

## Brain networks underlying novel metaphor production



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### ABSTRACT

Metaphors are widely used to convey abstract concepts and emotions in the arts and everyday life. Neuroimaging research suggests that dynamic interactions among large-scale brain networks, including the default and executive control networks, support the production of such creative ideas. However, the extent to which these networks interact to support other forms of creative language production such as metaphor remains unknown. Using functional magnetic resonance imaging (fMRI), we explored this question by assessing functional interactions between brain regions during novel metaphor production. 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 control (right intraparietal sulcus; IPS) networks. Seed-based analyses showed increased connectivity between these network hubs, and temporal connectivity analysis found early coupling of default (left AG) and salience (right anterior insula) regions that preceded later coupling of the left AG and left DLPFC, pointing to a potential switching mechanism underlying default and executive network interaction. The results extend recent work on the cooperative role of large-scale networks in creative cognition, and suggest that metaphor production involves similar brain network dynamics as other forms of goal-directed, self-generated cognition.

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### 1. Introduction

Researchers have long been interested in the cognitive and neural mechanisms underlying figurative language comprehension—how nonliteral language such as metaphor is processed and understood (Glucksberg, 2001; Mashal, Faust, Hendler, & Jung-Beeman, 2007; Rapp, Leube, Erb, Grood, & Kircher, 2004; Vartanian, 2012). Compared to this large literature, however, relatively little is known about how new figurative expressions are produced. Behavioral research has only recently explored the cognitive processes involved in metaphor production (Beaty & Silvia, 2013; Chiappe & Chiappe, 2007; Silvia & Beaty, 2012), and neuroimaging research has just begun to examine the neural mechanisms underlying metaphor production (Benedek, Beaty et al., 2014). Emerging evidence suggests that metaphor production involves brain systems involved in executive control, semantic integration, and self-generated thought. Nevertheless, it remains unclear how these different systems interact to support the production of new metaphorical expressions.

Cognitive neuroscience has increasingly shifted from analyzing brain regions in isolation to examining interactions between regions (i.e., networks; Medaglia, Lynall, & Bassett, 2015; Zabelina & Andrews-Hanna, 2016). Network-based approaches can reveal the extent of cooperation between large-scale brain systems such as the default network (DN) and the executive control networks (ECN; Cocchi, Zalesky, Fornito, & Mattingley, 2013)—networks associated with self-generated thought and cognitive control, respectively (Andrews-Hanna, Smallwood, & Spreng, 2014). Network methods have recently been employed to study neural networks underlying creative cognition, and mounting evidence suggests that the DN and ECN cooperate during creative idea production and evaluation (Beaty, Benedek, Silvia, & Schacter, 2016). An important next step in the study of metaphor production is to determine how individual brain regions interact during figurative language production. The present research thus seeks to address this question by examining brain networks underlying creative metaphor production.

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## 2. Figurative language and creative cognition

Neuroimaging research on figurative language has provided considerable insight into the neural mechanisms supporting metaphor comprehension (for reviews, see Rapp, Mutschler, & Erb, 2012; Vartanian, 2012). On the other hand, relatively little is known about how the brain actually produces new metaphors. To date, only a single study has examined neural correlates of metaphor production using functional magnetic resonance imaging (fMRI; Benedek, Beaty et al., 2014). 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 (e.g., “a supernova”) or literal expressions (e.g., “bright”). Compared to synonym production, metaphor production was associated with increased activation of several brain regions, with the strongest effect observed in the left angular gyrus (AG). The left AG is consistently activated during tasks involving semantic processing (Binder, Desai, Graves, & Conant, 2009), and it has been implicated during passive metaphor processing (Rapp et al., 2012). 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. In this context, the left AG may extract and relate shared semantic information between remotely associated concepts during metaphor processing.

Benedek and colleagues also reported increased activation of the posterior cingulate cortex (PCC). Although the PCC and the left AG are considered central components of the semantic memory system (Binder et al., 2009), these regions have also been identified as core hubs of the brain’s default mode network (Raichle et al., 2001), a network of midline and inferior parietal regions associated with spontaneous and self-generated thought (Andrews-Hanna et al., 2014). Default network regions are also commonly activated during various forms of imagination and mental simulation (Abraham, 2016; Jung, Flores, & Hunter, 2016), including spatial scene construction (Hassabis & Maguire, 2007), theory of mind reasoning (Buckner & Carroll, 2007), episodic future thinking (Schacter et al., 2012), and creative cognition (Beaty et al., 2016). Activation of default network regions may therefore reflect increased involvement of spontaneous imaginative processes during the construction of novel figurative expressions.

The study of figurative language production provides a new approach to understanding the brain basis of creative cognition, a rapidly evolving field of research (Green, 2016). Regions of the default network have been consistently implicated in the neuroimaging literature on creative cognition, especially the left AG (Gonen-Yaacovi et al., 2013; Wu et al., 2015). Moreover, 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 cognitive control (Seeley et al., 2007). The ECN and DN have shown an antagonistic or “anticorrelated” pattern of activity at rest and during cognitive tasks (Fox et al., 2005). During working memory tasks, for example, the ECN shows increased activity while the DN deactivates. Because DN activity is related to mind-wandering and spontaneous cognition (Andrews-Hanna, 2012), it has been hypothesized that DN deactivation reflects suppression of task-unrelated thoughts during executively-demanding cognitive tasks (Bressler & Menon, 2010; Seeley et al., 2007). Increasingly, however, research has begun to raise questions about this notion of network anticorrelation, citing evidence of network cooperation across a variety

of cognitive states (Christoff, Irving, Fox, Spreng, & Andrews-Hanna, 2016; Zabelina & Andrews-Hanna, 2016).

One such study examined brain network interactions during a divergent thinking creativity task (Beaty, Benedek, Kaufman, & Silvia, 2015). Whole-brain functional connectivity was assessed using multivariate pattern analysis (MVPA; Whitfield-Gabrieli & Nieto-Castanon, 2012), thus revealing a network of brain regions associated with creative idea production, which included regions of the default network (precuneus, PCC, and bilateral IPL) and control network (DLPFC). The precuneus and PCC also showed connectivity with bilateral insula and dorsal anterior cingulate cortex, core hubs of the salience network—a network involved in switching between the DN and ECN (Menon & Uddin, 2010; Uddin, 2014). A follow-up analysis explored the time-course of functional connectivity across the duration of the divergent thinking task: 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 DN and ECN (Menon & Uddin, 2010; Uddin, 2014), Beaty and colleagues interpreted early coupling between default and salience regions as reflecting an intermediate switching mechanism that facilitated subsequent coupling between the DN and ECN.

## 3. The present research

Recent evidence suggests that creative cognition involves cooperation between key nodes of the default and executive networks (Beaty et al., 2016; Jung, Mead, Carrasco, & Flores, 2013; Zabelina & Andrews-Hanna, 2016). But to what extent do these systems interact during other creative thought processes such as metaphor production? Benedek, Beaty et al. (2014) 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 (Andrews-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 used in Benedek, Beaty et al. (2014). A similar analytic approach as described in Beaty et al. (2015) 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 recent research reporting co-activation of the default and executive control networks during creative thinking tasks, a similar pattern of functional connectivity was expected to emerge during metaphor production. In sum, we hypothesized that metaphor production would be associated with activation of a network of brain regions involved in semantic integration, executive control, and spontaneously-generated thought.

## 4. Method

### 4.1. Participants

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 mm), resulting in a final sample of 35 (mean

age = 20.77, SD = 5.05; 22 women, 13 men). All participants self-reported right hand dominance and no history of psychiatric or neurologic disorder. After screening, an experimenter explained the purpose of the study, and participants completed an informed consent form. All study procedures were approved by UNCG's Institutional Review Board.

#### 4.2. 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, Beaty et al. \(2014\)](#). Both tasks presented short phrases relating a noun to an adjective in parentheses (e.g., “The lamp is [glaring]”; “The picture is [colorful]”; “The bread is [hard]”). The metaphor task required participants to generate a creative metaphor that conveys the meaning of the adjective and could replace it in the phrase. The synonym task required the generation of synonyms that convey the meaning of the adjective and could replace it in the phrase. 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.

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, Beaty et al. \(2014\)](#). In [Benedek et al.](#), participants produced valid responses (i.e., a metaphor in the metaphor condition and synonym in the synonym condition) 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 via an MRI-compatible microphone. The purpose of the response period was to ensure compliance and active engagement with the task; all trials were included in the subsequent analysis. Participants performed a total of 48 trials using 48 different stimulus phrases. 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.

#### 4.3. 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, Beaty et al. \(2014\)](#). 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 × 3.5 × 3.5 mm, distance factor 20%, FoV = 240 × 240 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 normalized to the Montreal Neurological Institute (MNI) template brain and smoothed with an 8 mm<sup>3</sup> isotropic Gaussian kernel.

Functional connectivity analysis was implemented in the CONN toolbox in Matlab ([Whitfield-Gabrieli & Nieto-Castanon, 2012](#)). For each participant, CONN implemented CompCor, a method for identifying principal components associated with segmented white matter (WM) and cerebrospinal fluid (CSF; [Behzadi, Restom, Liu, & 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.

#### 4.4. 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., 2015](#)).

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  $p < 0.001$  uncorrected, and a cluster-level threshold of  $p < 0.05$  familywise error (FWE) corrected.

## 5. Results

### 5.1. Multivariate pattern analysis

The MVPA task contrast (metaphor > synonym) revealed a distributed network of voxel clusters associated with metaphor pro-

duction (see Table 1 and Fig. 1). 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, Beaty et al. (2014). 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 DN.

### 5.2. Seed-to-Voxel analyses

Next, a series of post hoc analyses were conducted to further characterize functional connections between select regions of the DN (left AG and precuneus) and ECN (right IPS) found in whole-brain analysis. We thus defined three 10 mm spherical ROIs around the activation peaks from the MVPA (see Table 1). 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.,  $p < 0.05$ , 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 2 and Fig. 2A). 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.

Results for the precuneus seed revealed connectivity with eight voxel clusters (see Table 2 and Fig. 2B). The precuneus showed increased connectivity with several regions within the frontal lobes, including the left IFG (BA 47), left DLPFC (BA 9), and right rostralateral prefrontal cortex (RLPFC; BA 10). 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 (see Table 2 and Fig. 2C). 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.

### 5.3. Seed-to-voxel temporal connectivity

Temporal connectivity analysis was then conducted for the same three seed regions (left AG, left precuneus, and right IPS) to

determine whether these 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 Fig. 3). The precuneus showed increased coupling with a region in left MFG, and the right IPS showed coupling with bilateral superior parietal lobes (BA 7). Metaphor production was thus characterized by sparse connectivity between regions during the first time window.

During the second time window, the left AG showed sustained coupling with the precuneus (see Fig. 3). The left AG also increased coupling with a cluster in left somatosensory cortex (BA 40) and right anterior insula (BA 13). The precuneus showed a diffuse pattern of positive connectivity with clusters in occipital cortex, as well as with bilateral IPS and bilateral rostralateral 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).

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). The precuneus showed a similar pattern of connectivity with occipital and rostralateral prefrontal cortices during the third time window as it did during the second. Likewise, the right IPS showed the same pattern of connectivity with bilateral SPL as was found during the previous time window.

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. In sum, the temporal connectivity analysis revealed differential coupling of default, salience, and executive network regions during metaphor production.

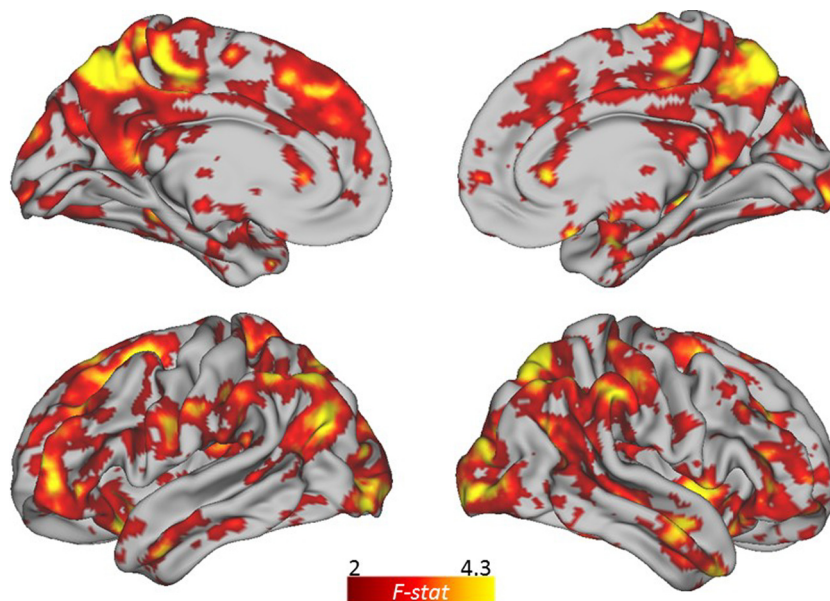
## 6. Discussion

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 execu-

**Table 1**

MVPA task effects (metaphor > synonym). BA = Brodmann area; L = left, R = right; C = cortex, G = gyrus. Results are corrected for multiple comparisons (FWE,  $p < 0.05$ ).

Region	BA	x	y	z	Voxels
L Angular G.	39	-38	-64	50	489
L Precuneus	7	-4	-66	54	1016
R Intraparietal S.	40	42	-50	46	100
L Middle Frontal G.	6/8	-20	8	58	484
L Superior Frontal G.	6	-10	38	60	56
L Inferior Frontal G.	47	-32	16	-18	165
L Precentral G.	31	-4	-26	46	301
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



**Fig. 1.** Multivariate pattern analysis of regions showing differential functional connectivity during metaphor production compared to synonym production.

**Table 2**

Seed-to-voxel results with default (left AG & precuneus) and executive (right IPS) network regions specified as seeds. L = left, R = right; C = cortex, G = gyrus, S = sulcus; DLPFC = dorsolateral prefrontal cortex. Results are corrected for multiple comparisons (FWE,  $p < 0.05$ ).

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

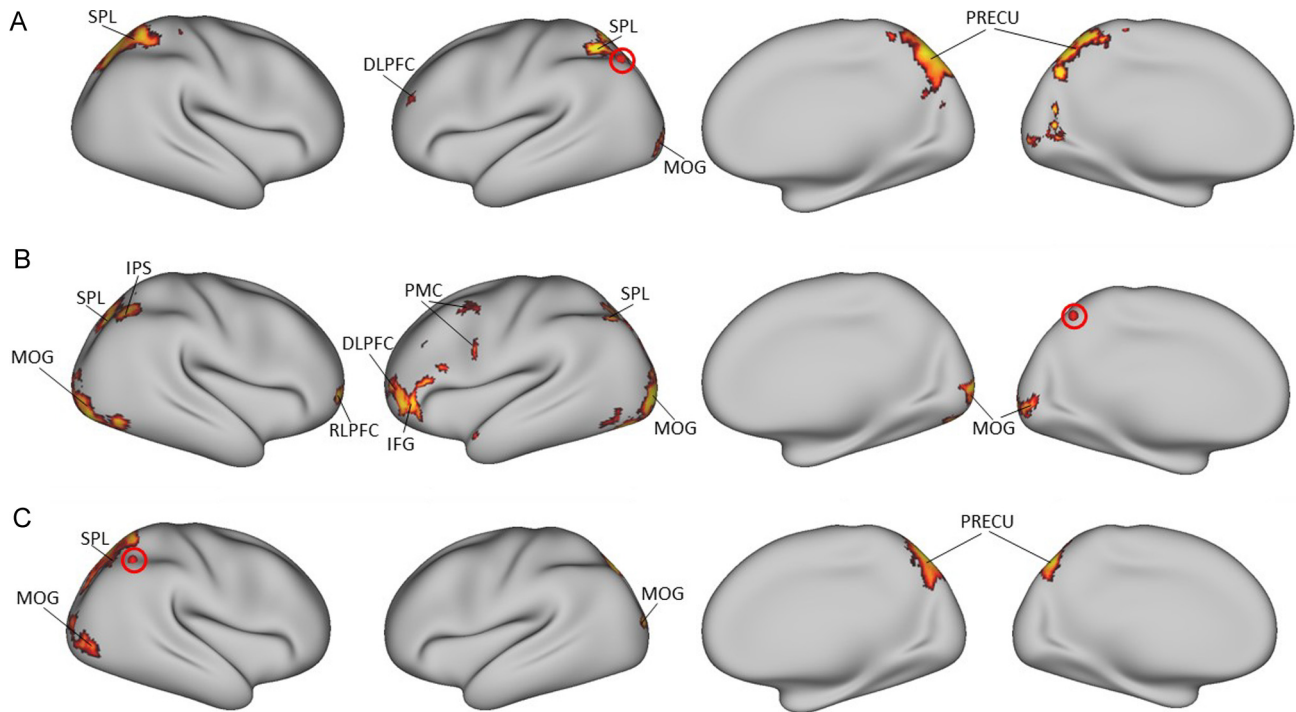
tive networks. Seed-based functional connectivity analysis showed direct functional connections between these regions, and temporal connectivity analyses showed differential coupling at different stages of metaphor production, including dynamic connectivity between default, salience, and executive network 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, 2016; Bashwiler, Wertz, Flores, & Jung, 2016; Beaty, 2015; Beaty et al., 2014, 2015; Jung et al., 2013; Mayseless, Eran, & Shamay-Tsoory, 2015; McMillan, Kaufman, & Singer, 2013; Mok, 2014; Zabelina & Andrews-Hanna, 2016).

We sought to replicate and extend Benedek and colleagues' original study of metaphor production in an independent sample of participants. To this end, we employed the same experimental paradigm, stimuli, and MRI protocol as Benedek, Beaty et al.

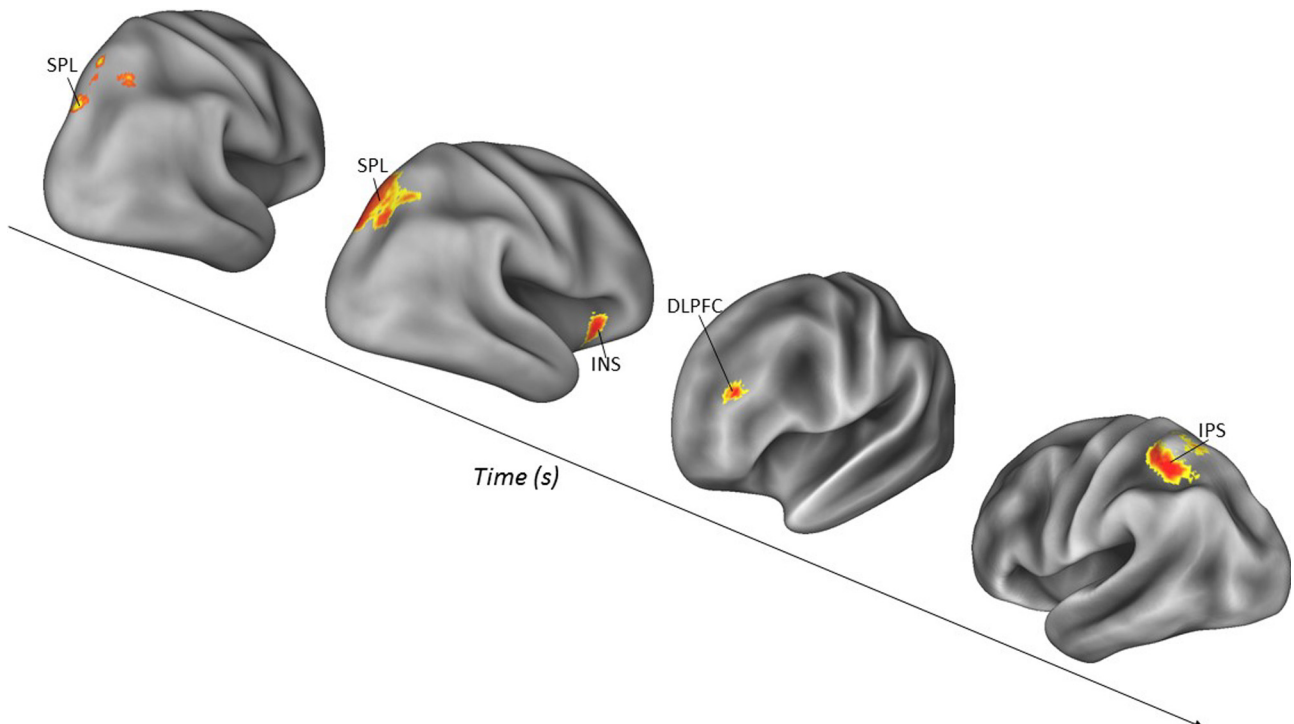
(2014). The main difference between studies, however, was the use of functional connectivity methods in the present research. Overall, the results of the two studies were largely similar: of the eight clusters associated with metaphor production in Benedek, Beaty et al. (2014) and Benedek, Jauk et al. (2014), the MVPA showed activation of seven clusters within close proximity. Across studies and types of analysis (multivariate 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.

## 7. Brain network dynamics underlying creative cognition

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; Hutchison &



**Fig. 2.** Seed-to-voxel connectivity maps for select regions of interest (metaphor > synonym). 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.



**Fig. 3.** Seed-to-voxel temporal connectivity maps with the left AG seed region showing connectivity during metaphor production compared to synonym production. 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.

Morton, 2015; Spreng et al., 2014). Both fields are beginning to challenge the notion that core brain networks like the DN and ECN always exhibit an antagonistic relationship (Beaty et al., 2016; Christoff et al., 2016; Zabelina & Andrews-Hanna, 2016). Instead, such work suggests that large-scale networks show

dynamic reconfigurations during cognitive processes such as future planning (Gerlach, Spreng, Gilmore, & Schacter, 2011), self-regulation (Hare, Camerer, & Rangel, 2009), emotional regulation (Buhle et al., 2014), memory suppression (Depue, Curran, & Banich, 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 DN and ECN, networks that typically act in opposition.

The results provide an interesting contrast to the recent work of Beaty et al. (2015) 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 network of regions that included several core hubs of the DN, 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. (2015), 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, 2014). 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 DN and ECN (Sridharan, Levitin, & Menon, 2008). The salience network is anatomically interposed between the core hubs of the DN 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 DN and ECN, Beaty et al. (2015) 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.

## 8. 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 DN 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 mentioned. Notably, we assume that the brain regions identified in this study correspond to specific large-scale networks (i.e., DN and ECN). However, the extent to which these regions correspond to established brain networks is somewhat unclear as ROI location can impact network affiliation. Future work should employ network-based methods (e.g., Independent Component Analysis) to further explore the contribution of large-scale networks to metaphor production.

Although we assume the metaphor production task used in this study assesses a facet of creative cognition, the task has yet to be formally validated against other established markers of creativity (e.g., alternate uses divergent thinking tasks), so conclusions regarding the involvement of creative thought processes remain somewhat tentative. We encourage future research on cognitive basis of metaphor production, especially studies examining its overlap with performance on other creative thinking tasks. Moreover, the temporal connectivity analysis assumed that participants had engaged in similar cognitive processes that uniformly unfolded across the idea generation period. However, the time windows may not have aligned to the same cognitive process for each trial across participants, especially if participants converged on a response at the beginning of the trial. Moreover, 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).

Another limitation of the present study concerns the extent to which participants were solely engaged in idea generation. Indeed, creativity theories suggest that creative cognition involves both idea generation and evaluation (Finke, Ward, & Smith, 1992). 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, Dobson, Beeman, and Christoff (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. Such findings may partially explain the temporal connectivity results of the present study: for example, idea generation may be related to early default network activity, whereas idea evaluation may be related to later executive network activity. Future research should further explore sub-processes underlying creative metaphor production.

## 9. Conclusion

The present research identified the brain network associated with metaphor production, including several core hubs of the default and executive networks. Results from temporal connectiv-

ity 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.

### Author note

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