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Sex differences in the relationship between white matter connectivity and creativity

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ABSTRACT

Creative cognition emerges from a complex network of interacting brain regions. This study investigated the relationship between the structural organization of the human brain and aspects of creative cognition tapped by divergent thinking tasks. Diffusion weighted imaging (DWI) was used to obtain fiber tracts from 83 segmented cortical regions. This information was represented as a network and metrics of connectivity organization, including connectivity strength, clustering and communication efficiency were computed, and their relationship to individual levels of creativity was examined. Permutation testing identified significant sex differences in the relationship between global connectivity and creativity as measured by divergent thinking tests. Females demonstrated significant inverse relationships between global connectivity and creative cognition, whereas there were no significant relationships observed in males. Node specific analyses revealed inverse relationships across measures of connectivity, efficiency, clustering and creative cognition in widespread regions in females. Our findings suggest that females involve more regions of the brain in processing to produce novel ideas to solutions, perhaps at the expense of efficiency (greater path lengths). Males, in contrast, exhibited few, relatively weak positive relationships across these measures. Extending recent observations of sex differences in connectome structure, our findings of sexually dimorphic relationships suggest a unique topological organization of connectivity underlying the generation of novel ideas in males and females.

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Introduction

Creative cognition is multifaceted, drawing on a wide range of mental faculties that enable individuals to develop novel and useful ideas (Stein, 1953). The process of creativity has been conceptualized as involving two stages: blind variation and selective retention (Campbell, 1960). The two stages utilize different brain regions in functional magnetic resonance imaging (fMRI) studies, suggesting that the blind variation and selective retention might represent distinct cognitive processes (Ellamil et al., 2012). Psychometrically, it is likely to be difficult to disentangle these two processes (Arden et al., 2010); however, divergent thinking has served as the primary measure most analogous to blind variation, as it measures an individual's ability to generate many ideas (Piffer, 2012).

Relative to the wealth of fMRI studies that have investigated divergent thinking, there are relatively few studies that have addressed the variation in underlying gray or white matter morphology and/or anatomical connectivity. Unlike other studies of cognitive abilities, increased creativity has been correlated to both increases and decreases in brain connectivity and cerebral volume elucidated through the use of proton magnetic resonance spectroscopic imaging (1H-MRSI), diffusion weighted imaging (DWI), and structural Magnetic Resonance Imaging (sMRI) (Jung et al., 2013). Two DWI investigations have examined the relationship between divergent thinking and Fractional Anisotropy (FA), a measure used to infer information about the underlying integrity of white matter fiber tracts (Johansen-Berg and Behrens, 2009). A whole brain voxel wise analysis found that increased FA near the bilateral prefrontal cortices, the body of the corpus callosum, the bilateral basal ganglia, the bilateral temporo-parietal junction and the right inferior parietal lobule was related to increased creative cognition (Takeuchi et al., 2010b). Examining FA values within a skeleton of the major white matter fiber pathways (Smith et al., 2006) Jung et al. (2010a) found lower FA to be related to increased scores on measures of divergent thinking within the left anterior thalamic radiation.

Studies that have examined volume and thickness of gray matter have found both increases and decreases across widespread regions related to higher creative cognition, with increases seen in the mid-brain,

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striatum, precuneus, dosolateral prefrontal cortex (Takeuchi et al., 2010a), superior parietal lobule (Gansler et al., 2011), posterior cingulate and right angular gyrus (Jung et al., 2010b). Additionally, cortical decreases related to higher creative cognition were found in the lingual, cuneus, angular gyrus, inferior parietal, fusiform gyrus, orbitofrontal cortex (Jung et al., 2010b) and the splenium of the corpus callosum (Gansler et al., 2011). From these studies, it is clear that the manifestation of creativity is associated with both excitatory and inhibitory relationship between cortical and subcortical regions spanning a widespread network of brain regions (Jung et al., 2013).

From functional connectivity analysis, there is increasing evidence showing correspondence between the regions implicated in creativity and the regions identified as being within the default mode network (DMN) (Jung et al., 2013). The DMN consists of regions where neural activity is higher during the baseline state than during an experimental task (Buckner et al., 2008; Greicius et al., 2003; Raichle et al., 2001; Shulman et al., 1997), and includes the medial prefrontal cortex (MPFC), medial temporal lobes (MTLs), and the posterior cingulate cortex (PCC)/retropslenial cortex (RCS). Many cognitive functions have been attributed to the DMN, including retrieval and manipulation of past events, both personal and general, in an effort to solve problems and develop future plans (Greicius et al., 2003). Buckner and Carroll (2007) suggest that the DMN is important in remembering the past, envisioning the future and considering the thoughts and perspectives of other people, all processes that could be construed as useful to developing novel ideas within a given context (i.e., creative).

Both the functional and structural studies of divergent thinking highlight the role of widespread variations in brain-behavioral relationships associated with creative cognition, although increasing evidence suggests that the DMN and the Executive Control Network (ECN) are predominant (Jung et al., 2013). The methods used in the vast majority of studies, to date, point to individual regions implicated in creativity; relatively few examined creativity in context of the network structure of the human brain. Instead of investigating the role of specific regions and pathways in isolation, fiber tractography can be used to construct and examine all of the connections in the brain, known as a connectome (Bullmore and Sporns, 2009; Craddock et al., 2013). By representing this information as a graph, measures of network organization can be extracted that indicate the extent of segregation and integration of connections (Rubinov and Sporns, 2010). Initial studies utilizing this approach characterized the brain as having a "small world" organization: in other words, the brain is organized such that there is a balance between local, clustered connectivity and global, long-range connectivity that facilitates efficient information transfer (Achard et al., 2006; Eguiluz et al., 2005; Sporns et al., 2004; Stam and Reijneveld, 2007b; van den Heuvel et al., 2008). The small world organization facilitates efficient information transfer via local processing within clusters that work in conjunction with several long-distance connections (Bullmore and Sporns, 2009; Latora and Marchiori, 2001; Watts and Strogatz, 1998a).

Small worldness is determined through the quantification of minimum path length, the shortest path needed to move from node i to j in a network, and clustering coefficient, the extent to which a node's neighbors are connected to each other (Bassett and Bullmore, 2006; Humphries and Gurney, 2008; Watts and Strogatz, 1998b). Using similar information, Latora and Marchiori (2001) proposed a measure of Global Efficiency that directly quantifies how efficiently information can be exchanged over the network. Evidence emerging through the use of both structural (diffusion weighted imaging) and functional imaging (fMRI, MEG) demonstrates that these measures are, in a general sense, quantifying local processing (high clustering) with an optimum number of long range paths (high efficiency) (Bullmore and Sporns, 2009; Stam and Reijneveld, 2007a). There is also growing interest in how these structural networks relate to the functional networks, with studies finding that the functional connectivity network organization is constrained by the underlying structural organization. In other words, the functional network can only be as efficient and clustered as its underlying connectivity (Greicius et al., 2009; Honey et al., 2009; van den Heuvel and Sporns, 2013a,b; van den Heuvel et al., 2009).

Individual differences in these network properties (i.e., higher efficiency) have been linked to measures of individual differences including intelligence (Li et al., 2009; van den Heuvel et al., 2009), and are being increasingly used to identify how variations in network metrics relate to cognitive dysfunction (de Haan et al., 2012; Fair et al., 2010). Several studies have found substantial sex differences in brain connectivity, suggesting that differential connectivity patterns may account for cognitive differences (Gong et al., 2009a, 2011; Ingalhalikar et al., 2013). While these studies posit potential cognitive differences resulting from the differing organization of male and female brains, they did not examine this relationship directly. Using other brain measures, such as the grey matter and white matter volumes and the functional and structural connectivities, there are numerous studies identifying sex differences in the relationship between brain measures and cognitive abilities (Gur et al., 1999), particularly with respect to higher order cognition, such as intelligence (Haier et al., 2005; Jung et al., 2005; Schmithorst, 2009; Schmithorst and Holland, 2007). In light of the recent studies emphasizing sex differences in structural brain organization and previous sex interactions in the relationship between brain structure and cognitive ability, this study investigates whether structural network properties significantly relate to creativity and whether the relationship between the structural connectome and creativity differ by sex. Second, we investigate whether variations in the network properties of individual regions of the brain are predictive of divergent thinking and if these regions are primarily within the DMN and ECN.

Materials and methods

Participants

Participants were young adults (21.53 +/− 2.93 years; 59 males, 47 females) recruited by postings in various departments and classrooms around the University of New Mexico. This study was conducted according to the principles expressed in the Declaration of Helsinki, and was approved by the Institutional Review Board of the University of New Mexico. All subjects provided written informed consent before the collection of data and subsequent analysis. One hundred and nineteen volunteers, with no history of neurological or psychological disorder, participated in the study. Thirteen individuals were excluded in the data analysis due to the low quality of their neuroimaging data (i.e. motion or image artifacts), resulting in 106 human subjects for analysis.

Behavioral measures

Four divergent thinking tasks were administered: Verbal and Drawing Creativity Tasks, Uses of Objects Test (UOT), described in detail elsewhere (Lezak et al., 2004; Miller and Tal, 2007) and generation of captions to New Yorker Magazine cartoons. Four independent judges (two females, two males) ranked the DT products of each participant using the consensual assessment technique (Amabile, 1982) from which a "Composite Creativity Index" (CCI) was derived. The raters were of the same cohort as the subjects (19–29; college student/graduate). Raters were instructed to rate each subject's DT product from 1 (lowest creativity) to 5 (highest creativity) according to their own notion of "creativity," and were instructed to bin rankings to conform to a normal distribution (e.g., 5% each 1's and 5's, 10% each 2's and 4's, 70% 3's). Rankings for each subject were averaged across the four measures and converted to a standard score to facilitate easy comparisons between FSIQ and the creativity measure, referred to as the Composite Creativity Index (CCI). The raters had excellent inter-rater reliabilities across the four measures of DT (i.e., CCI $\alpha = .81$).

To assess general intelligences, subjects were tested with the Wechsler Adult Inventory Scale (WAIS-III) (Wechsler, 1981). The

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