Table 3.4 and Figure 3.4 provide details for these nodes and associated connectivity results

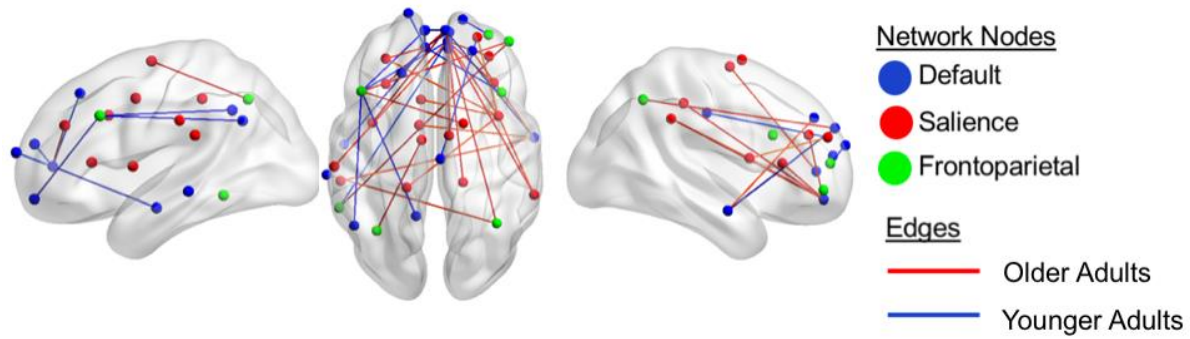


Figure 3.4. Group by behavior interaction for intrinsic connectivity correlated with divergent thinking, after controlling for scanner site and personality (openness to experience). The figure shows resting-state ROI-to-ROI functional connectivity that correlates with divergent thinking ability and is significantly different between young and older adults. Color coded nodes include regions from the default network (DN), fronto-parietal network (FPN) and salience network (SN). The color of the edges (connections between nodes) indicate the direction of the contrast. Red edges indicate greater connectivity between regions that are associated with divergent thinking in older adults, while blue edges indicate greater connectivity between regions that are associated with divergent thinking in young adults. Results correspond to findings in Table 3.4.

Table 3.4.

ROI-to-ROI connectivity correlating with divergent thinking ability contrasted between young and older adults (Older Adults > Young Adults), after controlling for the personality trait, openness to experience (BFAS-O) and scanner site.

<i>Network Hem Node</i>				<i>MNI Coordinates</i>			<i>T</i>	<i>p</i>	<i>Beta</i>
				<i>X</i>	<i>Y</i>	<i>Z</i>			
Young Adults									
<i>Between-Network Connectivity</i>									
<i>FPN-DN</i>									
<i>MFG</i>	FPN	L	108	-43	19.4	33.5			
PCC	DN	R	1	-11.2	-52.4	36.5	-4.34	0.0062	0.27
AG	DN	L	6	-47.2	-58	30.8	-4.04	0.017	0.22
medial FG	DN	L	116	-5.9	54.8	-11.3	-4.06	0.016	0.21
vmPFC	DN	R	279	7.2	48.4	-10.1	-3.46	0.016	0.19
vmPFC	DN	R	279	7.2	48.4	-10.1			
ITG	FPN	L	9	-55.9	-47.7	-9.3	-3.12	0.02	0.15
<i>Within-Network Connectivity</i>									
<i>DN-DN</i>									
vmPFC	DN	L	152	-6	44.9	6.3			
SFG	DN	R	322	8.2	53.8	14	-3.99	0.02	0.17
ITG	DN	L	127	-53.1	-11.4	-16	-3.51	0.03	0.17
SFG	DN	L	150	-6.5	54.7	18.1	-3.4	0.03	0.17
SFG	DN	L	151	-15.7	64.7	13.7	-3.37	0.03	0.18
SFG	DN	L	44	-19.5	30.1	45.5	-3.29	0.03	0.17
dorsomedial PFC	DN	R	323	5.9	54.9	29.4			
vmPFC	DN	R	279	7.2	48.4	-10.1	-3.76	0.01	0.14
SFG	DN	L	150	-6.5	54.7	18.1	-3.97	0.02	0.15
MTG	DN	R	290	57.5	-7.4	-16.4	-5.33	0.0002	0.21
Older adults									
<i>Between-Network Connectivity</i>									
<i>DN-FPN-SN</i>									

Medial PFC	DN	R	323	5.9	54.9	29.4				
IPS	FPN	R	261	35.7	-56.7	45.2	4.18	0.01	0.17	
Superior Insula	SN	L	81	-36.6	1.4	6.4	4.21	0.009	0.21	
<i>DN-SN</i>										
vmPFC	DN	R	279	7.2	48.4	-10.1				
TPJ	SN	R	180	16.2	-33.1	43.2	3.91	0.01	0.15	
Superior Insula	SN	R	249	34	24.4	10	3.91	0.01	0.15	
SMG	SN	R	219	57.5	-40.3	34.7	3.85	0.01	0.15	
MFG	SN	R	318	31.3	39.7	25.6	3.65	0.02	0.16	
Postcentral Gyrus	SN	L	105	-58.8	-23.9	31	3.41	0.01	0.18	
vmPFC	DN	L	152	-6	44.9	6.3				
MFG	SN	L	153	-28.8	38.3	28.2	3.6	0.03	0.15	
<i>Within-Network Connectivity</i>										
<i>FPN-FPN</i>										
IFG	FPN	R	240	42.8	48.3	-5.1				
ITG	FPN	L	9	-55.9	-47.7	-9.3	4.68	0.002	0.23	
MFG	FPN	L	108	-43	19.4	33.5	3.65	0.03	0.13	
<i>SN-SN</i>										
Superior Insula	SN	R	238	36.7	5.2	12.7	3.4	0.01	0.16	
SMG	SN	R	219	57.5	-40.3	34.7	3.33	0.01	0.16	
MFG	SN	L	153	-28.8	38.3	28.2	3.27	0.02	0.17	
mACC	SN	L	27	-8.4	14.6	33.8	3.16	0.02	0.17	

Note: AG- Angular Gyrus; DN – Default Network; FPN – Fronto-parietal Network; Hem – Hemisphere; IFG – Inferior Frontal Gyrus; IPS – Intra-parietal sulcus; ITG – Inferior Temporal Gyrus; L – Left; mACC – middle Anterior Cingulate Cortex ;MFG – Middle Frontal Gyrus; MNI – Montreal Neurological Institute; MTG – Middle Temporal Gyrus; PCC – Posterior Cingulate Cortex ; PFC – Prefrontal Cortex; R – Right; SMG – Supramarginal Gyrus ; TPJ – Temporo-parietal junction; SN – Salience Network; vmPFC – ventromedial prefrontal cortex.

Finally, as a further check on our approach to include the BFAS-O scores as a nuisance regressor in the regression model, we performed the above analysis on a subsample of the older adult participants (n=22 per age group) who were matched with young adults (n=22) on BFAS-O scores. These results are detailed in Appendix A and closely overlap the core findings described above (See Appendix A).

Discussion

We investigated whether creative ability, measured as performance on a divergent thinking task, was related to connectivity among the default, FPN and salience networks, and how patterns of RSFC associated with creativity differed between young and older adults. Both groups demonstrated equivalent performance on the divergent thinking task. However, unique intrinsic functional connectivity profiles were associated with creative ability in the two age groups. Older adults had a pattern greater functional connectivity between default and the broader executive control network, with connections observed between core nodes of the default, FPN, and salience networks that was associated with creativity. In contrast, while young adults showed default-executive coupling, it was limited to connectivity between default and sub networks of executive control (e.g. between default and salience network, default and FPN and, FPN and salience) rather than connectivity among all three networks.

Several studies of younger adults have investigated the relationship between neural network properties of the brain at rest and creative ability. Creative ability has been observed to be correlated with RSFC between the posterior cingulate cortex and medial PFC, core nodes of the default network (Takeuchi et al., 2012). Performance on a common measure of creative cognition, divergent thinking, has been also associated with greater connectivity within the default network, as well as connectivity between default and executive networks (Beaty et al.,

2018a). Importantly, this intrinsic network connectivity profile was able to predict creative ability in three independent participant samples, with the density of default to executive coupling identified as the most predictive feature. The current study replicated this pattern of intrinsic network connectivity associated with creativity in our young cohort. Significant connections were observed between hubs of the default network and salience network, as well as between the default network and the FPN, the default network and FPN and between FPN and salience networks. These findings add to the growing body of evidence suggesting that default to executive coupling is an important neural marker of creative thought in young adults.

Building from these young adult findings, here we show that the intrinsic neural substrate of creative thought is altered in older adulthood, with the most prevalent differences observed as greater coupling between the default and the broader executive control network, including nodes of both the FPN and salience sub-components. Consistent with a recently proposed neurocognitive aging model of aging, DECHA, (Turner and Spreng, 2015; Spreng et al., 2018) we interpret these results to suggest that older adults may access and manipulate information contained in their store of crystalized knowledge to generate creative responses. Based on the DECHA model, this greater default-executive coupling in typical aging may support cooperation between activated prior knowledge representations, mediated by default brain regions, and executive control processes necessary to leverage these representations to construct novel associations. Consistent with this idea, reliance on mnemonic processes during creative cognition has been recently been reported for older adults (Madore et al., 2016).

Our ability to detect creativity-RSFC associations during the resting state suggest that these age differences may be enduring and do not simply reflect changes in strategy or approach to the task. As the balance of cognitive resources shifts from controlled to crystalized capacities

across the lifespan (Park, 2001), we suggest that creativity becomes increasingly dependent on access to prior knowledge representations. With a lifetime of accumulated knowledge and experience, this engagement of prior knowledge in the service of goal-directed tasks reduces segregation between default and executive networks, with implications for multiple cognitive abilities. On tasks where prior knowledge is incongruent or distracting for task goals, greater default to executive coupling is associated with poorer task performance (e.g. Rieck et al., 2016; Spreng et al., 2018). Critically however, when access to prior knowledge is goal congruent, default to executive coupling is associated with better performance, at least in young (Beaty et al., 2016; Spreng et al., 2014). Here we provide evidence that this pattern also holds for older adults as greater default-executive coupling was more robustly predictive of creative cognition for older adults. We recently reported a similar pattern of default-executive coupling in the domain of autobiographical memory, with more semanticized recall associated with a pattern of greater default to executive coupling in older, but not younger adults (Spreng et al., 2018).

Our findings also highlight the role of vmPFC, a core default network node, in creative cognition in older adults. We observed that greater intrinsic bilateral coupling of vmPFC, as well as stronger between-network connectivity to executive control nodes, specifically within the salience network, was associated with creativity in our older participants. Our recent task findings also revealed greater coupling between vmPFC and the middle temporal gyrus, a region of the default network, during divergent thinking (Adnan et al., 2019). While speculative, the involvement of this region may hint at an alternative pathway supporting creative thinking in later life. The vmPFC is a core hub of the default network and comprises the anterior, self-referential subsystem of the network (Andrews-Hanna et al., 2010; Andrews-Hanna, 2012). Within-network connectivity of this region to medial temporal lobe subsystems as well as

between-network connections with executive control regions (such as the temporal-parietal junction, insula, middle frontal gyri, supramarginal gyrus) have been implicated in accessing and engaging autobiographical knowledge to support goal directed tasks (Andrews-Hanna et al., 2014). Consistent with this idea, the vmPFC has recently been posited as a gateway node, controlling access to consolidated, or more semanticized autobiographical memory (Bonnici & Maguire, 2018). Here we suggest that access to ones' store of consolidated, or crystalized experiential knowledge, reflected in the intrinsic connectivity patterns of the vmPFC, may be an important mechanism associated with creative cognition in later life.

Our findings suggest that intrinsic connectivity between the default and the executive control network (including both FPN and salience components) is associated with creative ability in later life. While default-executive coupling predicted divergent thinking ability in both young and older adults, the between-network connectivity pattern was more distributed and more robust for the older adult cohort. While these findings are broadly consistent with our recent task-based fMRI results (Adnan et al., 2019), these intrinsic connectivity data suggest that between-network coupling is not solely a task-specific neural response, but rather an entrained shift in the neural processes underlying creative thinking ability in later life. Moreover, we postulate that access to a comparatively preserved repertoire of stored personal knowledge and experiences in later life, reflected in greater within and between-network connectivity of the anterior default network, is associated with preserved creative thinking ability in older adulthood.

CHAPTER FOUR

Study Three: Cognitive Substrates of Divergent Thinking in Young and Older Adults

Introduction

Creativity is the ability to see the world in new ways. The creative individual is characterized by the ability to produce novel and useful ideas and to discern which ideas are appropriate and meaningful (Runco, 2003). Current models of creative thought conceptualize it as a dynamic, multi-stage process, characterized by interactions between stimulus- or salience-driven (i.e. bottom-up) attentional processes and intentional or goal driven (i.e. top-down) cognitive control. In the recent past, neuroscientific forays into creativity in younger adults have shown that large scale functional brain networks provide an essential neural substrate to support creative ability (Wu et al., 2015; Jung et al., 2013; Gonen-Yaacovi et al., 2013).

This work, mostly conducted with younger adults, has shown that the default network is involved in the productive process of idea generation while monitoring, or idea evaluation, processes are subserved by executive control systems including the fronto-parietal and salience networks (Beaty et al., 2016). During creative thought, these networks dynamically interact forming a connectivity profile that has been referred to as the ‘creativity network’ (Beaty et al., 2016; 2018). Studies one and two, demonstrated that this creativity network is altered in older adulthood, with greater coupling of default and executive control regions, as well as increased interactions between default and salience networks. While speculative, these results suggest that older adults may rely more on relatively preserved crystalized, or semantic knowledge representations, mediated by the default network, to generate or evaluate novel thoughts or actions.

Interestingly, recent neurocognitive theories also suggest that functional brain networks associated with fluid intelligence closely overlap the ‘creativity network’ (Hearne et al., 2016; Jung and Haier, 2007; Kenett et al., 2018). One prominent theory, the Parieto-Frontal Integration Theory of Intelligence, proposes frontal and parietal activation in relation to individual differences in intelligence (Jung and Haier, 2007).

Fluid intelligence abilities are known to be prominently impacted in the aging process (Horn and Cattell, 1967). In contrast, crystallized intelligence, the repertoire of stored knowledge about oneself and the world, remains stable and may even increase throughout the life span (Park et al., 2001). This shift from fluid to crystallized abilities, or the semanticization of cognition in later life, has been associated with the shifting network architecture of the brain towards greater coupling between default and executive regions (Spreng and Turner, in revision). Consistent with this idea, results from Studies one and two of the dissertation demonstrated that default-executive coupling, known to support creativity in young adults, is greater for older adults during divergent thinking (study one; Adnan et al., 2019). Further, greater intrinsic connectivity between these networks at rest was associated with creative ability in old but not younger adults (study two; Adnan et al., 2019b).

The central aim of the dissertation was to explore the neural network architecture of creative cognition in older adulthood. However, findings from the task and resting state neuroimaging studies, considered in the context of cognitive aging research showing a shifting balance of fluid versus crystallized intellectual capacities, suggested that the cognitive substrate of creativity may differ for younger and older adults. A definitive investigation of this hypothesis would require an individual differences study design, sufficiently powered to conduct the factor analytic studies necessary to map the cognitive correlates of divergent thinking. However, as all

of the participants in the resting state investigation (study two; Adnan et al., 2019b) completed tests of fluid and crystallized cognition as part of a larger study, a preliminary examination into the cognitive correlates of divergent thinking was conducted. The goals of this secondary analysis were twofold: First to provide additional data that may aid in the interpretation of the brain findings in Studies 1 and 2; and second, to inform hypothesis development for future investigations of the cognitive architecture of creativity in younger and older adults.

Thus, the rationale for this third, preliminary investigation is simple. Creativity is associated with fluid intelligence in young adults (Benedek et al., 2014; Benedek et al., 2017; Kenett et al., 2016). Yet, there is growing evidence that creativity is relatively preserved in later life (Palmiero et al., 2014), despite the loss of fluid intellectual capacity known to occur with age. As crystallized intelligence is relatively preserved in later life, this raises the possibility that access to a larger repertoire of prior knowledge may support creative cognition in older adults. The results of studies 1 and 2 suggest a neural mechanism, default-executive coupling, consistent with this possibility. There are two hypotheses for this study. First, fluid intelligence will be positively associated with creative cognition in young adults, with no additional contribution of crystallized intelligence. In contrast, crystallized intelligence will be positively associated with creative ability in older but not younger adults, with no significant additional contribution of fluid intelligence to creative task performance in the older cohort.

Methods

Participants.

52 older adults (mean age: 70.35, SD = 6.98; 28 females) and 22 young adults (mean age: 24.76, SD = 3.36; 15 females) participated in our study. Participants were recruited from the community and participated in a comprehensive cognitive test battery and magnetic resonance image (MRI) scanning. Participants received monetary compensation for their time (equivalent to \$50 for the

MRI scan and \$10 CAD per hour). To be eligible for the study, participants had to be: a) between ages 18-35 or over age 60; b) right-handed; and c) a fluent English speaker. Exclusion criteria included any MRI contraindications and/or a history of neurological, neuropsychiatric, or cardiovascular disease. All participants signed an informed consent form and completed an MRI screening procedure before participating in the study. All procedures were approved by the Institutional Review Board of York University. A subset of 32 older adults (mean age: 68.45, SD = 4.56; 20 females) and 18 young adults (mean age: 23.23, SD = 2.45; 12 females) had complete data for all measures detailed below and were included in the subsequent analyses.

Creative Ability.

The divergent thinking test battery was completed by all participants outside of the scanner and consisted of three paper-pencil alternate uses tasks (Kaufman et al., 2008) which are comparable to standard computer-based assessments (Lau & Cheung, 2010). The alternate uses tasks required participants to generate creative uses for three common objects: a box, a rope and a knife. Participants had three minutes to generate as many responses as possible, while they were recorded by the test administrator. After each task, participants were presented with their list of responses and asked to rank them for creative quality. Participants provided ranks for their top three responses. The main idea behind this ranking was to allow for the use of a top-scoring method where the originality score is based on the creativity evaluation of a predefined number of top-ideas (Silvia et al., 2008).

The top-ideas are identified by the participants themselves according to their subjective appraisal of the creativity of their ideas and then later scored by three trained raters using the subjective scoring method (Benedek, Mühlmann, Jauk, & Neubauer, 2013; Christensen, Guilford, & Wilson, 1957; Silvia et al., 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. We applied the Top 3 scoring procedure (Silvia et al., 2008) by selecting the three most creative responses indicated by participant rankings and averaged the three raters' scores. Overall creativity ratings were obtained by averaging ratings from the three raters for each of the three common objects.

Participants generated a total of 705 top three responses across all three tasks. Some participants only generated two responses for a given task and hence top-ranked those two responses in their top-ranking. Three independent raters were asked to evaluate the responses using a 1 (not at all creative) to 4 (very creative) scale. All raters received an initial training in a joint session where they were familiarized with the scale and the subcomponents of what constitutes an original response. The raters rated a small subset of responses ($n=10$) and discussed their ratings in the group setting. They then proceeded to rate the remaining responses using the scale. There was a moderate level of convergence between ratings provided by raters for the three tasks. The interrater reliability between the three raters was $ICC = 0.62, 0.59, 0.61$ for the tasks “box”, “rope” and “knife”. This level of moderate reliability has been reported and considered acceptable by others (Benedek et al., 2014), and hence, these ratings were used in further analyses.

Cognitive Ability.

Measures of crystallized and fluid intelligence were evaluated using the NIH Toolbox Cognition Battery (NIH Toolbox for Assessment of Neurological and Behavioral Function, 2013; Weintraub et al., 2013).

Crystallized Intelligence.

Crystallized Intelligence scores are calculated using a composite score of the NIHTB Oral Reading Word Test and Auditory word-visual picture matching.

Fluid Intelligence.

Fluid intelligence is assessed via the NIHTB Flanker Test of Executive Function-Inhibitory Control and Attention and the NIHTB Dimensional Change Card Sort Test of Executive Function-Cognitive Flexibility. Episodic memory is assessed using the NIHTB Picture Sequence Memory Test of Episodic Memory. Working memory, an integral component of executive function, is evaluated using the NIHTB List Sorting Working Memory Test. Finally, the NIHTB Pattern Comparison Processing Speed Test tests for processing speed. Raw scores of each test are processed according to the standardized NIH procedure to derive a composite measure of fluid IQ.

Personality Assessment.

Previous work has shown that both creative ability and intelligence (Feist, 1998; McCrae, 1987; Silvia, Nusbaum, Berg, Martin, & O'Connor, 2009) are predicted by one specific personality trait, openness to experience (BFAS-O). In our sample of participants, 18 young adults (mean age: 23.23, SD = 2.45; 15 females) and 32 older adults (mean age: 68.45, SD = 4.56; 24 females) completed a comprehensive personality inventory, the Big Five Aspect Scales (BFAS). We used this measure as a control variable in our analyses.

Analysis Approach.

Correlational Analyses.

To test our hypothesis, we conducted partial correlations between creative ability and intelligence (fluid and crystallized) for young and older adults, while controlling for openness to

experience. Confidence intervals (CI) for partial correlations (pr) were calculated from the bootstrap with 1000 resampling iterations, without replacement.

Results

Participant characteristics can be found in Table 4.1. Old and Young adults differed significantly on education ($t(48) = -2.83, p = 0.007$), measures of crystallized intelligence ($t(48) = 2.41, p = 0.02$) and the personality trait of openness to experience ($t(48) = 2.31, p = .02$).

Table 4.1

Participant Characteristics

	Young		Old		T test results	
	(N=18)		(N= 32)		p	T
	M	SD	M	SD		
<u>Age</u>	23.23	2.45	68.45	4.56	<.001*	1.68
<u>Education</u>	14.7	1.62	16	2.31	0.007*	-2.83
<u>Divergent Thinking</u>	2.79	0.58	2.71	0.38	0.55	-0.61
<u>Crystallized Intelligence</u>	122.43	20.13	133.54	12.59	0.02*	2.41
<u>Fluid Intelligence</u>	105.16	27.55	102.14	13.81	0.61	-0.51
<u>BFAS Openness to Experience</u>	3.47	0.53	3.8	0.45	0.02*	2.31

*significant at an alpha of 0.05

Correlation Results.

After controlling for effects of personality, divergent thinking in young adults showed a significant correlation with fluid intelligence [$pr(15) = 0.58, p = 0.016, 95\% CI: 0.181 - 0.85$]

as well as crystallized intelligence [$pr(15) = 0.59, p = 0.013, 95\% CI: -0.006 - 0.852$, see Figure 4.1].

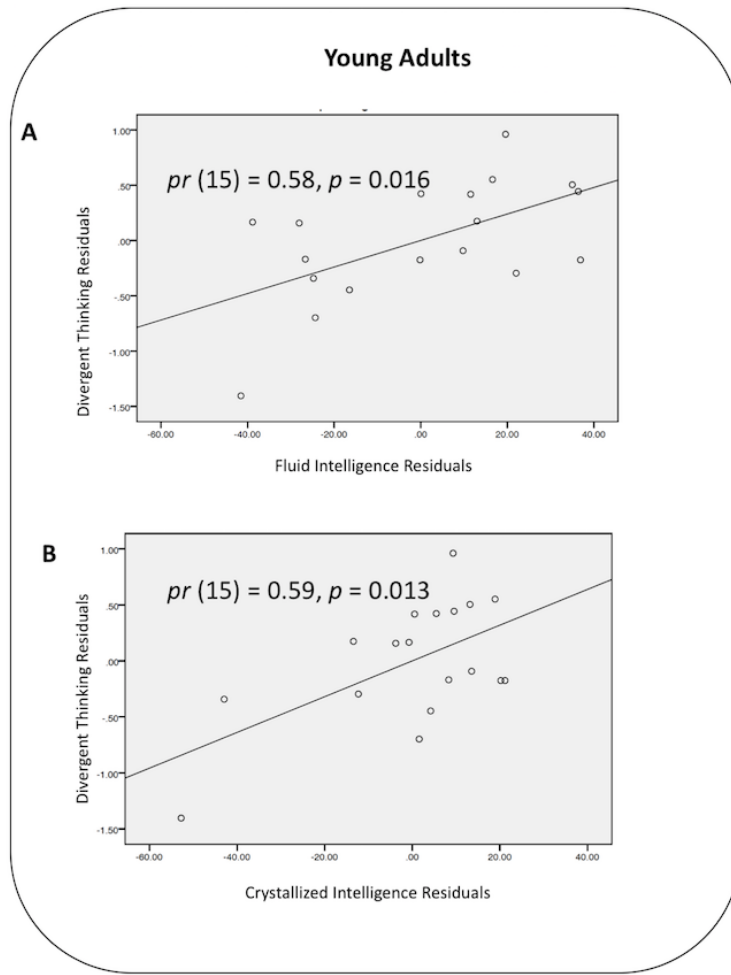


Figure 4.1. Partial correlation for young adults, after controlling for the effect of openness to experience, between fluid intelligence and divergent thinking (Panel A) and crystallized intelligence and divergent thinking (Panel B). X and Y axis values reflect residual values, after the effect of personality is controlled for.

In older adults, after controlling for personality, there was a significant correlation between divergent thinking and fluid intelligence [$r(29) = 0.38, p = 0.03, 95\% CI: -0.05 - 0.66$]. However, the correlation between divergent thinking and crystallized intelligence was not significant [$r(29) = 0.20, p = 0.28, 95\% CI: -0.19 - 0.49$]. A Z-transformation of these correlations showed that they were not significantly different between young and older adults ($Z = 0.738, p = 0.46$) Figure 4.2 shows these correlations.

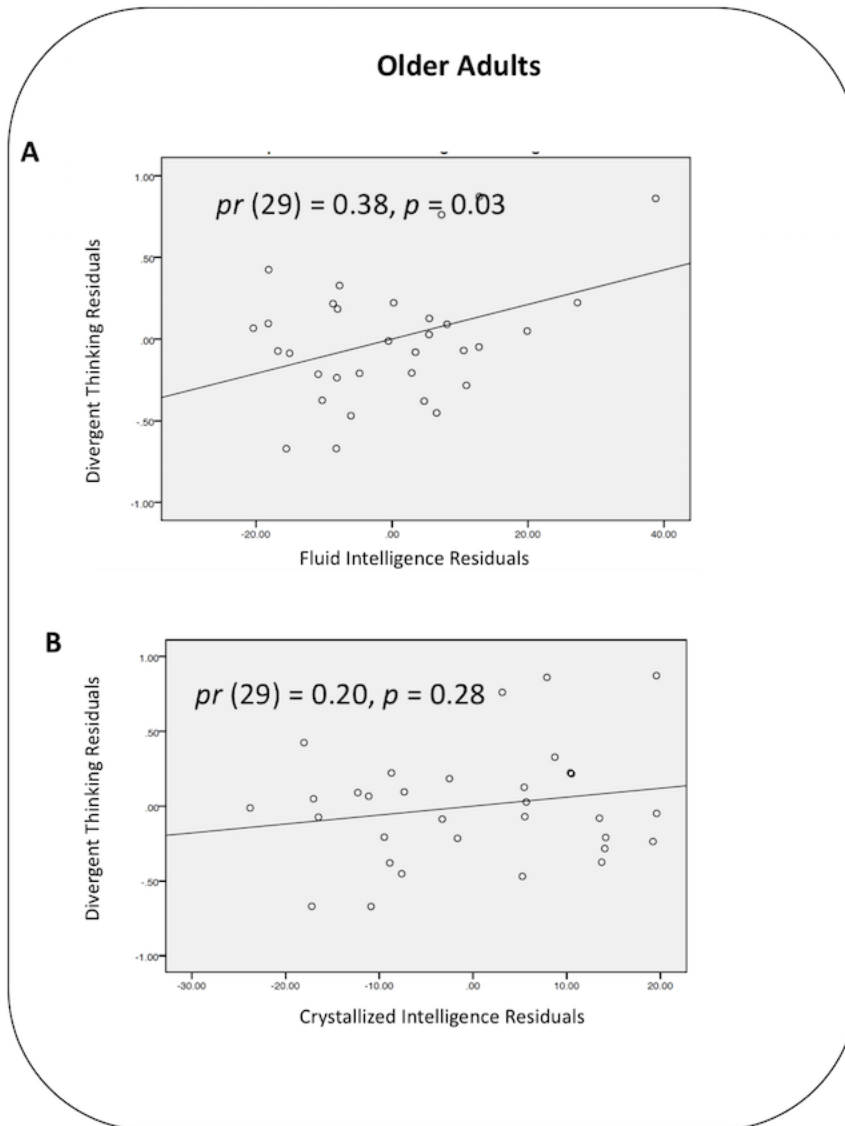


Figure 4.2. Partial correlation for older adults, after controlling for the effect of openness to experience, between fluid intelligence and divergent thinking (Panel A) and crystallized intelligence and divergent thinking (Panel B). X and Y axis values reflect residual values, after the effect of personality is controlled for.

Post-hoc Multiple Regression Analyses.

To further interrogate the associations between age, intelligence-type and creative ability, two additional multiple regression analyses were conducted. The first model investigated the predictive effect of personality, crystallized intelligence, age and the associated interactions of intelligence and age on divergent thinking. The model as a whole was significant, $F(4, 45) = 3.14, p = 0.02$. Openness to experience ($t(3) = 1.55, p = 0.14, \text{standard beta} = 0.19$), crystallized intelligence ($t(3) = 1.02, p = 0.31, \text{standard beta} = 0.006$) and age ($t(3) = -0.89, p = 0.31, \text{standard beta} = -0.92$) were not significant predictors of creative ability. The interaction between crystallized intelligence and age was also not a significant predictor of creative ability ($t(3) = 1.18, p = 0.25, \text{standard beta} = 0.009$).

The second post-hoc multiple regression analysis investigated the predictive effect of personality, fluid intelligence, and, age and, the associated interactions of intelligence and age on divergent thinking. The model as a whole was significant, $F(4, 45) = 4.71, p = 0.002$. Fluid intelligence was a significant predictor of divergent thinking across all participants ($t(3) = 2.023, p = 0.04, \text{standard beta} = 0.01$) and accounted for 23.25% of the variance observed in creative ability. Openness to experience ($t(3) = 0.75, p = 0.46, \text{standard beta} = 0.09$) and age ($t(3) = -0.19, p = 0.85, \text{standard beta} = -0.13$) were not significant predictors of creative ability. The interaction between fluid intelligence and age was also not significant in predicting creativity ($t(3) = 0.314, p = 0.75, \text{standard beta} = 0.002$).

Discussion

This preliminary investigation investigated whether age-related cognitive changes marked by a shift from fluid to more crystalized abilities resulted in a shift in the cognitive architecture associated with creative cognition from young to older adulthood. The results of

Studies 1 and 2 provided evidence for a shifting neural architecture towards default-executive coupling which was associated with creative ability in older adults. Consistent with previous work (Benedek et al., 2014; Silvia & Beaty, 2012), creative ability was associated with fluid intelligence in young adult in our sample. Surprisingly, there was also a reliable association between crystallized intelligence and creative ability in this younger cohort. Further, contrary to the hypotheses, there was a significant correlation between fluid intelligence, but not crystallized intelligence, for older adults. However, this relationship did not significantly differ between young and older adults, warranting further study. Post-hoc analyses revealed that fluid intelligence is a significant predictor of creative ability in both young and older adults.

These preliminary findings suggest that fluid intelligence is associated with creative ability for both younger and older adults. These data are consistent with prior work in young adults which posits a role for top-down, or goal-directed, control of attention to support creative ability. Much of the evidence for such an association is founded on latent variable studies showing effects of fluid intelligence (Beaty et al., 2015), working memory capacity (Lee and Theriault, 2013; Süß et al., 2002) and verbal fluency (Benedek et al., 2014; Silvia, Beaty and Nusbaum, 2013) on creative cognition. In young, these fluid cognitive abilities are hypothesized to facilitate divergent thinking by exerting the necessary top-down control of neural resources to guide memory retrieval and inhibit salient but unoriginal ideas (Beaty & Silvia, 2012; Silvia and Beaty, 2012; Benedek et al., 2014; Gilhooly et al., 2007; Beaty et al., 2014b).

Consistent with this idea theories of creativity have highlighted the importance of core executive functions including inhibition, updating and shifting in subserving creative ability (Koestler, 1964; Mednick, 1962; Nijstad, De Dreu, Rietzschel, & Baas, 2010). Investigations into the relationship between inhibition and working memory and creative cognition in young

have produced equivocal findings (Benedek et al., 2014; de Dreu et al., 2012; Dorfman et al., 2008; Lee & Therriault, 2013; Vartanian, Martindale, & Kwiatkowski, 2007). However, there is widespread consensus in investigations of shifting and creativity, that creative ability requires flexibility in thought processes (Ashby et al., 1999; Benedek et al., 2014; Rowe et al., 2007;). In the current study, fluid intelligence composite measures were computed using an aggregate score on assessments tapping each of these executive function abilities. Thus, while there may be process specific associations, fluid cognitive ability, more broadly appears to be positively associated with creative cognition. Moreover, this association was reliable for both young and older adults.

In contrast to the hypothesized findings, crystallized intelligence was not associated with creative cognitive ability for older adults, despite their larger repertoire of prior knowledge. In contrast, a significant relationship was observed between crystalized IQ and creative cognition for young adults, and post hoc analyses revealed that this a effect was indeed age-dependent. This absence of an association between prior knowledge and creative cognition in older adults was unexpected given the semanticization of cognition theory (Spreng and Turner, 2019) as well as the support for the default-executive coupling hypothesis in studies one and two. This could be in part due to two limitations of this study. First, this study was not designed as an examination of individual differences and was likely underpowered to detect differences. Future work investigating the relationship between intelligence and creativity in aging may need to account for this. Second, we were limited in this study to a composite measure for crystallized intelligence which was derived from two vocabulary-based measures. This estimate of crystalized intelligence, while based on commonly-reported measures of vocabulary knowledge, may be too narrow to detect an association between prior knowledge and experiences, more

broadly defined, and creative cognition. As suggested in studies one and two, default-executive coupling is indicative of greater reliance on internally directed, self-referential processes which in turn may be accessed to support creative thought in older adults. In this context, a broader estimate of prior knowledge, beyond simply vocabulary knowledge may be necessary to detect these associations. Consistent with this idea, a recent report demonstrated an association between semantic autobiographical memory and default-executive coupling in older but not younger adults (Spreng et al., 2018). Future studies will require a broader sampling across multiple domains of prior knowledge to better characterize the contribution of crystallized IQ to creative cognition.

This study provided an early investigation into the role of fluid and crystallized intelligence in creative ability for young and older adults. While our hypotheses were only partially supported by these preliminary findings, future research, involving larger sample sizes, individual difference study designs, and a more comprehensive assessment of prior knowledge, will be necessary to more accurately map the relationship between the shifting architecture of cognition and creative abilities across the adult lifespan. Specifically, adequately powered samples and latent variable analyses applied to multiple assays of executive function and crystallized cognitive abilities are needed to fully evaluate whether the cognitive substrate of creative cognition differs for younger and older adults. The brain-based investigations reported in studies one and two of the dissertation suggest that greater interplay between cognitive control and prior knowledge is a feature of creative cognition in older versus younger adults. Future examinations aimed at investigating the behavioural substrates of the reported neural correlates of creativity will be an important future direction for research in the field of creativity and aging.

CHAPTER FIVE

General Discussion

Creativity has been associated with adaptive and positive functioning across multiple domains of daily living (Runco, 2004). While much research has focused on younger adults, recent studies (e.g. Palmiero et al., 2014; Addis et al., 2016) suggest that creative cognitive ability is preserved into older age, and may be important for successful aging. Over the last decade a growing body of research has investigated how creative cognition is manifest in the functional network architecture of the brain, yet again much of this work has been conducted with younger adults (e.g. Vartanian et al., 2018; Gonen-Yaacovi et al., 2013; Wu et al., 2015; Beaty et al., 2015). Given the known changes in cognition and brain function that occur with age, this raises intriguing questions as to how creativity may be sustained into older adulthood and whether age-differences in brain and behavioural associations might suggest an altered architecture of creative cognition in later life. At the time of writing, there are no published reports examining the neural correlates of creativity in a typically aging population. To address this research gap, this dissertation sought to identify the neural network correlates of creative cognition in the aging brain. Two primary research questions were addressed. First, does the neural network architecture associated with creative task performance differ between older and younger adults? Study one provides the first evidence that, despite preserved performance on a creative thinking task, networks subserving creativity (Beaty et al., 2015) are altered in older adulthood. Study two investigated whether age-differences in the neural architecture of creative cognition are measurable at the level of intrinsic brain networks. The findings from study two show that this is indeed the case. Beyond task-driven differences, altered patterns of resting state functional connectivity associated with creative ability suggest that differences in the neural substrate of creative cognition are more entrained and durable, potentially reflecting an enduring

shift in the cognitive architecture of creativity across the adult lifespan. This latter possibility was explored in a final, preliminary study exploring the cognitive correlates of creative cognition in young versus older adults. This study showed that creativity, measured here as divergent thinking ability, was associated with fluid, or cognitive control ability in young and old. However, contrary to predictions, creativity was associated with crystallized or semantic abilities only for younger adults.

This general discussion first summarizes the key findings from the experiments designed to address each aim. Next areas of convergence and divergence between the task-based and intrinsic connectivity studies are discussed with respect to the shifting neural architecture of creativity in later life. The final section of the Discussion considers whether these results, while specifically addressing creativity, can inform a broader conceptualization of the shifting network architectures of cognition and brain function across the adult lifespan.

Key Experimental Findings.

Study one investigated whether there were age-related differences in neural networks during creative task performance. Despite equivalent behavioural performance between age groups, older adults displayed greater functional connectivity between nodes of the default and executive control networks, consistent with previous research showing a similar network in younger adults (Beaty et al., 2015). While the current studies cannot address this possibility directly, two recent reports suggest a potential explanation for these findings. In these studies, an episodic simulation technique was used to investigate the impact of episodic memory on creative cognition as measured by performance on a divergent thinking task (Madore et al., 2015, 2016). Both younger and older adult performance on the creativity task was enhanced following an episodic simulation. The authors considered this as evidence that creative cognition is, at least in

part, dependent on episodic memory processes. Importantly, older adults, despite known declines in episodic memory ability, continued to benefit from the episodic simulation technique. This suggests that older adults engage mnemonic processes to support creative cognition in later life. As memory is increasingly semanticized in later life (Spreng et al., 2018; Svoboda et al., 2006), a possible inference is that older adults would display relatively greater engagement of brain regions implicated in personal semantics, including nodes of the default network. In turn, engagement of executive control regions is modulated by demands for cognitive control during creative task performance (Beaty et al., 2015). As older adults show greater engagement executive control regions at a similar levels of task demand (e.g. Reuter-Lorenz and Cappell, 2008), older adults would be expected to co-activate executive control and default network brain regions during divergent thinking, reflecting engagement of both mnemonic and executive control processes to support task performance. Consistent with predictions, the task-based findings reported here align with a recent model of neurocognitive aging, the default-executive coupling hypothesis of aging (DECHA, Turner and Spreng, 2015). In this account, older adults demonstrate greater, and less flexible, coupling of default and executive control regions during goal-directed tasks. This enhanced coupling is postulated to reflect increased engagement of semantics, or stored prior knowledge representations, during task performance in older adults. On tasks where this prior knowledge is irrelevant or distracting to task goals, performance declines (Rieck et al., 2016; Turner and Spreng, 2015). However, to the extent that prior knowledge is congruent with task goals, this pattern of increased coupling is associated with enhanced performance, at least in young (e.g. Spreng et al., 2014). Taken together, the findings from the task-based study, and previous results involving episodic simulation (Madore et al.,

2016) suggest that increased default-executive coupling reflects greater recruitment of prior knowledge during divergent thinking in later life.

Having identified a task-driven mechanism associated with creativity in later life, the next study investigated whether the shift in brain networks towards greater default-executive coupling observed during divergent thinking in older adults may reflect a more enduring shift in network interactions, measureable at the level of intrinsic, or task-free, network connectivity. Consistent with the DECHA and earlier studies in young (Beaty et al., 2015) and old (e.g. Madore et al., 2015, 2016), the prediction was that greater intrinsic coupling of default and executive control brain regions would be positively associated with creative ability. To test this hypothesis, RSFC methods were used to derive measures of functional connectivity within- and between- networks implicated in task-based studies of creativity. In this second sample of younger and older adult participants, there were no significant age differences in creative cognition, measured on the divergent thinking task. Further, default and executive networks show greater and more distributed interactivity in older adults, and this pattern more robustly predicts creative ability. Specifically, older adults have greater intrinsic coupling between key nodes of the default network and both the fronto-parietal network and salience network components of the broader executive control network. In contrast, the brain-behaviour pattern observed in younger adults included greater within-network coupling and a more circumscribed pattern of default-executive coupling, as reported previously (Beaty et al., 2015).

These findings are consistent with those from the task-based study where, despite equivalent performance, older adults relied on greater default-executive coupling to support creative cognition. This indicates that the task-driven shift in neural architecture towards increased default-executive coupling, and presumably a greater reliance on prior knowledge, is

reflected in the intrinsic organization of the aging brain. Further, as default-executive coupling more robustly predicted older adult performance on a creative task, this pattern of network interactivity may serve as a neural marker of creativity in later life. A similar pattern of network interactivity has been observed in younger adults during creative task performance. These network interactions are postulated to support interference resolution as prior mnemonic representations intrude into creative thought processes necessitating cognitive control to overcome past knowledge representations and support novel idea generation (Beaty et al., 2017). In this context, greater intrinsic coupling of default and executive brain regions may reflect an entrained pattern of activation or suppression of a larger store prior knowledge in support of creative cognition. Unfortunately, we cannot distinguish between the suppression versus activation accounts with the current data. However, evidence that episodic simulation enhances creativity in older adulthood, in the context of declining control processes, suggests that accessing mnemonic representations may serve to enhance creative cognition in later life. Greater coupling at rest between default and executive networks may therefore reflect an entrained pattern of strategic semantic retrieval (a capacity well preserved in later life, Hoffman et al., 2018) to access and subsequently reconfigure prior knowledge to formulate novel constructs. This pattern of intrinsic functional connectivity, which is a robust predictor of creative ability in older adulthood, may serve to potentiate coupling of these regions during creative task performance, consistent with findings from study one. Whether the intrinsic functional connectivity patterns are a consequence or cause of the task-driven pattern cannot be determined using the cross-sectional, correlational design implemented here. However, these data provide an important empirical foundation for future research using causal (e.g. transcranial

magnetic stimulation) and longitudinal experimental designs. This possibility is discussed further as a future direction below.

Building upon these cognitive neuroscience investigations, which suggest that prior knowledge representations play a larger role in creative cognition in later life, a third exploratory behavioural study was conducted to investigate whether creativity was in fact correlated with an index of prior knowledge in older versus younger adults. While sample sizes were insufficient to conduct an adequately powered factor analytic investigation of the cognitive correlates of creative cognition (i.e. divergent thinking task performance), all participants were part of a larger study of cognitive and brain aging, enabling us to conduct a preliminary investigation of this possibility. Contrary to the hypotheses, there was no significant correlation between crystalized intellectual ability and divergent thinking performance for either age group. In contrast, fluid intelligence was a significant predictor of creativity for in both age cohorts. As discussed in study three, this may reflect a lack of statistical power to detect smaller associations. However, an alternate explanation concerns the measure of crystalized knowledge used here. Most investigations of semantic or crystalized knowledge involve vocabulary knowledge or knowledge of verbal concepts. It is possible, if not likely, that these forms of highly semanticized knowledge are difficult to reconfigure into novel constructs. In contrast, creative cognition in older adulthood may rely on personal experiential knowledge, a domain of prior knowledge not indexed by our standard measure of crystalized cognition. This interpretation is consistent with the prominent role for the ventral medial prefrontal cortex, identified in our resting-state analyses as a between-network hub. This core node of the default network has been associated with access to personal semantics, or crystalized experiential knowledge (Bonnici and Macguire, 2017).

Thus, functional connectivity of this region in older adulthood may signal greater reliance on personal semantics which we were unable to directly measure here.

Taken together, using an in-scanner task based approach and standard offline measures of divergent thinking, these studies demonstrate that creative ability is preserved in a typical aging. Greater and more distributed functional coupling between default and executive control networks, both during task and at rest, may be adaptive and facilitate creative cognition in older adulthood. The next section further integrates these findings towards the goal of developing a neural network model of the creative aging brain.

The Creativity Network in Older Adulthood: Integrating Evidence from Task and Rest.

Results from this dissertation drawing upon task-based and intrinsic connectivity approaches provide support for a default-executive neural network mechanism supporting creative cognition in older adults. In young adults, default-executive network coupling has been associated with creative thought (Beaty et al., 2016). Within this framework, the default network is postulated to support idea generation by engaging episodic and semantic processes in the service of task goals. Coupling between the default and the salience network component of the broader executive control network facilitates the redirection of attentional resources towards mnemonic representations necessary to generate novel ideas. Once ideas have been generated, default coupling shifts to the frontal parietal control network to filter out non-relevant information and determine alignment with task goals (Beaty et al., 2016). The findings from the studies reported here suggest that older adults express this network pattern more robustly and this may support creative cognition in later life. However, there are several areas of convergence and divergence between the task and resting state studies that may help to further characterize the neural mechanisms underlying creativity in healthy aging.

Evidence from both resting-state and task-based functional connectivity studies highlight the role of the vmPFC in creative cognition in older adults. The vmPFC is a core node of the default network implicated in self-referential processing (Andrews-Hanna et al., 2010). During task-based creativity in older adults, the left vmPFC is significantly functionally connected to the left middle temporal gyrus, a region critical for supporting semantic knowledge (Levy, Bayley and Squire, 2004). The current data suggest that during the divergent thinking task, older adults generate creative ideas in part through access to personal and general semantics mediated by coupling of vmPFC and middle temporal gyrus regions (Table 2.2; Figure 2.3). The vmPFC may be a critical node facilitating engagement of a vast repertoire of personal semantic knowledge as well as general semantic knowledge mediated by the medial PFC and lateral temporal lobes respectively. During both task and rest, connectivity of the left and right vmPFC was predictive of creative cognition, possibly signalling relatively greater reliance on internal mentation processes, including activation of prior knowledge of oneself and the world to support creativity.

Functional connectivity among key nodes of the salience network was also associated with creative cognition during both task and rest. The salience network is implicated in the direction and reallocation of attentional resources to task goals (Seeley et al., 2007; Uddin et al., 2015). Here, greater connectivity within the salience network for older adults may reflect increased demand for internally directed attention necessary to engage default network brain regions related to idea generation. Consistent with this idea, within-network coupling of the salience network has been associated with default network function (Chiong et al., 2013; Jilka et al., 2014; Sridharan et al., 2008).

In contrast, a different pattern of between-network connectivity was observed during rest versus task. Older adults showed extensive interactivity between default and executive control

subsystems (fronto-parietal and salience) at rest that was associated with creativity. However, during task performance this connectivity pattern was more circumscribed. Resting state functional connectivity reflects entrainment of task-based connectivity patterns repeated over time. This may, in turn, lead to a potentiation of these intrinsic connectivity patterns during task performance, albeit in more circumscribed connectivity profile driven by specific task demands (Stevens & Spreng, 2014). In this model, the default network couples with the salience network and the fronto-parietal network at different stages of creative thought. For younger adults, idea generation involves the coupling of (1) posterior cingulate cortex and right anterior insula, followed by idea evaluation marked by coupling of (2) posterior cingulate cortex and the right dorsolateral PFC during idea evaluation (Beaty et al., 2015). In our study, older adults showed a different pattern of task-based connectivity of the right insula, that was limited to the left inferior temporal gyrus, with other salience network nodes showing a more diffuse pattern of connectivity to posterior cingulate cortex and vmPFC. This suggests a different neural mechanism for creative idea generation in older adults. While speculative, this may reflect a redirecting of attentional resources to access general and personal knowledge based representations associated with salience default network coupling. This age-related difference in functional connectivity patterns may suggest greater reliance on mnemonic retrieval processes or post-retrieval monitoring processes, affiliated with anterior nodes of the default network.

A second area of divergence between the task-based and resting-state findings can be observed in the connectivity profile of the vmPFC, a core anterior node of the default network. During the divergent thinking task, the left vmPFC was significantly more functionally coupled with the left middle temporal gyrus (See Figure 2.3). However, during rest, connectivity of this region is more widespread to homologous regions as well as default and salience network nodes

(See Figure 3.2). While both patterns suggest a relationship between within-network default network connectivity and creativity, the different connectivity profiles of the vmPFC again suggest that task demands may alter the core intrinsic features of the creativity network, and its default aspect specifically. The vmPFC is implicated in the consolidation of autobiographical memories (Bonnici and Maguire, 2017) while the middle temporal gyrus is associated with general semantics, or crystalized knowledge such as word meaning (Jeffries, 2013). Task-based connectivity between vmPFC and middle temporal regions may reflect engagement of word meaning, elicited by the task stimuli, and subsequent integration with personal experiential knowledge of the displayed object, mediated by the vmPFC.

‘Novelty’ is fundamentally a relative term, adjudicated by its dissociation from prior knowledge. Thus, engaging personal past knowledge is a precondition for generating novel object uses. At the level of the brain, it follows that accessing word meanings, and mapping those meanings to personal semantics is necessary to determine whether a thought or action is indeed novel. Interestingly, intrinsic connectivity between vmPFC and middle temporal lobe structures did not predict creativity for older adults. This further highlights the enduring importance of vmPFC as an amodal gateway, within the broader creativity network, charged with accessing personal past knowledge necessary for generating and evaluating a response as novel. In contrast, connectivity to middle temporal lobes during the divergent thinking task may reflect a more modality-specific access to word meaning in response to visual or possibly, visual to verbally-transformed, task stimuli, prior to mapping these meanings to past experiential knowledge. This explanation is also consistent with our failure to observe significant correlations between measures of crystallized intelligence and divergent thinking performance in older adults. While standardized measures of crystallized intelligence typically assess general knowledge, a

measure of personal semantics may be necessary to detect the role of prior knowledge in creative task performance on older adulthood.

Default-Executive Coupling and Creative Cognition

In the context of equivalent divergent thinking performance, the results of the task and resting state neuroimaging studies suggest that greater coupling of default and executive control networks may support creative cognition in older adulthood. These findings are consistent with the scaffolding theory of aging and cognition (STAC; Reuter Lorenz and Park, 2009). In this account, the typically aging brain undergoes both structural and functional changes that may lead to age associated cognitive decline. These changes include cortical thinning, regional atrophy, loss of white matter integrity, dopamine depletion (Spreng and Turner, 2018). There are also changes in functional activation in the aging brain, including bilateral activation of prefrontal cortices in older adults. Within the STAC model, cognitive functioning is determined by a combined effect of both the negative effects of structural and functional changes, but also beneficial processes referred to in the STAC model as compensatory scaffolding. Compensatory scaffolding can offset the deleterious consequences of changes in the aging brain. Specifically, this scaffolding involves the recruitment and engagement of additional brain regions to provide the necessary neural support to sustain cognitive function into older age. Compensatory recruitment can occur in the form of bilateral activation in prefrontal regions or additional engagement of frontal and parietal regions (Cabeza and Dennis, 2012; Spreng et al., 2010).

Consistent with a compensatory scaffolding model, these data suggest that greater default-executive coupling in older adults may serve as a compensatory neural scaffold to support creative cognition. Older adults demonstrated greater connectivity between the right inferior frontal gyrus and medial superior frontal gyrus (Figure 2.5). In young adults, the right

inferior frontal gyrus via its connectivity with the bilateral inferior parietal lobes (Beaty et al., 2014; 2018; Vartanian et al., 2018) exerts top down control to support creative cognition (Beaty et al., 2014; Vartanian et al., 2018). In older adults, right inferior gyrus was engaged during creative thought; however, it is more connected to the medial PFC node of the default network, as compared to the middle temporal gyrus and inferior parietal lobe in young adults (Vartanian et al., 2018). This evidence supports the STAC model, where compensatory scaffolding stemming from the right inferior frontal gyrus to the self-referential subsystem of the default network (Campbell et al., 2013), including the medial superior frontal gyrus, supports creative thought in older adults. Here, the self-referential system of the default network may serve to activate prior experiential knowledge which is later reconfigured during novel idea generation. As noted by Beaty and colleagues, this process is aided by inhibitory and monitoring processes during the ideas evaluation stage. This coupling of critical default and executive nodes can allow for successful reliance on semanticized knowledge and its effective use, when the task demand of creativity can benefit from processes subserved by the default network. This may reflect a compensatory shift in strategy towards greater reliance on acquired and accumulated knowledge.

The hypothesis of compensatory default-executive scaffolding in aging as a neural mechanism supporting creative cognition is further supported by the examination of differences in connectivity between salience and default networks in older versus younger adults. For young adults, the right anterior insula is implicated in switching from idea generation to idea evaluation (Beaty and Schacter, 2016). In the task-based experiment, a similar pattern is observed during divergent thinking for young adults. In young adults, the right anterior insula is functionally connected to hubs of the default network including the posterior cingulate cortex and precuneus at early stages of divergent thinking (Beaty et al., 2015). This is thought to be a facilitative

mechanism allowing default and executive control mechanisms to couple during the latter, idea evaluation stage of creative thought. In older adults, during the same task, the right anterior insula is functionally connected to the inferior temporal gyrus node in the default network in older adults, and that other salience network nodes show greater connectivity to the default network (Figure 2.5). This pattern of increased between-network connectivity for older adults is interpreted here as reflecting greater reliance on representational knowledge (both general and personal semantics) to support equivalent divergent thinking abilities for older adults.

Further evidence to suggest that default-executive coupling may serve as a scaffold to support creative cognition in older adulthood can be found in the connectivity patterns of the vmPFC both during task (Figure 2.5) and rest (Figure 3.3). During rest, older adults showed greater connectivity between left and right vmPFC and between bilateral vmPFC and other default and salience network nodes. During the divergent thinking task, the left vmPFC showed greater connectivity with the middle temporal gyrus and the precentral gyrus. Its coupling at rest with other nodes of salience and fronto-parietal networks is notably different than the connectivity profiles observed in young, where dorsomedial prefrontal regions are more connected to core nodes of the default (posterior cingulate cortex) and salience (anterior insula) networks (Beaty et al., 2018). In the resting state findings reported here, young adults showed greater connectivity between left vmPFC and other nodes of the default network as well as nodes of the fronto-parietal and salience networks. Further, older adults in the task-based study demonstrated connectivity between the vmPFC and the middle temporal gyrus in older adults that is not observed in young. As noted above, the vmPFC is important for memory consolidation (Bonnici and Maguire, 2017). During divergent thinking, it is connected with the middle temporal subsystem of the default network necessary for memory construction and future

projection (Schacter et al., 2007). Here the scaffolding necessary to support divergent thinking can be inferred as arising from the engagement of general and personal semantic representations, which may be reconstituted to support novel idea generation.

Future Directions

Examinations of creativity from a biopsychosocial perspective suggest that creativity into older adulthood is critical for maintaining an agentic self-view, independence and a positive personal self-view that promotes better mental health (Duhamel, 2016; Runco, 2004). Future investigations of creative ability in aging may provide a novel lens through which we can understand the implications of creative thought in successful aging. In this dissertation while conducting resting state and task-based investigations to examine the neural correlates of creativity in older adults, it was not possible to establish if these patterns of connectivity were causal. The analyses reported here are unable to establish if task-based patterns of functional connectivity during creative thought processes were influenced by changes in the intrinsic connectivity patterns of the aging brain or vice versa. One line of investigation can potentially examine both intrinsic and task-based functional connectivity during creativity in a larger subset of older adults, using an individual differences approach. Within this approach, it is important to consider longitudinal methods and data sampling over multiple time points, to establish if creative thought processes subserved by default-executive coupling lead to changes in the intrinsic connectivity of the brain or vice versa. Within this approach, fMRI based investigations can take advantage of repeated measurements of performance on creative measures and intrinsic connectivity to investigate whether they influence each other.

An important future direction for research is to investigate causal mechanisms, not only between patterns of intrinsic and task-based connectivity related to creativity, but also within

specific network nodes. Current mathematical and neuroimaging modelling has provided a path for this work to emerge, and early work has examined the casual effects of nodes within the creative network (Vartanian et al., 2018). Using dynamic causal modelling, this work has shown that the right inferior frontal gyrus unilaterally controls activation in the middle temporal gyrus and inferior parietal lobe in young adults during creative thought processes, suggesting a causal role of the inferior frontal gyrus in mediating between-network connectivity. Following this line of investigation and modelling approach will be equally important in older adults, where it is unknown if the pattern of default-executive coupling giving rise to creativity may be similarly influenced by critical nodes allowing greater access to prior knowledge. The vmPFC could be a key node in this regard by providing a gateway to vast repertoire of stored representational knowledge. Through a dynamic causal modelling approach using resting state analyses in a larger subset of older adults, this hypothesis can be directly tested by examining the nature of control exerted by the vmPFC on other nodes of the creativity network in young and older adults.

Another approach to establishing causality and determining which nodes are key in giving rise to creativity, or even improving creativity, is via the use of neurostimulation techniques. Early work in this domain has used transcranial direct current stimulation (tDCS) of the left dorsolateral PFC to show that cathodal tDCS, that suppresses the left dorsolateral PFC, leads to greater creativity by reducing the effect of learned constraints (Chrysikou et al., 2012; Luft et al., 2017). Another recent study has shown that stimulation of the fronto-polar cortex, via anodal tDCS, leads to improvements in creative ability as measured by creative task performance (Green et al., 2016). While this work remains in its infancy, it provides a novel approach to examining the use of stimulation via both suppression and enhancement of cortical nodes that are implicated in creativity. Default-executive coupling, facilitating retrieval and access to stored

and representational knowledge, may be critical for maintaining creativity in older adults and may in part be mediated by the vmPFC. Through the use of tDCS and/or transcranial magnetic stimulation, future research can aim to modulate vmPFC activity indirectly via stimulation of lateral nodes (as in Chrysikou et al., 2012) and look at whether in older adults the ventromedial exerts a casual influence on creativity.

Thus far, the discussion has focused on domain general forms of creative cognition. Domain specific forms of creativity and their associated neural underpinnings, such as musical and artistic ability, are an under-studied area of research in the aging population. Earlier the pattern of default-executive coupling supporting creative cognition into older adulthood was identified as a putative compensatory neural scaffold. Given this, it is important to consider if this compensatory scaffold is also important in subserving other forms of creative cognition, such as those that are domain specific such as musical ability, that are representative of cognitive reserve (Stern, 2003). An aspect of cognitive reserve is the participation in leisurely activities, some of which may be hobbies such as music, creative writing and so forth. Future investigations of creativity focused at domain specific forms of cognition in aging may hence be useful in furthering this program of research in understanding the neural correlates of compensatory scaffolding that can be beneficial to older adults. Finally, from a translational standpoint, these data, suggesting that default-executive coupling may support creativity in older adulthood, opens potentially novel avenues for intervention design to sustain cognitive health in later life. First, as creativity is associated with successful aging, interventions aimed at strengthening default-executive coupling, for example leveraging tDCS techniques (see above) may serve to sustain creativity in later life. Alternatively, training in divergent thinking may be integrated into multifaceted cognitive training interventions to enhance the flexibility of default-executive

coupling in older adulthood. This in turn may lead to more generalized gains in goal-directed cognition where prior knowledge may be leveraged to support or potentially compensate for declining control abilities.

Conclusions

Overall, findings reported in this dissertation demonstrate that the neural network architecture of creativity differs between younger and older adults. Previous work has shown that large scale functional networks of the brain, including default and executive control networks show coordinated patterns of activity that give rise to creative cognitive processes in young adults. The default-executive coupling hypothesis of aging proposes that this pattern of network coupling reflects an overall age-related shift towards semanticized cognition and is beneficial to older adults when they faced with tasks whose demands rely on stored representational knowledge. The findings reported here suggest that default-executive coupling may serve as a compensatory neural scaffold to help sustain creative cognition into older adulthood. Further, across both task-based and resting state analyses examining creativity, the vmPFC emerged as a key node. These data implicate the vmPFC as a gateway node in allowing older adults to access semanticized knowledge to generate creative ideas. Investigating the role of the vmPFC and as between-network hub regions will be an important avenue for future research.

Given the infancy of creativity research in particularly the aging population, a focus on proof-of-concept studies using well-established tasks, beyond divergent thinking, should be a key focus of future research programs. A focus on more functional or real-world tasks, will allow researchers to examine whether the afore mentioned pattern of default-executive coupling in aging is generalized across different forms of creative cognition and its expression in more

ecologically-valid contexts. Taken together, research investigating the neural network basis of creativity in older adulthood will lay the necessary foundation for more translational research to sustain creative cognition in later life.

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Appendix A

Methods

Participants

22 old (mean age = 68.9 years, $SD = 5.27$; 11 females) and 22 young (mean age: 24.76, $SD = 3.36$; 15 females) were included in the current study and were recruited from the community and participated in a comprehensive cognitive test battery and magnetic resonance image (MRI) scanning as part of a larger ongoing study. Participants received monetary compensation for their time (equivalent to \$50 for the MRI scan and \$10 CAD per hour). To be eligible for the study, participants had to be: a) over age 60; b) right-handed; and c) a fluent English speaker. Exclusion criteria included any MRI contraindications and/or a history of neurological, neuropsychiatric, or cardiovascular disease. All participants provided informed consent consistent with procedures approved by the Institutional Review Board of York University. All participants were cognitively healthy based on subjective reports and had MMSE scores greater than 24.

Previous work has shown that both creative ability (Feist, 1998; McCrae, 1987; Silvia, Nusbaum, Berg, Martin, & O'Connor, 2009) and default network engagement (Beaty et al., 2018b) are predicted by the 'Big-Five' personality trait of 'openness'. Given that our participants were a subsample of a larger ongoing study, we chose to match our participants on the personality trait of openness. Previous work has shown that intrinsic coupling between networks implicated in creativity are also related to openness to experience (Beaty et al., 2018) and that divergent thinking is associated with openness to experience (Feist, 1998; McCrae, 1987; Silvia, Nusbaum, Berg, Martin, & O'Connor, 2009). Thus, we chose to match our young and older

adults on personality to ensure that between group differences were not due to differences in personality.

In the larger sample of participants, 22 young adults (mean age: 24.76, $SD = 3.36$; 15 females) and 44 older adults (mean age: 69.80, $SD = 7.05$; 24 females) had completed both the divergent thinking measures and a comprehensive personality inventory, the Big Five Aspect Scales (BFAS). A two-tailed t-test revealed that there was a significant difference in self-reported openness to experience between young ($M = 3.52$, $SD = 0.26$) and older adults ($M = 3.81$, $SD = 0.24$), $t(64) = -2.19$, $p = 0.032$, Cohen's $d = 1.16$). Given prior work associated creativity and personality and the rationale set up above, we matched a subset of older adults to our young adult sample on the personality trait of openness to experience, based on Big-Five Openness (BFAS-O) scores. We obtained two groups with 22 young (mean age = 24.76 years, $SD = 3.39$) and 22 older adults (mean age = 68.9 years, $SD = 5.27$) who were then subsequently used in analyses and did not differ significantly BFAS-O scores, $t(42) = -1.05$, $p = 0.29$.

Analysis Approach

Regions of interest

Next, we took a within-group approach to examine creativity associated patterns of RSFC among our networks of interest in young and older adults. Here, we examined within group patterns of connectivity (young and older adults) independently, and offline measures of creativity were used as a second level regressor of interest in both analyses. Results were corrected for multiple comparisons using a false discovery rate threshold of 0.05, at the ROI level. For both groups, positive findings reflect patterns of ROI-to-ROI connectivity that positively correlate with creative ability, while negative findings indicate negative correlations with creative ability.

Second, to look at age related differences in creativity, we used a between group analysis. Here,

we contrasted group level maps of ROI-to-ROI functional connectivity correlating with offline measures of creativity. This contrast was specified as *Older Adults > Young Adults*. Results were corrected for multiple comparisons using a false discovery rate threshold of 0.05, at the ROI level. For this analysis, positive findings reflect patterns of functional connectivity that correlate with creative ability in older adults; in contrast, negative findings indicate findings in young adults.

Results

Within-Group Patterns of Functional Connectivity Associated with Creative Ability

Young adults showed a distributed pattern of between-network functional connectivity that positively predicted divergent thinking performance outside of the scanner. Functional connectivity between nodes of the salience network (left anterior insula) and FPN (left inferior frontal gyrus) and between FPN (left inferior temporal gyrus) and default networks (right ventromedial PFC) positively correlated with creativity ratings on the divergent thinking task. Right dorsolateral PFC, a node of the FPN, was significantly connected to bilateral posterior cingulate cortex as well as left anterior cingulate cortex, nodes of the default network and positively predicted creative ability in the young adult cohort. Supplementary Table 1 and Supplementary Figure 2 provide details for these nodes and associated connectivity results.

For older adults, both within- and a more spatially distributed between- network connectivity profile was positively associated with creative task performance. Within-network connectivity was observed between nodes of the salience network (left insula and left supplementary motor area). Between-network connectivity was observed among default (right middle temporal gyrus) and salience (right cingulate gyrus) network nodes as well as between salience network (supplementary motor area) and FPN (inferior temporal gyrus) nodes.

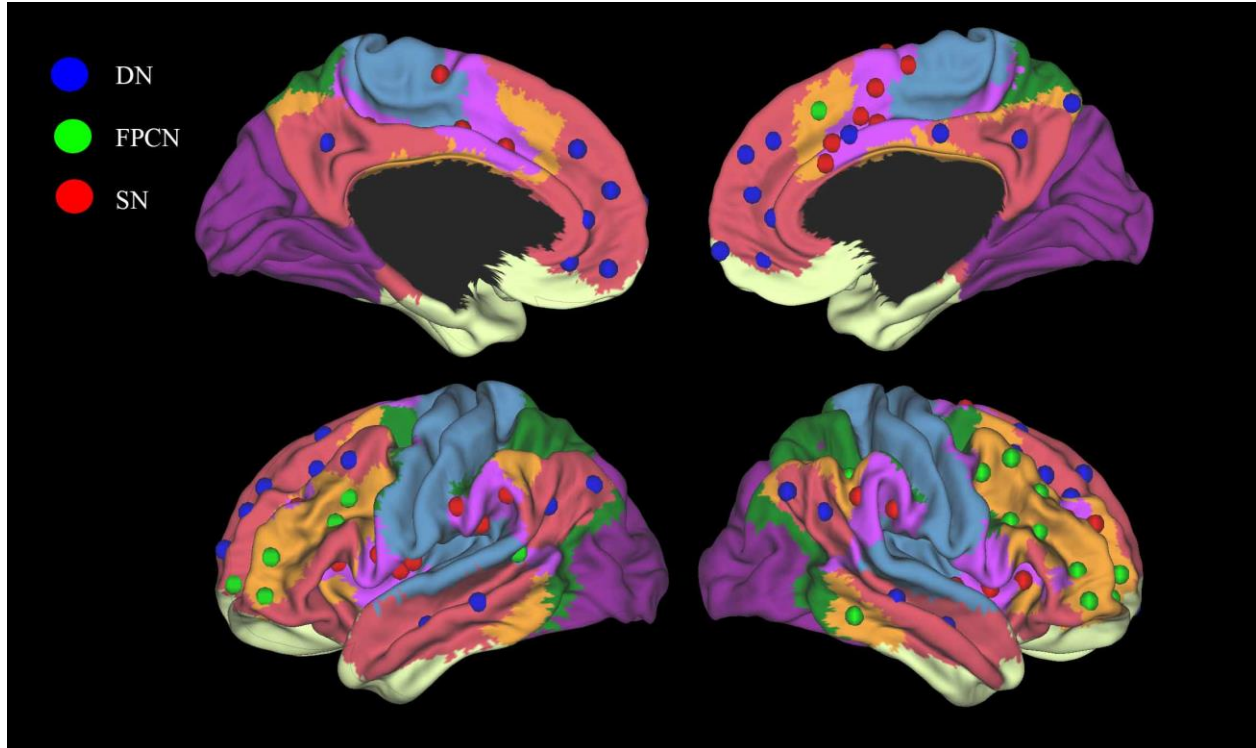
Additional between-network connectivity that was positively associated with creativity was observed between nodes of the default network (right superior temporal gyrus) and the FPN (right superior frontal gyrus). Supplementary Table 2 and Supplementary Figure 3 provide details for these nodes and associated connectivity results.

Age Differences in Patterns of Functional Connectivity Associated with Creative Ability

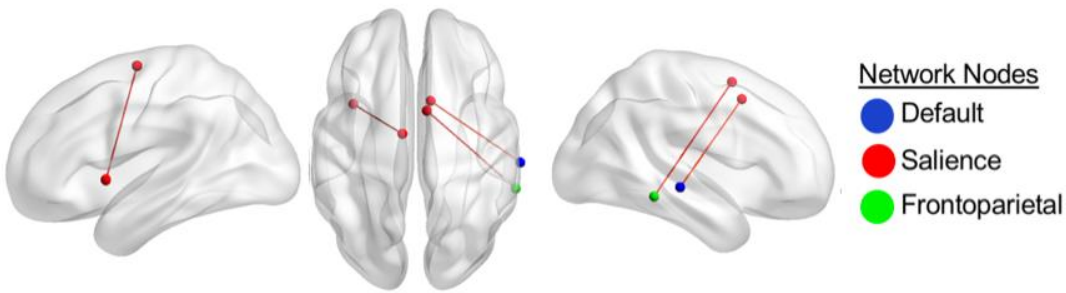
When the brain and behavior correlation maps for both age groups were directly contrasted, a pattern of greater within-network connectivity was associated with better divergent thinking performance for the younger cohort. Specifically, greater connectivity between default network nodes, including between left ventromedial PFC and left superior frontal gyrus, left medial frontal gyrus, left superior temporal gyrus and right dorsomedial PFC was associated with better divergent thinking ability for the younger participants. Young adults also had greater functional connectivity between default and FPN nodes associated with better divergent thinking ability, specifically between left inferior precentral sulcus and bilateral posterior cingulate cortex and between left ventromedial PFC and right inferior frontal gyrus and posterior middle temporal gyrus.

In older adults, greater between-network functional connectivity was associated with better divergent thinking ability. Greater between-network functional connectivity, associated with better task performance, was also observed between salience and default networks (right ventromedial PFC and right intraparietal sulcus) as well as among nodes of the default, FPN and salience networks (left ventromedial PFC, right anterior PFC and right middle frontal gyrus). One significant within-network connection, between the left and right ventromedial PFC nodes of the default network, was correlated with better creative ability for older adults (Supplementary Figure 4, Supplementary Table 3).

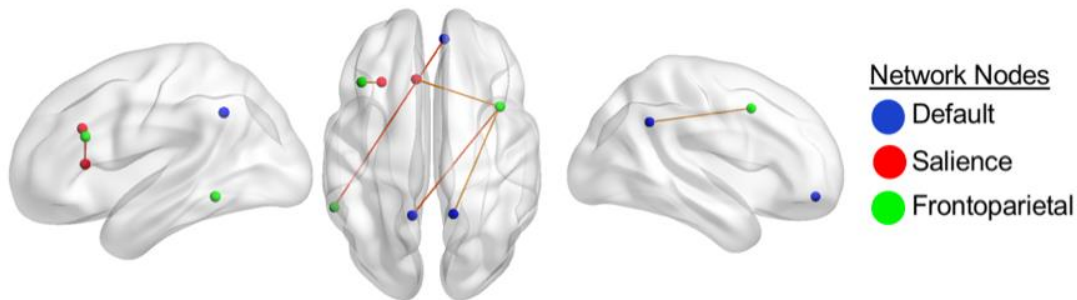
Supplementary Figures



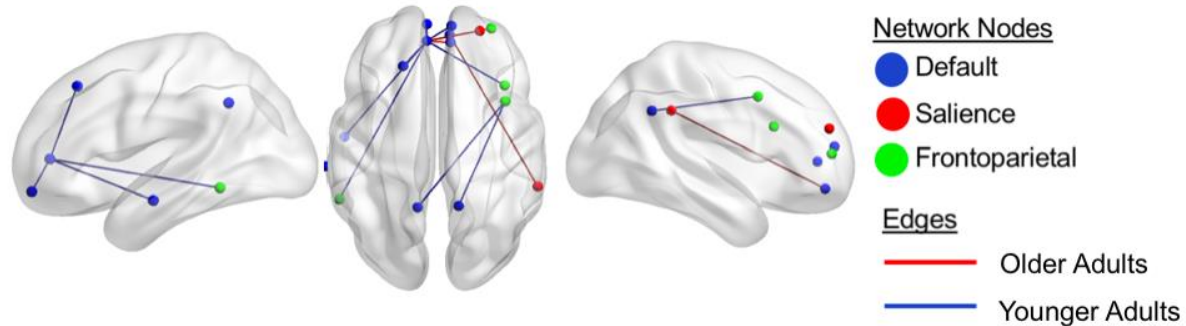
Supplementary Figure 1. Visualization of our networks of interest. Regions of Interest for the default, cingulo-opercular and frontoparietal control networks were taken from a resting state parcellation by Gordon and colleagues (2014) and are represented as spheres. For illustrative purposes, regions of interest were superimposed on an overlay (Yeo et al., 2011) to validate functional network assignment. The cingulo-opercular nodes from Gordon et al (2014) overlap with the salience network identified in Yeo et al (2011) and is referred to as the salience network in our analyses.



Supplementary Figure 2. Resting state functional connectivity correlating with divergent thinking ability in young adults. Color coded nodes include regions from the default network (DN), frontoparietal network (FPN) and salience network (SN). The color of the edges denotes the direction of correlation between functional connectivity and divergent thinking ability. Only positive correlations between ROI-to-ROI functional connectivity and divergent thinking ability survived a seed-level FDR correction at an alpha level of 0.05. Results correspond to findings in Supplementary Table 1.



Supplementary Figure 3. Resting state functional connectivity correlated with divergent thinking ability in older adults ($n = 22$) matched with younger adults on the personality trait, openness to experience. Color coded nodes include regions from the default network (DN), frontoparietal network (FPN) and salience network (SN). The color of the edges denotes the direction of correlation between functional connectivity and divergent thinking ability. Only positive correlations between ROI-to-ROI functional connectivity and divergent thinking ability survived a seed-level FDR correction at an alpha level of 0.05. Results correspond to findings in Supplementary Table 2.



Supplementary Figure 4. Group by behavior interaction for intrinsic connectivity correlated with divergent thinking. The figure shows resting-state ROI-to-ROI functional connectivity that correlates with divergent thinking ability and is significantly different between young and personality-matched older adults. Color coded nodes include regions from the default network (DN), fronto-parietal network (FPN) and salience network (SN). The color of the edges (connections between nodes) indicates the direction of the contrast. Red edges indicate greater connectivity between regions that are associated with divergent thinking in older adults, while blue edges indicate greater connectivity between regions that are associated with divergent thinking in young adults. Results correspond to findings in Supplementary Table 3.

Supplementary Table 1. ROI-to-ROI connectivity positively correlating with divergent thinking ability in young adults (corresponding to Supplementary Figure 1).

	<i>Network</i>	<i>Hem</i>	<i>Node</i>	<i>MNI Coordinates</i>			<i>T</i>	<i>p</i>
				<i>X</i>	<i>Y</i>	<i>Z</i>		
Young Adults								
Between Network Connectivity								
SN-FPN								
Anterior Insula	SN	L	84	-28.8	23.7	8.4		
IFG	FPN	L	109	-43	19.4	33.5	4.24	0.04
FPN-DN								
ITG	FPN	L	9	-55.9	-47.7	-9.3		
vmPFC	DN	R	279	7.2	48.4	-10	4.23	0.043
FPN-DN-SN								
DLPFC	FPN	R	328	38.9	9.6	42.7		
PCC	DN	L	1	-11.2	-52.4	36.5	4.07	0.046
mACC	SN	L	28	-9	25.3	27.7	3.72	0.047
PCC	DN	R	162	12.3	-51.6	34.5	0.74	0.047

Note: DN - Default Network ; DLPFC – Dorsolateral prefrontal cortex; FPN - Fronto-parietal network; Hem = Hemisphere; IFG – Inferior Frontal Gyrus; ITG – Inferior Temporal Gyrus; SFG – Superior Frontal Gyrus; PCC – Posterior Cingulate Cortex; mACC – Middle Anterior Cingulate Cortex; MTG – Middle Temporal Gyrus; R – Right; L – Left; vmPFC – Ventromedial Prefrontal Cortex

Supplementary Table 2. ROI-to-ROI connectivity positively correlating with divergent thinking ability in older adults (corresponding to Supplementary. Figure 2).

		<i>Network</i>	<i>Hem</i>	<i>Node</i>	<i>MNI Coordinates</i>			<i>T</i>	<i>p</i>
					<i>X</i>	<i>Y</i>	<i>Z</i>		
Older Adults									
<i>Between Network Connectivity</i>									
<i>DN-FPN</i>									
SFG	FPN	R	277	28.4	57	-5.1			
STG	DN	R	290	57.5	-7.4	-16	3.78	0.001	
<i>DN-SN</i>									
Cingulate Gyrus	SN	R	187	8.8	10.8	45.9			
MTG	DN	R	225	62.5	-25.6	-5.5	2.93	0.008	
<i>SN-FPN</i>									
ITG	FPN	R	170	59.7	-41	-11			
SMA	SN	R	181	6.7	5	55.9	3.09	0.006	
<i>Within Network Connectivity</i>									
<i>SN-SN</i>									
SMA	SN	L	34	-8	8.7	62.9			
Insula	SN	L	82	-37.3	8.9	-0.9	3.25	0.004	

Note: DN - Default Network ; ; FPN - Fronto-parietal network; Hem = Hemisphere; ITG – Inferior Temporal Gyrus; SFG – Superior Frontal Gyrus; SMA – Supplementary Motor Area; PFC - Prefrontal Cortex; PCC – Posterior Cingulate Cortex; MTG – Middle Temporal Gyrus; R – Right; L – Left.

SupplementaryTable 3. ROI-to-ROI connectivity correlating with divergent thinking ability contrasted between young and personality-matched older adults (Older Adults > Young Adults). Hence, Positive *T* values reflect ROI-to-ROI functional connectivity predicting divergent thinking in older adults, while negative *T* values correspond to ROI-to-ROI functional connectivity predictive of divergent thinking in young adults (corresponding to Supplementary Figure 3).

		Network	Hem	Node	MNI Coordinates			T	p
					X	Y	Z		
Young Adults									
Between Network Connectivity									
FPN – DN									
Inferior Precentral Sulcus	FPN	L	328	38.9	9.6	42.7			
	PCC	DN	R	162	12.3	-51.6	34.5	-4	0.028
	PCC	DN	L	1	-11.2	-52.4	36.5	-3.9	0.019
vmPFC	DN	L	152	-6	44.9	6.3			
	IFG	FPN	R	276	38.6	18.8	25.5	-3.9	0.033
	Posterior MTG	FPN	L	9	-55.9	-47.7	-9.3	-3.2	0.042
Within Network Connectivity									
DN-DN									
vmPFC	DN	L	152	-6	44.9	6.3			
	MFG	DN	L	116	-5.9	54.8	-11	-3.6	0.034
	SFG	DN	L	44	-19.5	30.1	45.4	-3.6	0.034
	STG	DN	L	127	-53.1	-11.4	-16	-3.4	0.035
	Dorsomedial PFC	DN	R	322	8.2	53.8	14	-3	0.047
Older Adults									
Between Network Connectivity									
SN-DN									
IPS	SN	R	219	57.5	-40.3	34.7			
vmPFC	DN	R	279	7.2	48.4	-10	4.35	0.009	
DN-FPN-SN									

Ventromedial PFC	DN	L	152	-6	44.9	6.3			
Anterior PFC	FPN	R	320	30.9	52.2	9.9	3.36	0.035	
MFG	SN	R	317	24.4	50.8	24.3	3.22	0.042	
<i>Within Network Connectivity</i>									
<i>DN-DN</i>									
vmPFC	DN	L	152	-6	44.9	6.3			
vmPFC	DN	R	184	7.7	44.1	5.5	3.13	0.042	

Note: DN - Default Network ; FPN - Fronto-parietal network; Hem - Hemisphere; IFG – Inferior Frontal Gyrus; IPS – Intraparietal Sulcus; MFG- Middle Frontal Gyrus; SFG – Superior Frontal Gyrus; STG – Superior Temporal Gyrus; SMA – Supplementary Motor Area; PFC - Prefrontal Cortex; PCC – Posterior Cingulate Cortex; MTG – Middle Temporal Gyrus; R – Right; L – Left.