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Metaphor is a common form of figurative language, yet little is known about how the brain produces novel figurative expressions. Related research suggests that dynamic interactions between large-scale brain systems support a range of complex cognitive processes, particularly those requiring focused internal attention and cognitive control. However, the extent to which these networks interact to support core processes of figurative language production remains unknown. The present research explored this question by assessing functional interactions between brain regions during novel metaphor production. Participants completed a metaphor production task and a literal control task during functional magnetic resonance imaging (fMRI). Whole-brain functional connectivity analysis revealed a distributed network associated with metaphor production, including several nodes of the default (precuneus and left angular gyrus; AG) and executive (right intraparietal sulcus; IPS) networks. Seed-based analyses showed direct function connections between core hubs of the default, salience, and executive networks. Moreover, analysis of temporal network dynamics found early functional coupling of the left AG and right anterior insula that preceded subsequent coupling of the left AG and left DLPFC, pointing to a potential switching mechanism underlying default and executive network interaction. These results extend recent work on the cooperative role of large-scale networks during complex cognitive processes, and suggest that metaphor production involves dynamic cooperation between brain systems linked to cognitive control, semantic integration, and spontaneously-generated thought.

BRAIN NETWORKS UNDERLYING FIGURATIVE LANGUAGE PRODUCTION

by

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CHAPTER I

INTRODUCTION

Metaphor is widely used to express abstract concepts and complex emotions, both in the arts and everyday life. Researchers have long been interested in the cognitive and neural processes underlying metaphor comprehension—how nonliteral language is processed and understood (Glucksberg, 2001; Mashal, Faust, Hendler, & Jung-Beeman, 2007; Rapp, Leube, Erb, Groot, & Kircher, 2004). Compared to the large literature on metaphor comprehension, however, little is known about how figurative language is actually constructed. Behavioral research has only recently begun to explore the cognitive processes involved in metaphor production (Chiappe & Chiappe, 2007; Silvia & Beaty, 2012; Beaty & Silvia, 2013), and neuroimaging research has shed light on the neural mechanisms underlying metaphor production (Benedek et al., 2014a). Thus far, such work suggests that metaphor production taps cognitive and neural systems involved in executive control, semantic integration, and self-generated thought. Nevertheless, it remains unclear how these different systems interact to support metaphor production.

Neuroscience research has increasingly shifted from analyzing brain regions in isolation to examining interactions between regions (i.e., functional connectivity; Sporns, 2014). A functional connectivity approach can reveal the extent of cooperation between large-scale brain systems such as the default mode network (DMN) and the executive control networks (ECN; Cocchi, Zalesky, Fornito, & Mattingley, 2013), networks associated with internal attention and executive control, respectively (Andrews-Hanna, 2012). Such methods have recently been

employed to study neural networks underlying creative cognition, and emerging evidence suggests that the DMN and ECN cooperate during creative idea production (Beaty, Benedek, Kaufman, & Silvia, in press) and evaluation (Ellamil, Dobson, Beeman, & Christoff, 2012). An important next step in the metaphor production literature is to determine how individual brain regions interact to support figurative language production. The proposed research thus seeks to address this question by examining brain networks underlying creative metaphor production.

Behavioral Correlates of Metaphor Production

The property attribution model of metaphor comprehension (Glucksberg, 2001) is one of the most influential cognitive models in the metaphor literature. According to this model, metaphor comprehension involves establishing an abstract link between a topic (a referent concept; e.g., “music”) and a vehicle (a conceptually similar exemplar; e.g., “medicine”). Metaphor comprehension is facilitated by means of an attributive category, which extracts and relates semantic information from two seemingly unrelated concepts stored in long-term memory. For the metaphor “music is a medicine,” for example, the attributive category “something that is healing” can be used to link conceptually similar information about music and medicine, which are otherwise unrelated concepts. In this context, metaphor comprehension can be conceived as a series of complex search and retrieval processes requiring the executive control of attention and cognition.

An attributive category involves the generation and maintenance of specific memory retrieval parameters (e.g., “search memory for something that is healing”). This process should benefit from executive mechanisms due to high demands on controlled retrieval and inhibitory processes. In addition, the process of identifying appropriate semantic properties for a candidate vehicle requires the suppression of conceptually irrelevant information. For example, “music” and “medicine” are conceptually dissimilar in many ways (music is an auditory phenomenon,

medicine is a branch of science), so these features must be suppressed for their common attributes (e.g., “healing properties”) to be established. Executive mechanisms thus appear to play a central role in the complex process of metaphor comprehension.

Early behavioral research on metaphor production employed an individual differences approach to study cognitive processes involved in conventional metaphor production. Conventional metaphors are culturally familiar expressions of figurative language—most people have encountered them before, and they are relatively easy to comprehend (e.g., “Life is a journey”; Glucksberg, 2001). In their first study, Chiappe and Chiappe (2007) explored whether individual differences in various cognitive abilities predicted the aptness of participant-generated metaphors. The authors examined the contribution of working memory capacity, verbal fluency, and vocabulary knowledge in the production of conventional metaphors. The metaphor production task presented participants with short phrases (e.g., “Some jobs are _____”) and properties (e.g., “something that is confining and constraining”); responses were rated for aptness by trained raters.

Results revealed large effects of vocabulary knowledge on aptness ratings, and smaller but significant effects of working memory capacity. These results provided seminal insight into the cognitive basis of metaphor production, and suggested that constructing conventional metaphors draws more upon acquired knowledge than executive processes. Research on conventional metaphor, however, has limitations for researchers interested in the cognitive processes underlying creative metaphor production. Unlike conventional metaphors, which are simply recalled from long-term memory (Chiappe & Chiappe, 2007), creative metaphors are novel, so they must be generated “on the spot” by combining stored conceptual knowledge into novel mental representations.

Silvia and Beaty (2012) sought to extend the metaphor production literature by employing a new task to assess creative metaphor production. Similar to Chiappe et al. (2007), the study also explored whether executive processes contributed to metaphor production. In contrast to the relatively constraining task prompts used by Chiappe and colleagues, Silvia and Beaty asked participants to respond to open-ended prompts based on past emotional experiences. For example, one prompt asked participants to construct a novel metaphor to describe the experience of consuming a disgusting food or drink. Responses were coded for creative quality by three trained raters using the subjective scoring method (Silvia et al., 2008). To assess the role of cognitive abilities, participants completed a battery of non-verbal fluid intelligence (Gf) tasks (e.g., Ravens Advanced Progressive Matrices). Latent variable models revealed a large effect of Gf on the creative quality of metaphor responses—as Gf increased, participants generated increasingly novel metaphors. This study extended the earlier work of Chiappe and colleagues by demonstrating that executive abilities also influence novel metaphor production.

The results of this study were interpreted within the context of the property attribution model of metaphor (Glucksberg, 2001). Although initially conceived as a model of metaphor comprehension, Silvia and Beaty (2012) adapted the model to explain the cognitive processes underlying metaphor production. When constructing a metaphor, one must generate an attributive category to relate conceptual information from two exemplars (e.g., searching memory for “something that is healing” when relating “music” and “medicine”). As noted above, salient but irrelevant conceptual information can become activated during the search process, thus disrupting the idea generation process. Executive processes may facilitate metaphor production by providing the inhibitory control needed to suppress task-irrelevant knowledge and maintain higher-order attributive categories during such complex search processes.

In a follow-up study, Beaty and Silvia (2013) explored the role of other potentially relevant cognitive abilities in metaphor production. They also sought to determine the relative contribution of these abilities in creative and conventional metaphor production, in light of Chiappe and colleagues' work showing effects of working memory and vocabulary knowledge. Participants completed the creative metaphor task of Silvia and Beaty (2012) and the conventional metaphor task of Chiappe and Chiappe (2007). The property attribution model posits that metaphor processing involves the generation and maintenance of higher-order attributive categories, which guide the retrieval of concepts from semantic memory (Glucksberg, 2001). Because of the high theoretical demands on selective retrieval mechanisms, Beaty and Silvia (2013) assessed individual differences in broad retrieval ability (Gr) with verbal fluency tasks. Fluency tasks require participants to selectively retrieve exemplars from memory by generating and maintaining search cues—a process that may involve retrieval mechanisms relevant for metaphor production. The authors also assessed general knowledge with several measures of crystallized intelligence (Gc). Although past work had reported contributions of general knowledge to conventional metaphor production (Chiappe & Chiappe, 2007), it remained unclear whether this ability similarly predicted creative metaphor production.

Latent variable models assessed the contribution of the cognitive ability variables (Gf, Gr, and Gc) on conventional and creative metaphor production. Replicating their previous study, Beaty and Silvia (2013) found that Gf strongly predicted creative metaphor—as Gf increased, participants generated metaphors that were rated as more creative. Results also showed a large effect of verbal fluency (Gr) on creative metaphor, and a moderate but nonsignificant effect of general knowledge (Gc). Regarding conventional metaphor, only general knowledge showed a significant effect on aptness ratings; the effects of Gf and Gr were small and nonsignificant. The results for conventional metaphor were largely consistent with past work: Chiappe and Chiappe

(2007) reported large effects of general knowledge, and relatively small effects of cognitive abilities (e.g., working memory capacity). Beaty and Silvia (2013) interpreted the results as evidence for a role of executive processes in creative metaphor production, and a role of crystallized knowledge in conventional metaphor production.

Neural Correlates of Metaphor Production

Behavioral research on metaphor production has been supplemented by a recent neuroimaging study examining the neural correlates of metaphor production (Benedek et al., 2014a). Using functional magnetic resonance imaging (fMRI), Benedek and colleagues explored brain regions involved in the production of creative metaphors, compared to a baseline condition requiring the production of synonyms. Participants were presented with brief phrases relating objects to characteristics (e.g., the lamp is [glaring]) and asked to complete the phrases with metaphors or literal expressions. Based on the available evidence on metaphor processing and creative idea generation, Benedek et al. expected metaphor generation to be associated with increased activity in the left hemisphere, especially the left inferior parietal cortex, a region involved in semantic integration (Binder, Desai, Graves, & Conant, 2009). Moreover, the authors expected the creative quality of metaphor responses to be associated with left prefrontal brain activation, regions involved in executive control processes, in light of past work on metaphor novelty and creativity.

Results revealed that compared to synonym production, metaphor production was associated with increased activation of several brain regions, primarily located in the left hemisphere. The strongest effect was observed in the left lateral parietal cortex, peaking in the left angular gyrus (AG). Metaphor production was also related to activation in the left middle frontal gyrus (MFG), left superior frontal gyrus (SFG), bilateral posterior cingulate cortex (PCC), ventral precuneus, bilateral parahippocampal and fusiform gyri, the left lingual gyrus, and the

right posterior cerebellum. The reversed contrast (synonym > metaphor) did not reveal further significant effects. Notably, however, a conjunction analysis revealed several regions common to metaphor and synonym production, including the left inferior frontal gyrus (IFG) and right middle temporal gyrus (MTG), regions involved in strategic memory retrieval and semantic processing, respectively.

Benedek and colleagues found that metaphor production was related to activation of the left AG, a region commonly implicated during passive metaphor processing (Rapp et al., 2012). In a meta-analysis of 120 neuroimaging studies, the left AG was identified as the most consistently activated during tasks involving semantic processing (Binder et al., 2009). Due to its involvement in a variety of semantic processes, the left AG has been conceived as a supramodal association area, and it is presumed to play a key role in strategic knowledge retrieval and complex information integration. Further overlap with regions involved in metaphor processing was observed in the parahippocampal gyri, regions essential for declarative memory (Squire, Stark, & Clark, 2004). Together, these regions are assumed to contribute to nonliteral language processing in general, both comprehension and production, by extracting and relating shared semantic information between remotely associated concepts.

Both the PCC and the left AG are considered central components of the semantic memory system (Binder et al. 2009). However, these regions have also been identified as core hubs of the brain's default mode network (Raichle, Leube, Erb, Grodd, & Kircher, 2001), a network of midline and inferior parietal regions associated with internally directed attention and self-referential cognition (Andrews-Hanna, 2012). Default network regions are also commonly activated during various forms of mental simulation, including spatial scene construction (Hassabis & Maguire 2007), theory of mind reasoning (Buckner & Carroll 2007), and episodic future thinking (Schacter et al., 2012). In this context, activation of default network regions may

reflect increased involvement of spontaneous imaginative processes during the construction of novel figurative expressions.

Brain Networks and Creative Cognition

The study of figurative language production provides a new approach to understanding how the brain produces creative ideas. Previous neuroimaging studies have used a range of tasks to investigate the neural correlates of creative cognition, such as insight problem solving, divergent thinking, story generation, and musical improvisation (e.g., Beaty, 2015; Bowden et al. 2005; Fink et al. 2009; Howard-Jones et al. 2005; for reviews, see Arden et al. 2010; Fink & Benedek, 2014). Early reviews on the neuroscience of creativity showed largely inconsistent findings (Arden et al., 2010), possibly due to a wide range of experimental tasks used to assess creative thought. However, studies focusing on divergent thinking—the generation of novel solutions to open-ended problems—have revealed a relatively consistent pattern of results (Gonen-Yaacovi et al., 2013; Wu et al., in press). Neuroimaging research on divergent thinking may provide insight into the neural basis of metaphor generation, as both processes involve the construction of novel mental representations.

One of the most commonly activated regions in the neuroimaging literature on divergent thinking is the left inferior parietal lobe (IPL; Gonen-Yaacovi et al., 2013). Fink and colleagues (2009) compared performance on tasks with greater creative demands (generating novel uses for objects) and tasks with lower creative demands (generating typical characteristics of objects). Generating creative ideas was associated with increased activation in the left IPL and decreased activation in the right temporoparietal junction (see also Abraham et al., 2012). Furthermore, Benedek and colleagues (2014b) assessed the novelty of verbal responses to an alternate uses task during functional imaging. Generating novel uses (responses participants identified as unfamiliar to them prior to scanning) was related to stronger activation in the left IPL compared to

generating previously known uses (responses participants had retrieved from memory). As noted above, the left IPL—and more specifically, the left AG—plays an important role in semantic integration (Binder et al., 2009) and mental scene construction (Hassabis & Maguire, 2007). And as a core hub of the DMN, the left IPL is also thought to contribute to the brain’s ability to flexibly recombine stored information in memory into novel mental representations (e.g., episodic future thinking; Schacter et al., 2012). Notably, the left IPL showed strong activation during metaphor production (Benedek et al., 2014a), and it is commonly implicated in studies of metaphor comprehension (Rapp et al., 2012).

Although regions of the DMN appear to be important for creative thought, a large body of evidence suggests that executive processes also play a central role. Several studies implicate regions within the executive control network (ECN)—a set of lateral prefrontal and superior parietal regions that show increased activation during tasks involving focused external attention (e.g., pre-potent response inhibition; Seeley et al., 2007). The ECN and DMN typically show an antagonistic or “anticorrelated” pattern of activity at rest and during cognitive tasks (Andrew-Hanna, 2012). During working memory tasks, for example, the ECN shows increased activity while the DMN shows decreased activity. Because DMN activity is related to mind-wandering and spontaneous cognition (Andrews-Hanna, Smallwood, & Spreng, 2014), researchers hypothesize that DMN deactivation reflects suppression of task-unrelated thoughts during executively-demanding cognitive tasks (Bressler & Menon, 2010; Seeley et al., 2007).

Co-activation of DMN and ECN regions, however, raises questions about how these seemingly opposing networks interact to support creative thought. Beaty and colleagues explored this question by examining dynamic interactions between brain regions during a divergent thinking task (Beaty et al., in press). Participants completed an alternate uses divergent thinking task (generating creative uses for common objects) and an object characteristics tasks (generating

typical characteristics of the objects; cf. Fink et al., 2009; Kleibuker, Koolschijn, Jolles, De Dreu, & Crone, 2013). Whole-brain functional connectivity was assessed using multivariate pattern analysis (MVPA). Unlike conventional univariate analysis, MVPA tests for differences in whole-brain (voxel-to-voxel) connectivity, thus revealing brain regions showing differential correlation as a function of task condition (Whitfield-Gabrieli & Nieto-Castanon, 2012). Beaty et al. also explored temporal connectivity patterns to determine the time-course of functional coupling across the duration of the task.

The whole-brain connectivity analysis revealed a distributed network of regions associated with divergent thinking, including several clusters in frontal, temporal, and parietal cortices. In line with past research, divergent thinking was related to increased activation of default network regions, such as the precuneus, posterior cingulate cortex (PCC), and bilateral IPL. However, the network also included a core hub of the executive network—right dorsolateral prefrontal cortex (DLPFC)—as well as the left inferior frontal gyrus (IFG), a region associated with controlled memory retrieval. In sum, results from the whole-brain analysis pointed to increased cooperation of brain networks associated with cognitive control (e.g., DLPFC) and spontaneous imaginative processes (e.g., PCC).

Beaty and colleagues also examined which regions within the network were more strongly connected during the task. The default (precuneus and PCC) and executive (DLPFC) regions identified in the whole-brain analysis were specified as regions of interest for further seed-based functional connectivity analysis. Results revealed increased functional connectivity between the default network seeds (precuneus and PCC) and executive network regions (DLPFC). The precuneus and PCC seeds also showed connectivity with bilateral insula and dorsal anterior cingulate cortex, core hubs of the salience network—a network involved in switching between the DMN and ECN (Menon & Uddin, 2010; Uddin, 2015). Likewise, the right

DLPFC seed showed increased connectivity with several default regions, including the right IPL, precuneus, and PCC. These results extended the whole-brain analysis by revealing direct functional connections between the core hubs of the default and executive networks.

A follow-up analysis explored the time-course of functional connectivity across the duration of the divergent thinking task. Results revealed differential functional coupling of network regions at different stages of divergent thinking. At the beginning of the task, the precuneus and PCC showed increased functional connectivity with regions of the salience network (bilateral insula and ACC). But at later stages of the task, the PCC showed increased connectivity with the right DLPFC, pointing to delayed interaction between default and executive networks. This pattern of results was mirrored with the DLPFC seed: the DLPFC only increased its connectivity with default regions (right IPL and PCC) later in the task. In sum, results from the temporal connectivity analysis revealed dynamic coupling among default, salience, and executive regions at different stages of divergent thinking: default regions coupled with salience regions at the beginning of the task and with executive regions at later stages. Because the salience network is involved in switching between the DMN and ECN (Menon & Uddin, 2010; Uddin, 2015), Beaty and colleagues interpreted early coupling between default and salience regions as reflecting an intermediate switching mechanism that facilitated subsequent coupling between the DMN and ECN.

The Present Research

The recent work of Beaty et al. (in press) suggests that creative cognition involves cooperation between key nodes of the default and executive networks. But to what extent do such networks interact during other creative thought processes such as metaphor production? Benedek et al. (2014a) found that metaphor production recruited the left angular gyrus and the posterior cingulate—core default network regions associated with semantic processing and spontaneous

imaginative processes (Andrew-Hanna, 2012; Binder et al., 2009; Buckner & Carroll, 2007; Schacter et al., 2012). Yet the authors also reported activation of regions within the prefrontal cortex associated with cognitive control, such as the superior and middle frontal gyri. It therefore remains unclear whether interaction between executive and default regions similarly underlies metaphor production, or whether such regions act in isolation.

To address this question, the present study examined brain networks during performance on a metaphor production task. Participants completed the metaphor and synonym production tasks from Benedek et al. (2014a). A similar analytic approach as described in Beaty et al. (in press) was employed to assess functional connections among brain regions during metaphor production, and temporal connectivity analyses explored whether metaphor production involves similar network interactions as divergent thinking. In light of Beaty et al. (in press) and other recent work reporting co-activation of the default and executive control networks during creative thinking tasks (e.g., Ellamil et al., 2012), a similar pattern of functional connectivity was expected to emerge during metaphor production. A secondary goal of the study was to replicate the univariate findings of Benedek et al. (2014a). Because the same experimental design was employed, it was expected that this analysis would reveal increased activation of regions reported in Benedek et al. (e.g., left AG and PCC). In sum, metaphor production was expected to be related to a network of brain regions involved in semantic integration, executive control, and spontaneous imaginative processes.

CHAPTER II

METHOD

Participants

Participants were recruited from the UNCG Psychology Department subject pool and from announcements in undergraduate psychology classes. Subject pool participants received credit toward a research option in their psychology course, and participants recruited in psychology classes received \$20 in cash; all participants were given a free anatomical image of their brain on CD as a thanks for their participation in the study. Prior to the study, participants were sent an IRB-approved MRI safety screening form via email. The form included questions regarding medical history (e.g., psychiatric disorders) and potential contraindications to participating in MRI research (e.g., metal implants in the body). Due to the language-intensive nature of the cognitive tasks, non-native English speakers were not invited to participate in the study. All participants also self-reported right hand dominance. After screening, participants completed an IRB-approved consent form (see Appendix A).

The original sample consisted of 36 young adults from the University of North Carolina at Greensboro (UNCG). Data from one subject was excluded from the analysis due to excessive head movement ($> 15\text{mm}$), resulting in a final sample of 35 (mean age = 20.77, $SD = 5.05$; 22 women, 13 men).

Procedure

Participants completed two tasks during functional imaging: a metaphor production task and a synonym production task. The experimental procedure and stimuli were exactly the same as

in Benedek et al. (2014a). Both tasks presented short phrases relating a noun to an adjective in parentheses; for example, “The lamp is (glaring).” The metaphor task required participants to generate a creative metaphor that conveys the meaning of the adjective and could replace it in the phrase (e.g., “a supernova”). The synonym task required the generation of synonyms that convey the meaning of the adjective and could replace it in the phrase (e.g., “bright”). Prior to scanning, participants received thorough training on the metaphor and synonym tasks with an experimenter. The training session involved a brief tutorial on the difference between metaphors and synonyms, followed by eight practice trials (four metaphor, four synonym). The sequence of these trials followed the sequence of events in the scanner.

Figure 1 depicts the experimental paradigm. A block began with a fixation period (5 s), followed by a cue (5 s) indicating the task to be performed in that block (metaphor or synonym). After the cue, six trials were presented separated in time by jittered (3-7 s) fixation null periods. Additional 10-s fixation periods were presented at the beginning and end of the session. Task stimuli were presented in white letters at the middle of a black screen. In both tasks, participants had 10 s to think of a response. This duration was sufficient to elicit a response in Benedek et al. (2014a): on average, participants produced valid responses in 87% of metaphor trials and 90% of synonym trials, and self-reported task difficulty ratings collected after the experiment showed no significant differences between tasks.

If participants produced a response in less than 10 s, they were encouraged to come up with an even more creative metaphor or a more appropriate synonym, respectively. After the 10 s, the stimulus turned green for 5 s, indicating that participants should vocalize their response (see Figure 1). The temporal separation of idea generation and response periods is commonly employed in neuroscientific studies on creative idea generation to avoid artifacts related to overt responses (Fink & Benedek, 2014).

Participants performed a total of 48 trials using 48 different stimulus phrases (see Appendix B). For each participant, half of the phrases were randomly assigned to either task (i.e., metaphor and literal). To maximize the power of the task contrast, trials were grouped into eight task blocks (four metaphors, four synonyms) in an ABBAABBA/BAABBAAB fashion, with each block containing six trials of one task.

MRI Data Acquisition and Preprocessing

Participants completed the metaphor and synonym tasks in a single fMRI run. The scanner and data acquisition settings were the same as in Benedek et al. (2014a). Whole-brain imaging was performed on a 3T Siemens Magnetom MRI system (Siemens Medical Systems, Erlangen, Germany) using a 16-channel head coil. BOLD-sensitive T2*-weighted functional images were acquired using a single shot gradient-echo EPI pulse sequence (TR = 2400 ms, TE = 30 ms, flip angle = 90°, 35 axial slices, 3.5 x 3.5 x 3.5 mm, distance factor 20%, FoV = 240x240 mm, interleaved slice ordering) and corrected online for head motion. The first two volumes were discarded to allow for T1 equilibration effects.

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) 8 package (Wellcome Institute of Cognitive Neurology, London). Functional volumes were coregistered and resliced to a voxel size of 2mm³, normalized to the Montreal Neurological Institute (MNI) template brain and smoothed with an 8 mm³ isotropic Gaussian kernel.

Functional connectivity analysis was implemented in the CONN toolbox (<http://www.nitrc.org/projects/conn>; Whitfield-Gabrieli & Nieto-Castanon, 2012) in Matlab. For each participant, CONN implemented CompCor, a method for identifying principal components

associated with segmented white matter (WM) and cerebrospinal fluid (CSF; Behzadi, Restom, Liau, & Liu, 2007). These components were entered as confounds along with realignment parameters in a first-level analysis. Because CompCor accounts for the effects of subject movement (Chai, Nieto-Castanon, Ongur, & Whitfield-Gabrieli, 2012), the global BOLD signal was not regressed.

Analytic Approach

The functional connectivity analysis was conducted in two steps. First, to identify brain regions showing significantly greater functional connectivity during metaphor production compared to synonym production, whole-brain connectivity was analyzed with MVPA (Whitfield-Gabrieli & Nieto-Castanon, 2012). MVPA assesses the entire multivariate pattern of pairwise connections between all voxels in the brain. First-level voxel-to-voxel covariance matrices were computed for each participant and for both tasks, permitting second-level analyses that tested for differences in whole-brain connectivity between conditions by means of a statistical F-test. In contrast to standard univariate analysis, which considers the effects of each voxel cluster separately using the general linear model, MVPA accounts for multivariate dependencies in the data. Hence, the second-level statistical analysis yields voxel clusters showing significantly greater functional connectivity with some other region (or regions) during metaphor production compared to synonym production.

Next, regions of interest (ROI) were extracted based on peak activation clusters from the whole-brain analysis. Because MVPA is an omnibus statistical test, such post-hoc analyses are needed to determine specific connectivity patterns in the data (Whitfield-Gabrieli & Nieto-Castanon, 2012). Seed-to-voxel analyses were conducted to assess correlations between these ROIs and the rest of the brain across the task duration. Temporal changes in functional connectivity were also assessed by dividing the total task duration into four 2.4 s intervals,

corresponding to the total task duration (10 s) divided by the repetition time of the fMRI sequence (2.4 s; see also Beaty et al., in press).

T-tests on Fisher's Z -transformed correlations were used to test for differences in functional connectivity between task conditions. Unless otherwise noted, all results are reported when significant at a voxelwise threshold of level of $p < .001$ uncorrected, and a cluster-level threshold of $p < .05$ familywise error (FWE) corrected.

CHAPTER III

RESULTS

Multivariate Pattern Analysis

The MVPA task contrast (metaphor > synonym) revealed a distributed network of voxel clusters associated with metaphor production (see Table 1 and Figure 2). The network consisted of several frontal and parietal regions, including regions within the default network—the precuneus and left angular gyrus (AG). The network also included the right intraparietal sulcus (IPS, BA 7), a region of the executive network. Several other regions reported in Benedek et al. were associated with metaphor production, including the left superior frontal gyrus (SFG), middle frontal gyrus (MFG), right parahippocampal gyrus (PHG), left lingual gyrus, and the cerebellum; the network also included a cluster in the right anterior middle temporal gyrus (MTG) and left IFG, regions reported in parametric analyses in Benedek et al (2014a). In sum, the whole-brain analysis revealed several of the same regions reported by Benedek and colleagues, including the precuneus and left angular gyrus, core hubs of the DMN.

Univariate Analysis

A secondary goal of the present study was to replicate the results of Benedek et al. (2014a). Thus, a general linear model was specified in SPM to assess univariate effects for the main task contrast (metaphor > synonym). Results revealed several of the same clusters reported in Benedek et al.; however, results only showed significance at a less conservative statistical threshold ($p < .001$ uncorrected; see Figure 3 and Table 2). Metaphor production was associated with greater activation in bilateral AG (BA 39) and left MFG (BA 8). A large cluster was also

found in the left precuneus (BA 7) and a smaller cluster was found in the right PCC (BA 30). Finally, the reverse contrast (synonym > metaphor) revealed significant activation in the right parahippocampal gyrus (BA 35). In sum, the univariate analysis found activation of several of the same brain regions as in the univariate analysis of Benedek et al. (2014a) and the multivariate analysis reported above.

Seed-to-Voxel Analyses

Next, a series of post-hoc analyses were conducted to further characterize functional connections between select regions of the DMN (left AG and precuneus) and ECN (right IPS) found in whole-brain analysis. The average BOLD signal within each ROI was correlated with the average signal within all other voxels in the brain during metaphor production, and a conservative statistical threshold was applied to the resulting clusters (i.e., $p < .05$, FWE corrected).

The first analysis assessed connectivity between the left AG and the rest of the brain during metaphor production. The left AG showed increased functional connectivity with two large clusters that peaked in bilateral precuneus. Both clusters extended to superior parietal cortex (BA 7; see Table 3 and Figure 4a). The left AG also showed increased coupling with a cluster of voxels in left dorsolateral prefrontal cortex (BA 46)—a key node of the ECN—as well as a cluster in occipital cortex. Notably, the DLPFC cluster did not appear in the whole-brain analysis, suggesting that its connectivity with the AG during metaphor production may have been transient.

Results for the precuneus seed revealed connectivity with eight voxel clusters (see Table 3 and Figure 4b). The precuneus showed increased connectivity with several regions within the frontal lobes, including the left IFG (BA 47), left DLPFC (BA 9), and right rostrolateral prefrontal cortex (RLPFC; BA 10). Thus, the precuneus was more strongly connected to several regions involved in executive control processes during metaphor production.

Finally, the right IPS (an ECN region) was specified as a seed to explore its connectivity with the rest of the brain during metaphor production. The IPS showed increased connectivity with two clusters that peaked in the precuneus (BA 7) as well as with clusters in occipital cortex (BA 19); no additional connectivity differences were found for the right IPS seed. The seed-to-voxel analyses thus revealed increased functional coupling between key nodes of the default and executive networks during metaphor production.

Seed-to-Voxel Temporal Connectivity

Temporal connectivity analysis was then conducted to determine whether the default and executive network regions showed differential coupling across the duration of the task. This approach could reveal whether regions not identified in the whole-brain or seed-to-voxel analyses reported above showed transient or sustained connectivity with the default and executive ROIs at different stages of metaphor production.

At the beginning of the task, the left AG showed increased coupling with a cluster in the right precuneus that extended to the right superior parietal lobe (see Figure 5). The precuneus showed increased coupling with a region in left MFG, and the right IPS showed coupling with bilateral superior parietal lobes (BA 7). In sum, metaphor production was characterized by sparse connectivity between regions during the first time window, with no apparent connections between default and executive network nodes.

During the second time window, the left AG showed sustained coupling with the precuneus (see Figure 5). The left AG also increased coupling with a cluster in left somatosensory cortex (BA 40) and right anterior insula (BA 13). Connectivity between the left AG and right insula points to increased cooperation between default and salience network nodes at an intermediate stage of metaphor production. The precuneus showed a diffuse pattern of positive connectivity with clusters in occipital cortex, as well as with bilateral IPS and bilateral

rostrolateral prefrontal cortex (RLPFC; BA 10). Finally, the right IPS showed positive coupling with two clusters in superior parietal cortex that extended to the precuneus (BA 7). The second time window of metaphor production was thus marked by cooperation between default and salience network nodes, consistent with Beaty et al. (in press).

During the third time window, the left AG showed sustained coupling with the precuneus, and novel coupling with a large voxel cluster peaking in the right IPS. The left AG also showed increased coupling with a cluster in the left DLPFC (BA 9), pointing to increased cooperation between the left AG and two key nodes of the ECN (i.e., right IPS and left DLPFC). The precuneus showed a similar pattern of connectivity with occipital and rostrolateral prefrontal cortices during the third time window as it did during the second window. Likewise, the right IPS showed the same pattern of connectivity with bilateral SPL as was found during the previous time window. Thus, the third window revealed increased cooperation between default and executive regions.

Finally, during the fourth window, the left AG showed sustained coupling with the right IPS and novel coupling with a cluster in the left IPS. The precuneus remained functionally connected to occipital cortex and the left DLPFC, and the IPS remained coupled with bilateral SPL. Functional connectivity between regions thus remained largely unchanged from the third to fourth windows, with the exception of increased coupling between the left AG and the left IPS, a region of the ECN, pointing to increased cooperation between DMN and ECN regions at later stages of metaphor production.

CHAPTER IV

DISCUSSION

The present study explored brain networks underlying figurative language production. Multivariate pattern analysis was used to determine brain regions showing greater functional connectivity during metaphor production compared to synonym production. Results revealed a distributed network associated with metaphor production, including several core hubs of the default and executive networks. Seed-based functional connectivity analysis showed direct functional connections between these regions, and temporal connectivity analyses showed differential coupling at different stages of metaphor production, including transient connectivity between default, salience, and executive network regions. Taken together, the results extend previous research on metaphor production by elucidating patterns of functional connectivity related to figurative language production, providing further support for the notion that creative cognition involves cooperation between brain regions associated with executive control and spontaneous thought (Abraham, 2014; Beaty et al., 2014a, in press; Jung et al., 2013; McMillan et al., 2013; Mok, 2014).

The whole-brain MVPA revealed several significant voxel clusters related to metaphor production (see Table 1). These included two core regions of the DMN, the left AG and precuneus, as well as the right IPS, a core hub of the ECN. The whole-brain network also included clusters in frontal and occipital cortices, regions associated with executive control and mental imagery, respectively. Post-hoc analyses were used to determine relations among specific regions. The precuneus seed showed widespread connectivity with several regions during metaphor production. The precuneus was functionally connected to regions in the frontal lobes,

including the left IFG and the left DLPFC, areas associated with controlled memory retrieval and executive processes. The precuneus was also coupled with clusters in superior parietal cortex, including the intraparietal sulcus (IPS)—a region of the ECN associated with the manipulation of information in working memory (Koenigs, Barbey, Postle, & Grafman, 2009). In addition, the precuneus showed increased connectivity with clusters in occipital cortex, pointing to a potential cooperation with a region involved in visual mental imagery manipulation (Sasaoka, Mizuhara, & Inui, 2013). The diffuse connectivity profile of the precuneus is consistent with its role as a multimodal convergence zone (Binder & Desai, 2011). Moreover, although the precuneus is often associated with the default network and spontaneous cognition (Andrews-Hanna, 2012), specific regions of the precuneus have been associated with cognitive control (Margulies et al., 2009). Taken in the context of metaphor production, the precuneus may manage and synthesize information from other regions involved in semantic integration (AG), executive processes (IPS and DLPFC), and mental imagery (MOG).

The left AG showed a similar pattern of connectivity during metaphor production. Seed-based analyses revealed direction connections between the left AG, precuneus, posterior parietal cortex, and inferior frontal cortex. Like the precuneus, the left AG also showed coupling with the left DLPFC, a core region of the ECN. Moreover, the right IPS—an ECN region associated with manipulation of information in working memory (Koenigs et al., 2009)—showed increased coupling with the precuneus during metaphor production. Such coupling suggests that metaphor production involves cooperation between default and executive regions, consistent with the recent research on creative idea production (Beaty et al., in press) and evaluation (Ellamil et al., 2011).

The temporal connectivity analyses provided further insight into dynamic interactions within the network during metaphor production. Interestingly, increased coupling between the left

AG and left DLPFC was only found later in the task (time window 3), pointing to transient connectivity between these regions at latter stages of metaphor production. However, the left AG showed increased coupling with right anterior insula, which preceded connectivity with the left DLPFC. The anterior insula is a core region of the salience network (Uddin, 2015), and it plays a central role in switching between other large-scale networks, such as the DMN and ECN (Menon & Uddin, 2010). Such findings are consistent with Beaty et al. (in press), which found that coupling between default and salience regions preceded coupling between default and executive regions during a divergent thinking task. Thus, early transient connectivity between default and salience regions may facilitate later connectivity between default and executive regions, pointing to a potential switching mechanism underlying creative cognition.

Comparing Findings with Previous Research on Metaphor Production

The present research sought to replicate and extend Benedek and colleagues' original study of metaphor production. To this end, this study used the same experimental paradigm, stimuli, and MRI protocol as Benedek et al (2014a). A univariate analysis was used to contrast brain activation related to metaphor production compared to synonym production, providing insight into individual brain regions associated with the task conditions. The main difference between studies, however, was the use of functional connectivity methods in the present research. This approach permitted an assessment of functional relations between regions during metaphor production—a procedure which was not reported by Benedek and colleagues.

Overall, the results of the two studies were largely similar. Using univariate analysis, both studies found significant activation of the left AG and the precuneus, two core default mode regions. Both studies also reported activation of the left middle frontal gyrus (MFG), a region associated with executive functions. Notably, Benedek et al. also reported activation of several regions that were not found in the present univariate results, including the left lingual gyrus, left

superior frontal gyrus (SFG), right posterior cerebellum, and bilateral parahippocampal gyrus. The present study found that the right parahippocampal gyrus was more strongly activated during synonym production during metaphor production, which may be due to various differences between the two culturally distinct samples. Future research should thus further clarify the role of the hippocampus in metaphor production.

Interestingly, the MVPA results actually showed closer similarity to Benedek et al. (2014a). Of the eight clusters associated with metaphor production in that study, the MVPA showed activation of seven clusters within close proximity. Moreover, the MVPA showed activation of the left IFG and right MTG, regions also reported in Benedek et al., albeit in a conjunction analysis (left IFG) and a parametric analysis (right MTG). But across studies and types of analysis (MVPA and univariate), the two regions showing the most robust activation were the left AG and the precuneus. The precuneus and left AG may therefore comprise a core network underlying creative metaphor production.

Creative Cognition and Brain Network Dynamics

A primary goal of this study was to explore brain network dynamics associated with metaphor production. This approach informs recent work in the field of creativity neuroscience as well as the growing literature on large-scale network interactions during complex cognitive tasks (cf. Cocchi et al., 2013; Hearne, Cocchi, Zalesky, & Mattingley, in press; Hutchison & Morton, 2015; Spreng et al., 2014). Both fields are beginning to challenge the notion that core brain networks like the DMN and ECN always exhibit an antagonistic relationship (Andrews-Hanna et al., 2014). Instead, such work suggests that large-scale networks show dynamic reconfigurations during cognitive processes such future planning (Gerlach, Spreng, Gilmore, & Schacter, 2011), self-regulation (Hare, Camerer, & Rangel, 2009), emotional regulation (Buhle et al., 2014), memory suppression (Depue et al., 2007), and even cognitive control (Cocchi et al., 2013; Spreng

et al., 2014). The present results provide further evidence that creative cognition involves cooperation between the DMN and ECN, networks that typically act in opposition.

The results provide an interesting contrast to the recent work of Beaty et al. (in press) on brain networks underlying divergent thinking. Beaty and colleagues used MVPA to identify brain regions showing increased functional connectivity during divergent thinking (i.e., alternate uses generation). Similar to metaphor production, the MVPA results revealed a distributed network of regions that included several core hubs of the DMN, such as the left AG, precuneus, and PCC. The network also included the right DLPFC, a core hub of the ECN (Seeley et al., 2007). Likewise, the present study found that metaphor production was associated with activation of default (the left AG and precuneus) and executive (right IPS) network nodes. At the whole-brain level, MVPA showed that both divergent thinking and metaphor production recruit brain regions associated with cognitive control and spontaneous thought.

To further characterize network dynamics, Beaty and colleagues used similar seed-based analyses as in the present study. The authors focused on the default and executive network regions to determine whether these regions showed increased coupling during divergent thinking. Seed-based analyses revealed a similar pattern of default-executive network coupling: the precuneus showed increased connectivity with the left DLPFC, and the PCC showed increased connectivity with the right DLPFC. A similar pattern emerged in the present study—metaphor production was also associated with increased connectivity between the precuneus and the left DLPFC. Further metaphor-related connectivity was found between the precuneus and bilateral IPS which was not found in Beaty et al. (in press), possibly reflecting task-specific connectivity related to figurative language production.

The temporal connectivity results suggest that default-executive network coupling occurred at later stages of metaphor production. Beaty and colleagues also found a similar pattern

of temporal coupling during divergent thinking: default and executive regions were functionally disconnected at the beginning of the task, but showed strong positive coupling at later stages of the task. Another notable similarity between the studies was the transient connectivity between default and salience network regions early in the task. During metaphor production, the left AG showed early coupling with the right anterior insula—a core region of the salience network (Menon & Uddin, 2010)—that preceded later coupling with the DLPFC. Likewise, Beaty et al. found that the PCC showed early coupling with regions of salience network nodes (bilateral insula), and later coupling with executive network nodes (DLPFC). It therefore seems that early coupling between default and salience regions may facilitate later coupling between default and executive regions during tasks involving creative idea production.

As noted above, the insula is a core region of the salience network (Uddin, 2015). Together with the anterior cingulate cortex, the salience network plays a key role in orienting attention to salient external and internal information (Menon & Uddin, 2010). Menon and colleagues have further elucidated a critical role of the salience network in switching between other large-scale networks, especially the DMN and ECN (Sridharan, Levitin, & Menon, 2008). The salience network is anatomically interposed between the core hubs of the DMN and ECN, and is thus well-positioned to facilitate network switching (Menon & Uddin, 2010). In light of the salience network's role in switching between the DMN and ECN, Beaty et al. (in press) interpreted early coupling of the PCC with salience network nodes as reflecting an intermediate switching mechanism needed to facilitate subsequent coupling with the ECN. A similar interpretation may explain the pattern observed in the present study: early coupling between the left AG and right anterior insula may be required for later coupling with the ECN. Dynamic coupling between the default and executive networks during creative cognition may therefore be facilitated by means of intermediate coupling between the default and salience networks.

The notion that creative cognition involves cooperation between regions associated with cognitive control and spontaneous thought was further supported by a recent resting-state functional connectivity study (Beaty et al., 2014a). One of the most commonly implicated regions in the literature on divergent thinking is the left inferior frontal gyrus (IFG; Gonen-Yaacovi et al., 2013). The IFG is associated with experimental tasks that require controlled retrieval from semantic memory (Costafreda, Fu, Lee, Everitt, Brammer, & David, 2006; Poldrack, Wagner, Prull, Desmond, Glover, & Gabrieli, 1999). This region has consistently shown activation when demands on memory retrieval are increased, especially when a task involves selecting items among competing associates and when switching between semantic categories is required (Costafreda et al., 2006; Hirshorn & Thompson-Schill, 2006). Activation of the left IFG in studies of creative cognition is thus hypothesized to reflect selective retrieval mechanisms involved in the top-down control of complex search processes. The notion that creative cognition taps selective retrieval mechanisms is consistent with recent behavioral research on the role of verbal fluency ability in divergent thinking (Silvia, Beaty, & Nusbaum, 2013), which found large effects of verbal fluency on the creative quality of divergent thinking responses.

The resting-state study of Beaty et al. (2014) examined intrinsic functional connectivity patterns in participants of high- and low-divergent thinking ability. The authors hypothesized that if brain regions linked to both executive control (IFG) and spontaneous processes (DMN) are important for creative thought, such regions may show increased functional connectivity “at rest” in individuals of high-divergent thinking ability. High- and low-divergent thinking ability groups were defined based on performance on a battery of divergent thinking tasks completed outside of the scanner, and the IFG was specified as a seed region of interest for functional connectivity analysis. Compared to the low-creative group, the high-creative group showed increased functional connectivity between the left IFG and the core regions of the default network,

including medial prefrontal cortex (MPFC), posterior parietal cortex (PCC), and bilateral inferior parietal lobes (IPL). The high-creative group also showed increased connectivity between the right IFG and bilateral IPL, as well as the right DLPFC. These results suggest that individuals of high-divergent thinking ability show greater functional coupling between the inferior prefrontal cortex and the default network, pointing to an enhanced cooperation brain regions linked to cognitive control and spontaneous thought.

Further support for the cooperative role of controlled and spontaneous processes comes from a recent behavioral study (Beatty, Benedek, Nusbaum, Jauk, & Silvia, 2014b). This study assessed individual differences in executive function and associative ability to determine the relative contribution of these variables to divergent thinking. Participants completed several measures of fluid intelligence and verbal fluency. To assess associative ability, the authors used responses to verbal fluency tasks and a novel technique derived from latent semantic analysis (LSA), a software-based method that computes the semantic similarity of inputted terms based on a large database of written texts. Cue words for the verbal fluency tasks were compared with participant responses, and the resulting semantic similarity values were averaged for each participant and subtracted from one to derive a measure of semantic distance (cf. Prabhakaran et al., 2014). Thus, for the verbal fluency task “list synonyms for the word *good*”, highly semantically similar associates to the cue word (*good*) were assigned low scores (e.g., “great”) and interpreted as reflecting low associative ability. Participants completed two alternate uses tasks which were scored for creative quality using the subjective scoring method (Silvia et al., 2008).

In two studies, latent variable models assessed the unique contribution of executive and associative abilities in divergent thinking ability. Consistent with past work (e.g., Benedek, Jauk, Sommer, Arendasy, & Neubauer, 2014c; Silvia et al., 2013), results revealed significant effects of

executive abilities on divergent thinking—both fluid intelligence and verbal fluency showed unique effects on the creative quality of divergent thinking responses. Moreover, associative ability also predicted divergent thinking across both studies: as the average semantic distance between cue words and participant responses increased, the creative quality of divergent thinking responses increased. Importantly, the effects of the executive and associative ability variables remained robust predictors in the same model, pointing to an important role of both processes in creative cognition. Taken together, these results suggest that creative thought processes involve both the ability to exert cognitive control and spontaneous flexibility during memory retrieval.

Limitations and Future Directions

The present research identified brain networks underlying figurative language production. This work extends previous research on metaphor production and creative cognition by showing increased cooperation between regions of the DMN and ECN, large-scale brain systems involved in opposing modes of attention and cognition. Despite the strengths of the present work, some limitations should be noted. First, the experimental design was constrained by a rather brief period for idea generation (i.e., 10 s). With additional time to generate a response, participants may have been able to produce more creative metaphors, as time on task and creative quality are highly correlated (Silvia & Beaty, 2012). Nevertheless, a shorter period may be beneficial as it can isolate brain activity related to idea generation, whereas prolonged periods may be contaminated by brain activation unrelated to idea generation (cf. Fink & Benedek, 2014). In addition, technical difficulties with the MRI-compatible microphone lead to a loss of verbal response data for nearly one third of participants, which prevented an analysis of brain activity related to the creative quality of metaphor responses.

Another limitation of the present study concerns the extent to which participants were solely engaged in idea generation. Indeed, some participants may have generated a response

within the first few seconds of the task, leaving the remaining task duration for other processes (e.g., generating another response or elaborating on the first response). At the same time, there is behavioral evidence to suggest that creative idea generation does not occur within the first few seconds (e.g., Prabhakaran et al., 2014). For example, Prabhakaran and colleagues found that generating creative verbs took an average of 5 seconds, and a study of episodic simulation found that generating novel future events took participants an average of 7.5 seconds (Addis, Pan, Vu, Laiser, & Schacter, 2009). Notably, this study differentiated between idea generation and elaboration: participants were asked to make a button press once they had generated an idea, and to use the remaining time to elaborate on the idea.

Future research on metaphor generation should use similar approaches to identify brain activity related to idea generation and other related processes. Because the present study employed the same experimental paradigm as Benedek et al. (2014a), asking participants to make a button press once they had successfully generated a metaphor may have altered the results. Future work should explore network interactions underlying idea generation and evaluation in metaphor production, an approach that has been adopted in other studies of creative cognition. For example, Ellamil et al. (2012) asked visual artists to create book covers based on a series of prompts, and found differential brain network patterns for idea generation versus idea evaluation. Similar methods may be used to tease apart specific sub-processes underlying metaphor production. Such approaches may explain the temporal connectivity results of the present study: for example, creative idea production may be related to early default-salience coupling, whereas idea evaluation may be related to later default-executive coupling. Nevertheless, these interpretations remain speculative and rely on some degree of reverse inference (Poldrack, 2006). Future research should employ behavioral measures and test specific hypotheses regarding functional interactions between brain regions during creative cognition.

CHAPTER V

CONCLUSION

The present research identified a whole-brain network associated with metaphor production, including several core hubs of the default and executive networks. Results from temporal connectivity analyses revealed an intermediate switching mechanism within the salience network—the right anterior insula—that may facilitate later interactions between default and executive network regions. This pattern of functional coupling points to increased cooperation among brain regions involved in mental simulation, executive control, and semantic integration. Taken together, the results provide new insight into the brain networks underlying figurative language production, and highlight the importance of large-scale network interaction in creative cognition.

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APPENDIX A

TABLES

Table 1. Multivariate Pattern Analysis Task Effects

Region	BA	x	y	z	voxels
L Inferior Frontal G.	47	-32	16	-18	165
L Middle Frontal G.	6/8	-20	8	58	484
L Superior Frontal G.	6	-10	38	60	56
L Angular G.	39	-38	-64	50	489
L Precuneus	7	-6	-64	54	1016
L Precentral G.	31	-4	-26	46	301
R Intraparietal S.	40	42	-50	46	100
R Middle Temporal G.	21	58	-4	-20	301
R Parahippocampal G.	36	30	-36	-10	44
L Lingual G.	18	-4	-96	20	70
R Middle Occipital G.	18	32	-96	16	299
L Cerebellum	-	-12	-42	-36	98

Note. L = left, R = right; C = cortex, G = gyrus. Results are corrected for multiple comparisons

(FWE, $p < .05$).

Table 2. Univariate Analysis Task Effects

Region	BA	x	y	z	voxels
<i>Metaphor > Synonym</i>					
L Middle Frontal G.	6/8	-20	8	58	484
L Angular G.	39	-38	-64	50	489
R Angular G.	39	38	-62	32	138
L Precuneus	7	-6	-64	54	1016
L Posterior Cingulate	31	-4	-26	46	301
<i>Synonym > Metaphor</i>					
R Parahippocampal G.	35	22	-2	-28	40

Note. L = left, R = right; G = gyrus. Results are uncorrected for multiple comparisons ($p < .001$, $k > 20$).

Table 3. Seed-to-Voxel Functional Connectivity Results

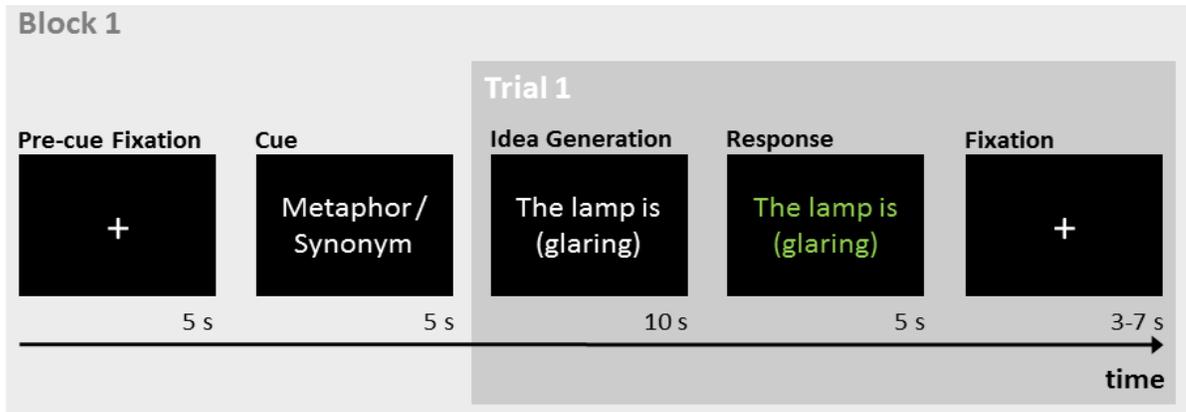
Seed/Region	BA	x	y	z	voxels
1. L Angular G.					
R Precuneus	7	12	-68	54	2369
L Precuneus	7	-14	-62	54	882
L Middle Frontal G. (DLPFC)	9	-42	46	30	173
L Middle Occipital G.	18	-12	-74	14	288
2. L Precuneus					
L Inferior Frontal G.	47	-50	42	-6	635
L Middle Frontal G. (DLPFC)	9	-52	12	36	230
R Superior Frontal G.	10	28	58	2	175
R Intraparietal S.	7	32	-66	36	566
L Intraparietal S.	7	-22	-70	40	269
R Middle Occipital G.	18	28	-86	-8	1065
L Middle Occipital G.	18	-30	-94	-2	1028
R Cerebellum	-	22	-78	-48	145
3. R Intraparietal S.					
R Precuneus	7	26	-68	60	1642
L Precuneus	7	-18	-70	48	459
R Middle Occipital G.	19	42	-82	0	241
L Middle Occipital G.	19	-32	-92	12	153

Note. Results are shown for select default (left AG & precuneus) and executive (right IPS) network regions. L = left, R = right; C = cortex, G = gyrus, S = sulcus; DLPFC = dorsolateral prefrontal cortex. Results are corrected for multiple comparisons (FWE, $p < .05$).

APPENDIX B

FIGURES

Figure 1. Schematic Sequence of the fMRI Task Paradigm



Note. Schematic sequence of first trial within a task block. After an initial fixation period, a cue will indicate whether participants should generate metaphors or synonyms in this block. Participants will have 10 s to complete the sentence by generating a metaphor or a synonym. Responses will be given in the subsequent response period (5 s) indicated by the stimulus word changing color to green. Trials will be separated by jittered fixation periods.

Figure 2. Multivariate Pattern Analysis for the Whole-Brain Task Contrast

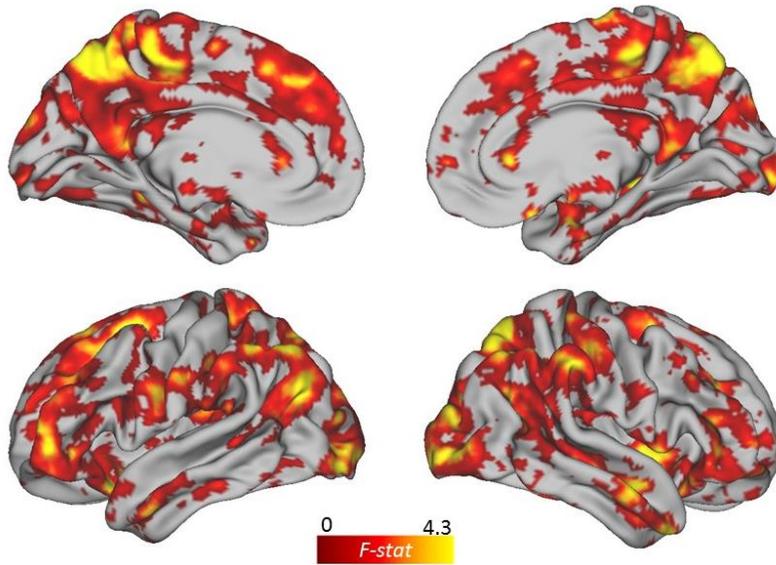


Figure 3. Univariate Analysis for the Whole-Brain Task Contrast

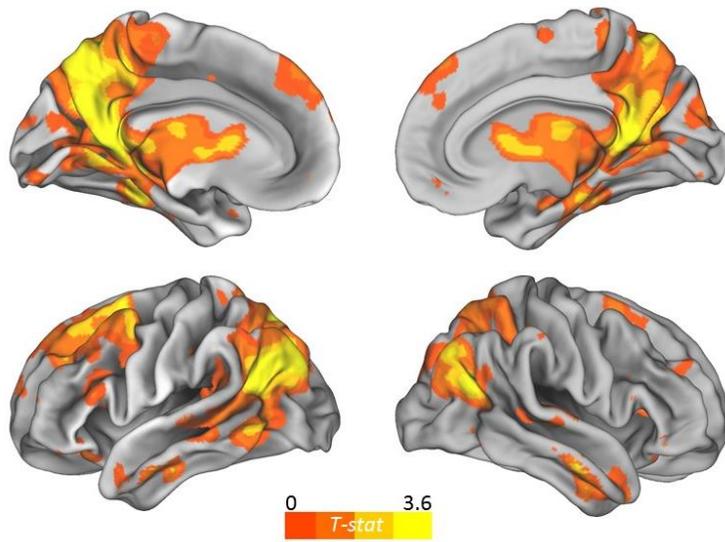
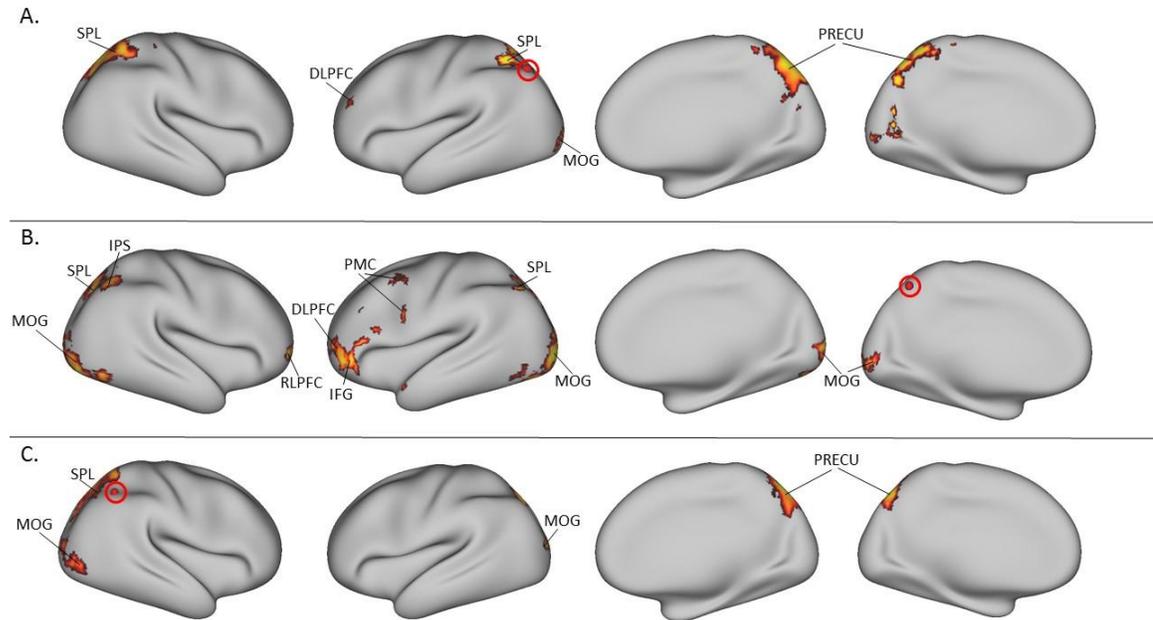
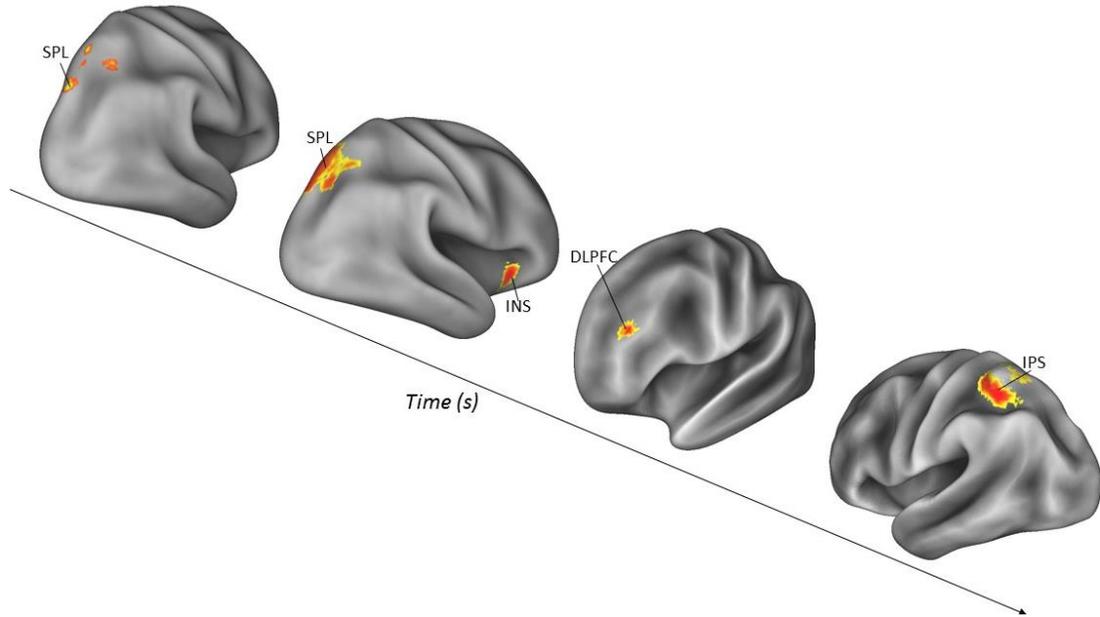


Figure 4. Seed-to-Voxel Analysis for Select Regions of Interest



Note. Results are shown for select default and executive network regions, including the left AG (A), left precuneus (B), and right IPS (C). Seed regions are located within red circles. AG = angular gyrus; DLPFC = dorsolateral prefrontal cortex; IFG = inferior frontal gyrus; IPS = intraparietal sulcus; MOG = middle occipital gyrus; PRECU = precuneus; RLPFC = rostralateral prefrontal cortex; SPL = superior parietal lobe.

Figure 5. Seed-to-Voxel Temporal Connectivity Analysis



Note. Each brain surface represents one time window (or TR; i.e., 2.4 s). DLPFC = dorsolateral prefrontal cortex; INS = insula; IPS = intraparietal sulcus; SPL = superior parietal lobe.

APPENDIX C

PARTICIPANT CONSENT FORM

UNIVERSITY OF NORTH CAROLINA AT GREENSBORO *CONSENT TO ACT AS A HUMAN PARTICIPANT: LONG FORM*

Project Title: Thinking Styles and Creativity

Project Director: Dr. Paul Silvia

Participant's Name:

What is the study about?

This is a research project. Your participation is voluntary. The study investigates different thinking styles, such as how people reason and come up with creative ideas. If you decide to participate in this research study, you will be asked to complete some computerized tasks and questionnaires, and then undergo functional magnetic resonance imaging (fMRI) at the Joint School of Nanoscience and Nanoengineering (JSSN). The study takes about two hours to complete. Your participation and all of the information from the assessment will be kept completely confidential. You will be assigned an identification number. All of the information regarding research participants will be identified by this number.

Why are you asking me?

People are eligible to participate if they are at least 18 years-old, right-hand dominant, and have signed up on Experimentrix.

MRI uses a very strong magnetic fields and powerful radio waves. While an MRI exam is safe for most people, there are a number of instances when it is unsafe (even potentially fatal) for someone to be in or around a MRI scanner. In order to make sure the MRI procedure will be safe for you, you will be asked to fill out a screening form before starting the study. It is important that you tell the researchers in this study:

- if you have a heart pacemaker
- if you have a neurological disorder
- if you take medications that affect the central nervous system
- if you have metal in your head (not including dental work)
- if you have metal in your spine or heart
- if there is the possibility of metal in your eyes,
- if you have any implanted medical device in your body,
- if you have an implant in your body held in place with a magnet,
- if you have had surgery in the last 6 weeks,
- if you weigh more than 450 pounds,
- if you are pregnant or there is the possibility that you are pregnant.

What will you ask me to do if I agree to be in the study?

People will be asked to travel to JSNN for function brain imaging; you will also be asked to complete some tasks and questionnaires that measure personality and thinking styles. We will provide you with directions and schedule a convenient time for you to complete the study at JSNN. The study will take about two hours. If you have any questions regarding this study, please contact Roger Beaty at rebeaty@uncg.edu.

Before your MRI exam is scheduled you will be asked to answer a series of questions about your medical history to determine if an MRI exam is safe for you. We are interested in knowing if you have any metal inside your body that could result in injury during the MRI exam. You will also be asked your height, weight, sex, and birthdate. After it has been determined that it is safe for you to have an MRI exam, your MRI exam will be done at the Joint School of Nanoscience and Nanotechnology in Greensboro, NC.

On the day of your scheduled MRI exam, you will be asked to answer the same questions again to verify that nothing has changed and that it is still safe for you to have an MRI exam. You will be in the MRI scanner for about 60 minutes.

For your safety, you will be monitored the entire time you are in the scanner. The study team will be able to talk to you and hear you talk during the exam through an intercom. You will also be given a safety-ball to squeeze with your hand if you want to stop the exam at any time for any reason. **You will be in the MRI scanner for about 60 minutes. This is a functional MRI (fMRI) study. During the fMRI study, you will be asked to complete several different computerized tasks; you will also be asked to rest silently with your eyes closed for five minutes. We will be measuring how the brain responds during different tasks, and the patterns of activity that occur during rest.**

For your safety, you will be monitored the entire time you are in the scanner. The study team will be able to talk to you and hear you talk during the exam through an intercom. You will also be given a ball to squeeze with your hand if you want to stop the exam at any time for any reason.

Is there any audio/video recording?

There is no audio or video recording in this experiment.

What are the risks to me?

One potential risk concerns a breach of confidentiality. However, several steps (discussed below in the section “How will you keep my information confidential?”) have been taken to minimize this risk and to ensure confidentiality. Another risk concerns your discomfort and/or embarrassment with the questionnaires. However, the questionnaires were carefully selected to avoid any questions that are inappropriate or intrusive. Second, the fMRI machine can be noisy and uncomfortable. We take every effort to minimize any potential discomfort you may experience throughout the scanning session, but you are free to end the session at any point if you do not feel comfortable. If you have any concerns about your rights, how you are being treated, or if you have questions, want more information or have suggestions, please contact the Office of Research Compliance at UNCG at (336) 256-1482. Questions, concerns or complaints about this project or benefits or risks associated with being in this study can be answered by Roger Beaty (rebeaty@uncg.edu) or Dr. Paul Silvia (p_silvia@uncg.edu).

The Institutional Review Board at the University of North Carolina at Greensboro has determined that participation in this study poses minimal risk to participants. MRI scanners have been in clinical use for about 20 years. When the MRI is used properly, there are no known risks to having an MRI scan for most people. Unlike X-rays, CT scans, and nuclear medicine studies, the MRI machine does not use X-rays or other forms of ionizing radiation. Instead, the MRI scanner uses strong magnetic fields and radio waves to measure your brain activity when you lay on a bed in a tube.

Metal objects: Metal objects within or on your body and clothing can cause harm to you, in addition to distorting the quality of the MRI images. Such things as keys, watches, and credit cards will be kept safely away from the machine. We will ask you to take off all removable metal (e.g. jewelry, piercings, etc.). People with devices or objects inside their body that are affected by strong magnetic fields (i.e. metallic foreign bodies inside your head or in your eyes, incompatible medical implants, pacemakers, brain stimulators, blood vessel clips, etc.) will not be allowed to participate under any circumstances. Knowingly participating in this study with these types of metallic implants can lead to serious injury or death. Although metal objects sensitive to strong magnetic fields are not allowed in the MRI scanner, there are many metal objects that are not sensitive to strong magnetic fields, such as dental work, pins or screws used during surgery, and even some tattoos contain metal. People with these types of metal objects may safely participate in this study. You will go through an extensive screening process to determine if the MRI scanner is safe for you before allowing have your MRI exam

Burn risks: In extremely rare cases, metal in the body (e.g., in tattoos) exposed to the powerful radio waves used in MRI may heat up. This heating occurs gradually but if it goes unreported during the MRI exam it could lead to burns. Such burns are easily prevented by reporting any heating sensations that you have to the technologists immediately. For your safety, you will be monitored the entire time you are in the scanner. The study team will be able to talk to you and hear you talk during the exam through an intercom. You will also be given a ball to squeeze with your hand if you want to stop the exam immediately and for any reason.

Fear of small places: MRI machines require you to enter a tube about 2 feet in diameter and place your head in small helmet. For people with a fear of small spaces this can cause anxiety. If you experience anxiety during your MRI exam please let the technologist know. If you decide that you cannot complete the scan, you will be removed immediately from the scanner, and released from the study.

Hearing loss: MRI scanners when taking a picture are very loud. You will be required to wear earplugs during the exam. When the earplugs are used properly, the noise from the MRI scanner is as loud as a garbage disposal or food blender. If the earplugs are not inserted into the ear canal then temporary hearing loss is possible. If at any time the noise from the MRI machine is too loud inform the technologist.

Muscle twitching and tingling: MRI machines turn magnetic fields on and off very quickly to make an image. In rare cases, this may cause your muscles to twitch and tingle. The muscle twitching and tingling are temporary and will stop as soon as the scanner stops. In some rare cases, some individuals find the muscle twitching and tingling to be uncomfortable and cannot continue with the MRI exam. If this happens to you let us know and you will be released from the study.

Other miscellaneous risks: There are other short-term effects that have been reported in very rare cases during the MRI exam. These effects range from dizziness, to taste sensations, to light flashes during the MRI exam. These effects are temporary and occur as you move in and out of the MRI machine. In most cases, these effects go away very quickly. If these sensations persist and you are unable to continue with the MRI exam, inform the researchers and you will be removed from the MRI exam and released from the study.

Pregnancy: It is unclear at this time whether strong magnets are a risk to unborn fetuses. Due to the unknown risk and potential harm to an unborn fetus from any MRI scan, pregnant women will be excluded. All women will be asked before entering the scanner if they are pregnant.

The MRI images completed as part of this study are not for clinical diagnostic purposes. The MRI images in this study will not be reviewed by a physician. If you would like to review these images with your physician, we will give you a copy of your images on a CD.

This research project asks questions about a wide range of feelings and behaviors, including feelings of being depressed. If any questions on the questionnaires make you feel uncomfortable, you may choose to skip that question. In addition, if you are concerned about feelings of depression or about any other mental health issues, we would like to make you aware of some services that are available to you on campus. One option is the Counseling Center, which is part of the Student Health Services ([336-334-5340](tel:336-334-5340)). The other is the UNCG Psychology Clinic ([336-334-5662](tel:336-334-5662)). If you would like to talk to someone about your feelings, there are professionals available who can meet with you and, if necessary, recommend treatment options.

Are there any benefits to me for taking part in this research study?

There are no direct benefits to participants in this study. You will receive a copy of your MRI on a CD.

Are there any benefits to society as a result of me taking part in this research?

Individuals' participation may contribute to scientific knowledge about the thinking processes and brain science related to how people remember and imagine experiences.

Will I get paid for being in the study? Will it cost me anything?

For this study, you will be asked to travel to the JSNN campus, and the transportation costs are not covered by the university. JSNN is approximately five miles from UNCG main campus.

How will you keep my information confidential?

All information obtained in this study is strictly confidential unless disclosure is required by law. The imagining data obtained via the fMRI scanner can only be accessed by the researchers. This information, as well as the electronic files containing the questionnaire data, will be stored on a computer that is kept in a locked office. Participants will be assigned an identification number and all of the information regarding participants will be identified by that number. A master list linking your name to your study ID number will be stored separate from the data in a locked office.

What if I want to leave the study?

You have the right to refuse to participate or to withdraw at any time, without penalty. If you do withdraw, it will not affect you in any way and you will still receive credit. If you choose to

withdraw, you may request that any of your data which has been collected be destroyed unless it is in a de-identifiable state.

What about new information/changes in the study?

If significant new information relating to the study becomes available which may relate to your willingness to continue to participate, this information will be provided to you.

Voluntary Consent by Participant:

By signing this consent form/completing this survey/activity (used for an IRB-approved waiver of signature) you are agreeing that you read, or it has been read to you, and you fully understand the contents of this document and are openly willing consent to take part in this study. All of your questions concerning this study have been answered. By signing this form, you are agreeing that you are 18 years of age or older and are agreeing to participate, or have the individual specified above as a participant participate, in this study described to you by the research assistant. All of your questions concerning this study have been answered.

Signature: _____ Date: _____

APPENDIX D

METAPHOR AND SYNONYM TASK ITEMS

The picture is (colorful)	The table is (round)	The car is (spacious)
The book is (big)	The wind is (gentle)	The man is (weak)
The boy is (thin)	The dish is (tidy)	The floor is (slippery)
The room is (dark)	The voice is (shrill)	The neighbor is (loud)
The alley is (narrow)	The friend is (strong)	The tower is (shaky)
The screen is (flat)	The sun is (warm)	Health is (precious)
The swimmer is (fast)	The fabric is (soft)	
The skin is (smooth)	The cat is (wild)	
The lamp is (glaring)	The music is (monotonous)	
The hat is (big)	The place is (quiet)	
The food is (marvelous)	The mosquito is (aggressive)	
The bread is (hard)	The plant is (fragile)	
The star is (bright)	The bus is (slow)	
The girl is (pretty)	The job is (boring)	
The room is (cold)	The billboard is (ugly)	
The dog is (small)	The room is (messy)	
The line is (curvred)	The bathroom is (dirty)	
The neighbor is (lazy)	The bar is (crowded)	
The hall is (empty)	The pillow is (comfortable)	
The shoe is (wet)	The cake is (square)	
The paper is (rough)	The woman is (devious)	