Executive and default network connectivity reflects conceptual interference during creative

imagery generation

Alexander P. Christensen [1,*], Mathias Benedek[2], Paul J. Silvia[1], & Roger E. Beaty[3]

[1] Department of Psychology, University of North Carolina at Greensboro, USA

[2] Institute of Psychology, University of Graz, Austria; BioTechMed Graz

[3] Department of Psychology, Pennsylvania State University, USA

* Corresponding author: Alexander P. Christensen at Department of Psychology, P. O. Box

26170, University of North Carolina at Greensboro, Greensboro, NC, 27502-6170, USA;

apchrist@uncg.edu

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Abstract

Functional neuroimaging research has recently begun to explore cognitive mechanisms of creativity that underlie the interactions between large-scale brain networks—specifically regions of the executive control (ECN) and default (DN) networks. Increased ECN-DN coupling has been shown to occur when participants are required to overcome conceptual interference (i.e., activation of salient conceptual knowledge); however, most studies have used creativity tasks with verbal stimuli. Here we examine whether overcoming conceptual interference elicits these interactions during a creativity task with visual stimuli, which may suggest that these interactions are a domain-general neural mechanism (i.e., across multiple modalities). We used independent component analysis to identify task-related functional connectivity networks during novel imagery generation under High- and Low-Constraint conditions (i.e., interference and no interference, respectively). Consistent with our expectations, our results showed greater connectivity between ECN and DN components during the High-Constraint condition compared to the Low-Constraint condition. In contrast to previous research using verbal tasks, our results showed that the ECN had greater connectivity with the posterior, rather than anterior, DN. Our results suggest that ECN-DN coupling may be a domain-general neural mechanism that underlies creative cognition, but stimulus modality may affect which specific regions within these networks are involved.

Keywords: creativity, mental imagery, cognitive control, stimulus modality, fMRI

1. Introduction

The activation, retrieval, and flexible combination of concepts stored in memory are core cognitive components of creativity (Abraham, 2018; Finke, Ward, & Smith, 1992). Modern theories of creative cognition emphasize the dual processes of memory where associative processes allow concepts to activate passively across a semantic network (i.e., spreading activation; Kenett, Anaki, & Faust, 2014; Mednick, 1962) and executive processes allow concepts to be strategically retrieved and flexibly combined (Beaty, Silvia, Nusbaum, Jauk, & Benedek, 2014b; Forthmann et al., 2019; Hass, 2017; Unsworth, Brewer, & Spillers, 2013). These associative and executive processes are supported by the brain's default (DN) and executive control (ECN) networks, respectively (Zabelina & Andrews-Hanna, 2016), and the interactions between these two networks facilitate creative cognition (Beaty, Benedek, Silvia, & Schacter, 2016; Beaty et al., 2018a).

To date, most neuroscience research has examined memory's effects on creative cognition using creativity tasks with verbal stimuli, with few studies examining whether its effects extend to other modalities. Indeed, stimulus modality may influence the extent to which these processes are involved; for example, verbal stimuli have been shown to use more associative-driven processes, while visual stimuli have been shown to use more executive-driven processes (Chrysikou, Motyka, Nigro, Yang, & Thompson-Schill, 2016). Therefore, it's unclear whether the same large-scale brain network interactions would occur in another modality (e.g., visual stimuli). In the present study, we developed an experimental paradigm that induced conceptual interference (i.e., making conceptual knowledge stored in memory salient) during a creativity task with visual stimuli to determine whether these network interactions extend to the visual domain.

1.1. The Role of Memory in Creative Cognition

A prominent theory of creative cognition is Mednick's (1962) associative theory, which suggests that the organization of associations in memory can facilitate the activation of more remote associations, which can be used in new and useful combinations, resulting in creative solutions. Support for this theory has been found using modern quantitative approaches (e.g., network science), showing that creative people tend to have a more interconnected organization of associations than less creative people (Kenett & Austerweil, 2016; Kenett et al., 2014, 2018). Some researchers, however, have suggested that there may be no differences in creative people's associative structure when controlling for association fluency (i.e., number of association responses; Benedek & Neubauer, 2013).

An executive account of creative cognition suggests that cognitive control can facilitate the search and retrieval of concepts in memory (Beaty et al., 2014b; Benedek & Fink, 2019). Working memory, for example, has been shown to support controlled search and retrieval of concepts in semantic memory (Unsworth et al., 2013), allowing more concepts to be flexibly combined (Beaty & Silvia, 2012; Benedek, Jauk, Sommer, Arendasy, & Neubauer, 2014b). Cognitive inhibition also has a significant role in creative cognition by constraining salient conceptual knowledge and allowing more remote associations to be reached (Beaty, Christensen, Benedek, Silvia, & Schacter, 2017; Chrysikou, 2019). In support of both associative and executive accounts, several studies have demonstrated that these processes have unique contributions to creative cognition, which independently and collaboratively lead to creative solutions (Benedek, Kenett, Umdasch, Anaki, Faust, & Neubauer, 2017; Kenett, Beaty, Silvia, Anaki, & Faust, 2016).

Memory is clearly important for creative cognition; however, there are times when

memory can constrain creative thinking. Prior knowledge, for example, can interfere with the

generation of creative ideas (i.e., creative fixation; Abraham, 2018). On the one hand, when

participants are given good or bad examples, their responses typically become more creative

(Shin, Cotter, Christensen, & Silvia, in press; Sio, Kotovsky, & Cagan, 2015). On the other hand,

when participants are given prototypical examples, they typically included features of the

examples in their responses, even when instructed not to (Smith, Ward, & Finke, 1995).

Similar results have been found for pictorial examples where seeing an example can lead

participants to be constrained to the example's features (Smith, Ward, & Schumacher, 1993),

while instructing participants not to use those features can mitigate these effects (Chrysikou &

Weisberg, 2005). Hence, there are mixed effects for how and when prior knowledge facilitates

creative ideation, which may depend on several factors, including stimulus modality (e.g., verbal

vs. visual; Chrysikou et al., 2016), the quality of examples when provided (Shin et al., in press),

and whether examples are provided by others (Smith, Ward, & Finke, 1995) or prompted

through one's own knowledge via semantic priming (Beaty et al., 2017).

1.2. Neuroscientific Evidence of the Relationship between Memory and Creative Cognition

The role of memory in creative cognition has been widely studied using neuroimaging

techniques. The default network (DN)—a set of cortical midline, medial temporal, and posterior

inferior parietal regions—has been shown to be activated during autobiographic (Buckner,

Andrews-Hanna, & Schacter, 2008), episodic (Thakral, Madore, & Schacter, 2017), and

semantic cognition (Vatansever et al., 2017). In creative cognition, the DN has been shown to

have increased connectivity with the inferior frontal gyrus (IFG) at rest (Beaty et al., 2014a) and

during a verbal divergent thinking (DT) task (i.e., an ill-defined, open-ended problem requiring

idea generation; Beaty, Benedek, Kaufman, & Silvia, 2015). The posterior inferior parietal lobe

(IPL), a core posterior hub of the DN, has also been linked to creative cognition, particularly during visual creativity tasks (De Pisapia, Bacci, Parrott, & Melcher, 2016; Ellamil, Dobson, Beeman, & Christoff, 2012; Pidgeon et al., 2016; Zhu et al., 2017). One study, for example, found greater activation in the posterior IPL (i.e., angular gyrus; AG) and left dorsolateral prefrontal cortex (dlPFC) when participants mentally combined three distinct shapes into a namable composite image compared to when they identified trisected shapes (Aziz-Zadeh, Liew, & Dandekar; 2013).

The executive control network (ECN)—lateral prefrontal and anterior IPL regions—has been implicated in supporting the control of attention (Seeley et al., 2007) and goal-directed cognition (Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010), especially during semantic selection (Jefferies, 2013). Several regions of the ECN have been implicated in creative cognition, including the left lateral prefrontal cortex during conceptual interference (Abraham, 2014a; Beaty et al., 2017). One study examining lesions in the left IFG found that the ability to appropriately combine remote ideas was impaired but the ability to generate them was spared (Bendetowicz et al., 2017). This suggests that the ECN may have an important role for the effective inhibition and evaluation of creative ideas (cf. Kleinmintz, Ivancovsky, & Shamay-Tsoory, 2019). These findings extend to the visual domain, with one study finding increased connectivity between the dlPFC of the ECN and posterior cingulate cortex (PCC) of the DN during a visual creativity task (De Pisapia et al., 2016).

The interactions between these two networks appear to support creative cognition through a cyclic and dynamic interplay of generation and evaluation processes (Abraham, 2018; Beaty et al., 2016; Bendetowicz et al., 2017; Chrysikou, 2019). Generation processes (i.e., DN) rely on search through semantic and autobiographical memory to reach remote associations,

while evaluation processes (i.e., ECN) inhibit salient knowledge and manipulate these associations into a creative product (Kleinmintz et al., 2019). The salience network (SN)— bilateral insula and anterior cingulate cortex (ACC) regions—is hypothesized to be the intermediate switching mechanism (Uddin, Supekar, Ryali, & Menon, 2011) that facilitates these dynamic interactions during creative ideation (Beaty et al., 2016, 2018a; Jung, Mead, Carrasco, & Flores, 2013).

1.3. The Facilitatory and Inhibitory Effects of Memory on Creative Cognition

Several studies have found effects of memory on creative cognition (Beaty et al., 2015, 2018). Episodic memory, for example, has been shown to activate similar brain regions as creativity tasks (Madore, Thakral, Beaty, Addis, & Schacter, 2017), and episodic induction paradigms that prime the involvement of episodic retrieval mechanisms have improved the number of responses in verbal DT tasks (Madore, Addis, & Schacter, 2015). In a recent study, researchers examined the conjunction of episodic retrieval, future simulation, and a verbal DT task, finding a core network comprised of several regions in the DN (medial prefrontal cortex; mPFC and middle temporal gyrus; MTG; Beaty, Thakral, Madore, Benedek, & Schacter, 2018b). This conjunctive overlap suggests that constructive episodic processes are involved in creative cognition.

Other studies have examined the effects of cognitive stimulation from other people's ideas, showing that examples may facilitate the retrieval and recombination of existing knowledge (Fink et al., 2010, 2012). In these studies, participants were exposed to meaningless words, common examples, and highly creative examples from a verbal DT task. Typically, they found that people generated their most creative responses when they were exposed to common examples. Compared to meaningless words, ideas generated when exposed to common examples

elicited greater activation in several regions associated with the DN (PCC, MTG, and AG) and ECN (SMG and superior frontal gyrus), suggesting that exposure to common ideas may facilitate creative cognition (Fink et al., 2010, 2012).

Nevertheless, examples—whether provided by others or prompted by one's own memory—can have inhibitory effects that stem from salient conceptual knowledge. In a recent study, we used a novel experimental paradigm where participants learned common noun-verb pairs (e.g., phone–call) and were asked to recall them later (Beaty et al., 2017). After this cued-recall task, participants completed the experimental task where they were either presented with a new noun or an old noun from the cued-recall task. Participants were instructed to generate novel verbs for the new nouns and to either recall old verbs or generate novel verbs for the old nouns. This paradigm allowed us to investigate the specific effects of conceptual interference when a salient response had been reinforced (old noun–new verb). We found that connectivity between the left ECN and anterior DN supported novel verb generation during conceptual interference (old noun–new verb) compared to when there was none (new noun–new verb). Notably, conceptual interference induced by salient conceptual knowledge decreased the semantic distance (measured by Latent Semantic Analysis, LSA; Green, 2016) between the noun and generated verb, which we interpreted as a less creative response.

1.4. Present Research

To date, the interactions between the ECN and DN have mostly been examined using creativity tasks with verbal stimuli. The interactions between these two networks are less understood, however, for other stimulus domains. Idea generation in verbal and visual domains have been shown to recruit similar brain regions, including the left dlPFC and left AG (Aziz-Zadeh et al., 2013; Gonen-Yaacovi et al., 2013); however, it's unclear whether the same

cognitive processes apply. To better understand whether ECN-DN coupling may be a domain-general neural mechanism underlying creative cognition, we sought to extend these interactions to the visual domain. One approach to experimentally examine the role of ECN-DN coupling in creative cognition is to induce conceptual interference via common examples (Beaty et al., 2017).

We developed a paradigm to induce conceptual interference using common example responses from a creativity task with visual stimuli. The experimental design started with participants first rating how related a label was to an incomplete figure. The labels were balanced with half being related (i.e., a common example; High-Constraint condition) and half being unrelated (i.e., a random example; Low-Constraint condition) to the incomplete figure. After rating the relatedness of a label to an incomplete figure, participants were then instructed to imagine new creative labels for the figure (the original label no longer being present), or to identify shapes in the figure (control condition). Participants then verbally reported a label for their image or shape.

We expected that greater conceptual interference would occur during the High-Constraint condition (relative to the Low-Constraint condition) because the highly rated labels increased the saliency of relevant but common response options. Based on previous research involving conceptual interference, we expected that this would lead to greater connectivity between the left dlPFC and the DN (Beaty et al., 2017). Given the visual stimuli used in the task, we expected that there would be greater connectivity between the left ECN (i.e., left dlPFC) and posterior DN, consistent with previous findings involving visual creativity tasks (De Pisapia et al., 2016; Zhu et al., 2017). Finally, we did not have specific expectations for whether the labels that

participants generated would be more creative for the High- or Low-Constraint conditions because of the mixed findings in the literature (Beaty et al., 2017; Fink et al., 2010, 2012).

2. Method

2.1. Participants

Thirty-three adults were recruited from the University of North Carolina at Greensboro and its surrounding community. Four participants were excluded from the analyses due to excessive head movement, leaving the final sample with 29 people (19 female, M_{age} = 21.4, range = 18 – 31). All participants were right-handed with normal or corrected-to-normal vision and reported no history of neurological disorder or psychotropic medication.

2.2. Experimental Task and Procedure

The experimental procedure consisted of one task with two phases: label rating and label generation. The label rating phase preceded the label generation phase. During the label rating phase, participants viewed an incomplete figure with either a related or unrelated label and were asked to rate how similar the label was to the incomplete figure (1 = *not at all related* to 4 = *highly related*). We instructed participants to "imagine the figure as its label" even if the label didn't immediately resemble the figure. The relatedness of the labels was determined by a pilot study on Amazon's Mechanical Turk (MTurk). In the pilot study, 55 English speaking adults were asked to generate a label for what each incomplete figure most resembled (see Lloyd-Cox, Christensen, Silvia, & Beaty, 2019). We identified a consensus label (i.e., a label that at least 20% of the participants generated) for each incomplete figure, which was used as the common example (i.e., related) label in our task. Unrelated labels were determined by randomly assigning related labels from other figures to each incomplete figure; the authors confirmed that each randomly selected label was unrelated.

After the label rating phase, the label generation phase started with a condition prompt that read either "Shapes" or "Imagine." For the "Shapes" trials, participants were told to identify common shapes in the incomplete figure (e.g., rectangles). For the "Imagine" trials, participants were told to "be creative" and imagine a novel creative label for the incomplete figure (Nusbaum, Silvia, & Beaty, 2014; Said-Metwaly, Fernández-Castilla, Kyndt, & Van den Noortgate, 2019). Participants were told that they could "mentally manipulate" (e.g., rotate, elaborate, expand on) the incomplete figure when generating labels. After the condition prompt, participants then performed the condition's instructions while viewing the incomplete figure with no label. Participants completed a total of 54 trials, including 18 trials of the Shapes condition and 36 trials of the Imagine condition.

The Imagine condition was further divided into two sub-conditions that differed based on the relatedness of the labels in the label rating phase. The related labels were used as the "High-Constraint" condition and the unrelated labels were used as the "Low-Constraint" condition. Because of this division, there were 18 trials for both the High-Constraint and Low-Constraint conditions. The High-Constraint condition was designed to induce conceptual interference due to the similarity of the label and incomplete figure stimulus, assuming that participants would have to inhibit the related label to generate a novel label. In contrast, the Low-Constraint condition was not expected to induce conceptual interference because of the lack of similarity between the label and incomplete figure. This task design allowed us to target a specific cognitive process (i.e., conceptual interference) during creative ideation (Benedek, Christensen, Fink, & Beaty, 2019). Finally, the Shapes condition (also 18 trials and equally balanced with High- and Low-Constraint conditions) served as a control condition to allow participants to engage in low-order perceptual processes (Aziz-Zadeh et al., 2013).
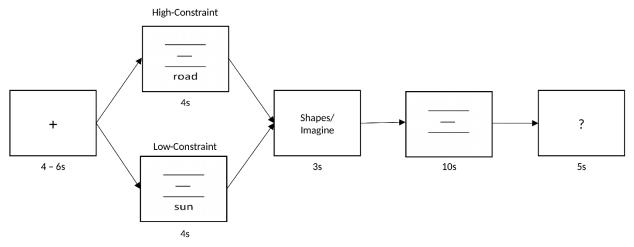
Figure 1. The fMRI experiment procedure beginning on the left and proceeding in order to the right. In the third frame, participants either saw "Shapes" or "Imagine." The duration in seconds (s) is presented below each frame.

The experimental procedure was identical across all conditions (Figure 1). Visual stimuli were projected onto a screen from a computer using E-Prime and viewed through a mirror attached to the head coil. First, participants were presented with a jittered fixation cross (4–6s) and then they performed the label rating task where they had 4 seconds to respond. Participants rated the labels using a Cedrus LSC-400B (San Pedro, California) four-button response box (button 1 = *not at all related* to button 4 = *highly related*). After the label rating task, the condition of Shapes or Imagine appeared on the screen for 3 seconds, followed by the incomplete figure without a label. Participants had 10 seconds to either identify a shape or imagined a novel image for the incomplete figure. After, participants were given 5 seconds to vocalize the shape or label for their image into the MRI-compatible microphone (Optoacoustics; Mazor, Israel), which were immediately recorded by an experimenter.

Inappropriate responses were flagged (and subsequently not included in the analyses) if the participant did not perform the appropriate instruction (i.e., if they generated a creative label

in the Shapes condition or a shape in the Imagine condition). The Imagine responses were then coded for semantic distance via LSA. Semantic distance was determined from the common example label. For the High-Constraint condition, this was the label that participants rated; for the Low-Constraint condition, this was the common example label for the incomplete figure, which the participants did not rate. To compute the LSA values, we used the one-to-many comparison program (freely available via the LSA website: http://lsa.colorado.edu/) with the default topic space of "General_Reading_up_to_1st_year_college" and "term to term" comparison type. The common example label was used as the "main text" and the responses were used as the "texts to compare." Semantic distance was computed by subtracting the LSA values from 1 (i.e., $semantic\ distance = 1 - LSA$; Prabhakaran, Green, & Gray, 2014). Larger sematic distance values were interpreted as more creative (Hass, 2017).

2.3. MRI Data Acquisition and Preprocessing

Participants completed the fMRI task in a single run. Whole-brain imaging was performed on a 3T Siemens Magnetom MRI system (Siemens Medical Systems, Erlangen, Germany) using a 16-channel head coil. Blood-oxygen-level-dependent (BOLD)-sensitive T2*-weighted functional images were acquired using a single shot gradient-echo EPI pulse sequence (TR = 2000 ms, TE = 30 ms, flip angle = 78°, 32 axial slices, $3.5 \times 3.5 \times 4.0$ mm, distance factor 0%, FoV = 192×192 mm, interleaved slice ordering) and corrected online for head motion. The first two volumes were discarded to allow for T1 equilibration effects. A high resolution T1 scan was acquired for anatomic normalization. Imaging data were slice-time corrected and realigned using the Statistical Parametric Mapping (SPM) 12 package (Wellcome Institute of Cognitive Neurology, London). Functional volumes were co-registered and resliced to a voxel size of 3mm^3, normalized to the MNI template brain (Montreal Neurological Institute), and smoothed

with an 8mm^3 isotropic Gaussian kernel.

2.4. Functional Network Connectivity

To assess functional network connectivity across conditions, we used independent component analysis (ICA) implemented in the CONN Toolbox in Matlab (Whitfield-Gabrieli & Nieto-Castanon, 2012). ICA is an exploratory, data-driven method that identifies spatiotemporal voxel clusters, referred to as functional connectivity networks (Calhoun, Adali, Pearlson, & Pekar, 2001). We used ICA to extract brain networks associated with the three task conditions, which were then used to examine the correlation patterns among these networks. Twenty independent components were identified using a dimensionality reduction of 64 (Calhoun et al., 2001). From these components, we extracted the networks of interest (i.e., group-level spatial maps) to examine the functional interactions between the networks during the task conditions. These components of interest were based on our previous work (Beaty et al., 2017) and included anterior default (mPFC), posterior default (PCC/precuneus and bilateral AG), left executive (left dlPFC and left anterior IPL), right executive (right dlPFC and right anterior IPL), and salience (bilateral insulae and ACC) components. We also retained other task-related networks recovered by the ICA for exploratory purposes, including networks with theoretical relevance to visuospatial creative thinking (e.g., dorsal attention and visual networks). These components were specified as regions of interest (ROI) to examine the between-network connectivity differences associated with the three task conditions.

Functional network connectivity analysis was conducted using the CONN Toolbox in Matlab (Whitfield-Gabrieli & Nieto-Castanon, 2012). In addition to the preprocessing steps listed above, we implemented CompCor via CONN Toolbox to identify principal components associated with segmented white matter and cerebrospinal fluid (Behzadi, Restom, Liau, & Liu,

2007). These components and realignment parameters were entered as confounds in the first-level analysis (Whitfield-Gabrieli & Nieto-Castanon, 2012). For second-level analyses, Fisher's Z-transformed correlations were computed between mean BOLD signal extracted from task-related component masks (i.e., functional networks) and t-tests were computed to assess potential differences between task conditions. All functional connectivity results reported have p-values at or below a false discovery rate (FDR) corrected threshold of $p < .05$. Univariate analyses are reported in the Supplementary Information but are not reported here because we did not have hypotheses for these results.

3. Results

3.1. Behavioral Results

For a manipulation check, we performed two paired samples t-tests to determine whether participants' average ratings of the related labels (High-Constraint condition) were more related to the incomplete figures than the unrelated labels (Low-Constraint condition) as well as whether participants' average response time for ratings was faster when the labels were more related to the incomplete figures. Indeed, the related labels ($M = 3.34$, $SD = 0.31$) were rated as more related to the incomplete figures than the unrelated labels ($M = 1.48$, $SD = 0.40$), $t(28) = 21.94$, $p < .001$, $d = 5.00$. Similarly, people responded significantly faster when the labels were related to the incomplete figures ($M = 2000$ ms, $SD = 288$ ms) than when they were unrelated ($M = 2310$ ms, $SD = 360$ ms), $t(28) = -4.63$, $p < .001$, $d = 0.89$.

We also examined semantic distance to determine the creative quality of the labels. Semantic distance was significantly greater for the High-Constraint condition ($M = 0.86$, $SD = 0.05$) than the Low-Constraint condition ($M = 0.75$, $SD = 0.08$), $t(28) = 6.74$, $p < .001$, $d = 1.77$. This suggests that when people saw a related label compared to an unrelated label in the rating

phase, they generated more semantically distant labels in the subsequent generation phase. Interestingly, in the Low-Constraint condition, people generated the common example label in their responses about 18% of the time ($SD = 14.2\%$), ranging from 0% to 55.2% for individual stimuli. This suggests that when the common example label was not provided many participants would generate the common example label themselves (cf. Lloyd-Cox et al., 2019).

3.2. Functional Network Connectivity

3.2.1 Group ICA Network Solution. First, we report group-level results from the ICA collapsed across the three task conditions (i.e., High-Constraint, Low-Constraint, and Shapes). This analysis yielded functional connectivity networks consistent with our previous study (Beaty et al., 2017) and past work using this ICA algorithm (Calhoun et al., 2001), including a posterior default cluster (PCC and AG), two anterior default clusters corresponding to dorsomedial PFC (dmPFC) and ventromedial PFC (vmPFC), a left executive cluster (left dlPFC/IFG and left anterior IPL), and two salience networks corresponding to the left anterior insula and right anterior insula extending to the right temporal pole. Several other canonical connectivity networks were recovered by the ICA: a dorsal attention cluster (bilateral superior parietal lobules), a visual cluster (occipital cortex), a ventral attention cluster (e.g., bilateral supramarginal gyrus and bilateral insula/IFG), a medial temporal cluster (e.g., bilateral superior temporal gyri and parahippocampal gyri), a subcortical cluster (e.g., thalamus and midbrain nuclei), a motor cluster (e.g. precentral and postcentral gyri), and a cerebellar cluster. One additional cluster with no clear allegiance to canonical networks was identified, corresponding to the right AG. These networks were entered into the following second-level functional connectivity analysis to assess potential differences in between-network connectivity associated with the task conditions.

3.2.2 Task Differences in Functional Network Connectivity. We began with the primary analysis of interest (i.e., contrasting between-network functional connectivity during the High and Low-Constraint conditions). Compared to the Low-Constraint condition, the High-Constraint condition was associated with increased connectivity between the left executive and posterior default networks ($t = 3.43$, $p = .02$; see Figure 2). This finding corroborates the results of Beaty et al. (2017) and points to an anterior/posterior dissociation, with left ECN coupling with anterior default in the prior verbal stimuli study and left ECN coupling with posterior default in the current visual stimuli study. In addition, our analyses showed increased coupling between the dorsal attention network and two other networks: ventral attention ($t = 3.52$, $p = .02$) and right salience/temporal ($t = 3.39$, $p = .03$). Notably, there were no significant connectivity differences found for the reverse contrast (i.e., Low-Constraint > High-Constraint).
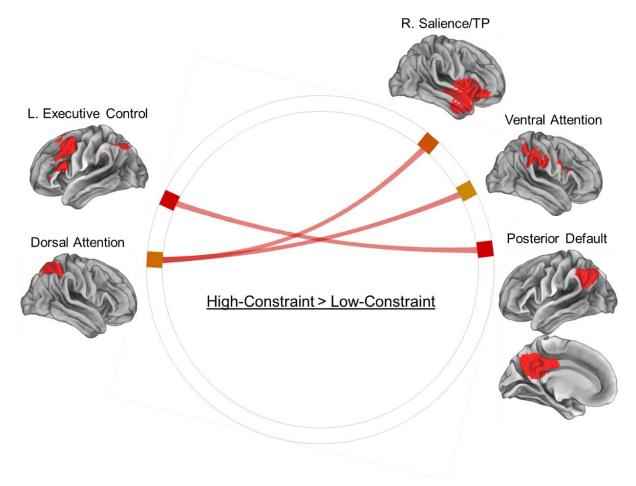
Figure 2. Functional connectivity results contrasting the High- and Low-Constraint conditions. L = left; R = right; TP = temporal pole. The analysis was FDR-corrected for multiple between-network comparisons ($p < .05$).

We then contrasted the label generation conditions separately against the Shapes condition. Compared to the Shapes condition, High-Constraint generation was associated with stronger functional connectivity between the visual network and two other networks: left executive ($t = 5.85$, $p < .01$) and dorsal attention ($t = 3.22$, $p < .01$); the reverse contrast showed stronger connectivity between executive and dorsal attention networks ($t = -3.56$, $p < .01$) as well as between left salience and two other networks: motor ($t = 3.20$, $p < .01$) and right AG ($t = -3.42$, $p < .01$). Contrasting Low-Constraint generation with the Shapes condition showed no significant differences; likewise, no significant differences emerged in the reverse contrast.

4. Discussion

The neurocognitive mechanisms underlying creative cognition have typically been studied using creativity tasks with verbal stimuli. In this study, we extended one of these mechanisms, conceptual interference, to the visual domain and identified a distinct pattern of functional connectivity. Specifically, we demonstrated that overcoming conceptual interference during creative idea generation elicits increased connectivity between the left ECN and DN, consistent with previous research (Beaty et al., 2017). This suggests that the coupling between the ECN and DN may be a domain-general neural mechanism that occurs during conceptual interference in creativity tasks with verbal and visual stimuli. People also produced more semantically distant, and thereby more creative, responses during the High-Constraint condition compared to the Low-Constraint condition. These results add to the growing literature that shows common examples may improve creative idea generation (Fink et al., 2010, 2012; Shin et al., in press; Yagolkovskiy & Kharkhurin, 2016).

Consistent with our hypotheses, we found the left ECN (including the left dlPFC and IFG) had increased connectivity with the DN in the High-Constraint condition compared to the Low-Constraint condition. This finding adds to work showing the left IFG to be involved in semantic retrieval, particularly when cognitive demands are high (Jefferies, 2013). A recent study showed that the left IFG may also resolve competing responses across many modalities (e.g., words and pictures) for both semantic and episodic memory (Stampacchia et al., 2018). Indeed, one study reported greater activity in the left medial frontal gyrus and left IFG when subjective difficulty increased during the drawing of a Pictionary word (Saggar et al., 2015). This suggests that greater connectivity with the left ECN may reflect increased evaluation and selection of memory content more generally. In contrast to previous findings involving

conceptual interference, we found that the left ECN was coupled with the posterior DN instead of the anterior DN (Beaty et al., 2017). This distinction may reflect the differences between the stimulus modalities (Chrysikou et al., 2016).

Several previous studies examining visual creativity appear to support this conclusion. A meta-analysis on visual creativity, for example, found several posterior DN regions—left angular gyrus, left IPL, and left fusiform gyrus—that had greater activation during visual creativity tasks compared to non-resting-state control tasks (Pidgeon et al., 2016). In a study that ours closely paralleled, the authors found increased activity in the left dlPFC and left AG (Aziz-Zadeh et al., 2013). Our results extend these findings to suggest that the connectivity between these regions is crucial for inhibiting salient examples to reach more creative solutions. Another study that examined the planning of a visual artwork found greater functional connectivity between the posterior cingulate cortex (PCC) and several regions of the ECN, particularly for artists compared to non-artists (De Pisapia et al., 2016). Taken together, our results suggest that the increased coupling between ECN and posterior DN regions may contribute to overcoming conceptual interference during visual imagery generation.

Broadly, our results extend the creativity neuroscience literature by identifying functional connectivity patterns that appear to be domain-general. Beyond the connectivity between the ECN and DN, we found greater connectivity between the SN (i.e., anterior insula) and attention networks (i.e., dorsal and ventral), particularly with the SMG. There is growing evidence that the SN has an influential role in identifying candidate ideas in creative cognition (Beaty et al., 2016, 2018), while recent work has shown that the SMG is involved in the generation and construction of original ideas from episodic memory (Benedek et al., 2014a, 2018). The connectivity between these regions, which were particularly greater in the High-Constraint than the Low-Constraint

condition, may support the integration of novel representations of imagery that are used for further evaluation and selection.

In support of this interpretation, we found that responses generated during the High-Constraint condition were more semantically distant, which we interpreted as more creative, than the Low-Constraint condition. Our findings parallel those found by previous neuroimaging example studies, which found that common examples stimulated more creative responses (Fink al., 2010, 2012). These results also align with Shin et al.'s (in press) results where the instruction to avoid bad examples improved creative responses. Although a common example may not be considered "bad," they tend to be generic and therefore lack originality. Indeed, for several Low-Constraint stimuli, participants often generated the common example label, suggesting that many responses were not novel at all. This may have been a consequence of the salience of the stimuli, which could have had one strong, closely-related visual association that made it hard for people to come up with alternatives in a short time and when not explicitly told to avoid it (Beaty et al., 2019; Chrysikou & Weisberg, 2005).

We note, however, that the behavioral results of our previous study found that semantic distance was greater in the Low-Constraint condition rather than the High-Constraint condition (Beaty et al., 2017). One critical difference between these two studies was how conceptual interference was induced. In our previous study, participants had related responses (i.e., noun-verb pairs) reinforced through learning and memory tests, while in this study participants were presented with related examples immediately prior to stimulus exposure (i.e., no reinforced responses). This task difference represents what Abraham (2018) calls "passive" and "active" contextual influences, respectively. Passive contexts refer to knowledge that is implicitly activated from representations in long-term memory, while active contexts refer to knowledge

that is conditionally salient from representations in short-term memory (Abraham, 2014b). The contrast in our findings suggest that the context of how conceptual interference is induced may affect behavioral performance on creativity tasks, despite showing similar neurocognitive mechanisms (e.g., ECN-DN coupling).

4.1. Limitations and Future Directions

One limitation of this study is that LSA may not be an optimal rating for the creativity of a response, especially for visual stimuli. Although the responses were verbal and therefore semantic in nature, it's possible that an incomplete figure could have a label that is semantically distant from the common label, yet still be closely related to the image (via subjective ratings). Therefore, future research should use subjective ratings rather than LSA to determine the subjective creativity of responses in visual creativity tasks (Silvia et al., 2008). Another limitation is that our study still had a verbal component to the task. Although participants were asked to imagine a new creative label for visual stimuli, they still provided a verbal label for their imagery. This concedes some potential for participants to not evoke any mental imagery at all. Future research should attempt to mitigate this possibility by having participants imagine a novel image and then draw, rather than vocalize, their response in the scanner (cf. Ellamil et al., 2012).

5. Conclusions

In this study, we showed that there is increased coupling between the ECN and DN when overcoming conceptual interference in a creativity task with visual stimuli. Overcoming conceptual interference seems to be a particularly potent cognitive mechanism for eliciting these brain network interactions. Importantly, our task design allowed us to target a specific cognitive mechanism of creativity (i.e., conceptual interference); however, to explicitly dissociate the anterior and posterior DN coupling with the ECN involved in creativity tasks with verbal and

visual stimuli (respectively), future research should assess conceptual interference during these tasks in the same study (Benedek et al., 2019). This proposition extends to other cognitive mechanisms such as conceptual expansion (Abraham, 2014a, 2018) and episodic simulation (Madore et al., 2017). More research is necessary to elaborate on these and other cognitive mechanisms to examine whether they elicit similar neural interactions across stimulus modalities. Finally, the influence of contextual information on behavioral performance of creativity tasks and their neurocognitive representation possesses promising avenues for future research. Such research would not only expand our understanding of creative cognition but also clarify how stimulus modality and contextual information influence the complex and dynamic interactions between these neurocognitive systems.

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