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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 comprehensionhow 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 selfgenerated thought. Nevertheless, it remains unclear how these different systems interact to support the production of new metaphoric expressions.

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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 systemss 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 coactivation 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

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