One-way traffic

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One-way Traffic: The Inferior Frontal Gyrus Controls Brain Activation in the Middle Temporal Gyrus and Inferior Parietal Lobule During Divergent Thinking

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Abstract

Contrary to earlier approaches that focused on the contributions of isolated brain regions to the emergence of creativity, there is now growing consensus that creative thought emerges from the interaction of multiple brain regions, often embedded within larger brain networks. Specifically, recent evidence from studies of divergent thinking suggests that kernel ideas emerge in posterior brain regions residing within the semantic system and/or the default mode network (DMN), and that the prefrontal cortex (PFC) regions within the executive control network (ECN) constrain those ideas for generating outputs that meet task demands. However, despite knowing that regions within these networks exhibit interaction, to date the direction of the relationship has not been tested directly. By applying Dynamic Causal Modeling (DCM) to fMRI data collected during a divergent thinking task, we tested the hypothesis that the PFC exerts unidirectional control over the middle temporal gyrus (MTG) and the inferior parietal lobule (IPL), vs. the hypothesis that these two sets of regions exert bidirectional control over each other (in the form of feedback loops). The data were consistent with the former model by demonstrating that the right inferior frontal gyrus (IFG) exerts unidirectional control over MTG and IPL, although the evidence was stronger in the case of the MTG than the IPL. Our findings highlight potential causal pathways that could underlie the neural bases of divergent thinking.

Keywords: Creativity, divergent thinking, Dynamic Causal Modeling (DCM)
1. Introduction

Early neuroimaging research focusing on the brain bases of creativity was largely characterized by a search to localize the neural correlates of creative thought in isolated brain regions. However, perhaps demonstrated most clearly by large-scale meta-analyses that focused on the output of those earlier studies, it has since become evident that creativity has a distributed neural representation throughout the brain (see Boccia et al., 2015; Gonen-Yaacovi et al., 2013; Wu et al., 2015). In turn, the contribution of any specific brain region to the emergence of creativity has been shown to vary as a function of task demands. For example, different brain regions have shown reliable engagement or interaction depending on whether the creative task under consideration is verbal vs. non-verbal, requires generating vs. combining ideas, or whether it supports analogical vs. metaphorical thinking (Gonen-Yaacovi et al., 2013; Vartanian, 2012; Zhu et al., 2017). Thus, as has been shown to be the case with other higher-order cognitive capacities such as reasoning (Goel, 2007), clusters of brain regions appear to reconfigure dynamically in response to the demands of the task and the context within which creativity must be manifested.

However, the search for the neural correlates of creativity has entered a new phase in which the focus has shifted from brain mapping per se to an examination of the interactions between brain regions and networks that give rise to idea generation. This focus on the interactions has been facilitated by the discovery of large-scale networks within the brain (see Zabelina & Andrews-Hanna, 2016). Specifically, by focusing on brain networks—defined as brain regions that exhibit similar patterns of fMRI activity
fluctuations—one can study their interactions (and dynamics) in the service of various types of thinking, including creative cognition as well as related forms of thought such as spontaneous cognition and mind wandering (Christoff et al., 2016). Recent work using this approach has demonstrated that divergent thinking involves interactions between the default-mode network (DMN) and the executive control network (ECN). Specifically, a series of studies have revealed that the DMN and the ECN cooperate in the course of creative cognition across a wide range of tasks including divergent thinking (Beaty et al., 2015; Mayseless et al., 2015), creative drawing (Ellamil et al., 2012), poetry generation (Liu et al., 2015), and musical improvisation (Pinho et al., 2016), among others (reviewed in Beaty et al., 2016). Interestingly, the DMN and ECN also exhibit greater connectivity in creative people when the focus is shifted to resting-state fMRI data (see Beaty et al., 2014). By and large, these data have been interpreted using a two-step model of creative thinking according to which creative ideas emerge when an initial blind variation (i.e., generation) step is followed by a secondary selective retention stage, ultimately resulting in the emergence of output that is appropriate based on task and contextual demands (Campbell, 1960; Eysenck, 1993; Simonton, 1999). As suggested by Beaty et al. (2016), within such a model the DMN could contribute to the generation of candidate ideas through retrieval from long-term memory and/or recombination, given its role in internally-oriented cognition. In turn, the ECN could contribute to the selective retention of ideas that meet task demands with an eye toward executing a response, although the extent of such top-down regulation is heavily dependent on the organism’s goals and the features of the task (Chrysikou et al., 2014).
A framework similar to the one that involves the interaction between ECN and DMN has been proposed in relation to the interplay between prefrontal cognitive control regions and the semantic system during creative cognition. Conceptually, such models are rooted in historically important process-based approaches to studying the components of the cognitive machinery underlying creativity, including semantic memory. For example, according to the Geneplore model (Finke et al., 1996; Ward et al., 1995, 1997), creative ideas emerge following a two-step process whereby the first step involves the generation of potential ideas (i.e., “preinventive structures”), whereas the second step involves the exploration and elaboration of those potential ideas leading to output. Consistent with the Geneplore model, Abraham (2014) has argued that a critical aspect of the process is conceptual expansion—defined as “the ability to widen one’s conceptual structures to include unusual or novel associations” (p. 1)—and that this process is underwritten by the brain’s semantic network. In turn, regions of the brain that underlie cognitive control and executive functions are engaged to regulate the degree of (conceptual) constraints placed on those (kernel) ideas in the service of generating creative output.

Aside from the behavioural data that support the contribution of associative and executive processes to creative cognition (Beaty et al., 2014; Benedek et al., 2014; see also Kaufman et al., 2010), there are two lines of neuroimaging evidence that have also provided support for this two-step model. First, using Latent Semantic Analysis (LSA) coupled with independent component analysis of intrinsic functional connectivity networks, Beaty et al. (2017) have shown that the ECN can interact with the DMN to
inhibit salient conceptual knowledge (i.e., pre-potent responses) retrieved from memory during creative idea production. Their findings indicate that the ECN acts on the DMN to constrain its output to meet task demands. Secondly, Beaty et al. (2015) have also shown that the time course of ECN and DMN coupling varies as a function of the stage of divergent thinking. Specifically, when divergent thinking trials were examined based on 2-second increments of time, the coupling between ECN and the posterior cingulate cortex (PCC)—a core hub of the DMN—was stronger in the later phases of divergent thinking, precisely when one would expect ECN to exert control over DMN activity prior to response generation.

1.1 Present study

Although several lines of evidence suggest that the DMN, the semantic system and ECN cooperate during creative cognition, there is no direct evidence to demonstrate that ECN exerts control over DMN and/or the semantic system activity during the process. The aim of the present study was to test that possibility using Dynamic Causal Modeling (DCM; Daunizeau et al., 2011; Stephan et al., 2010), in the form of two competing hypotheses. Specifically, one can imagine that the ECN might exert unidirectional control over the DMN and/or the semantic system during creative cognition (hypothesis 1). According to this model, the DMN and/or the semantic system would generate candidate ideas either through retrieval from episodic and/or semantic memory (or recombination of ideas from memory), which would in turn undergo selection by the ECN before a response is outputted. However, another possibility might be that the ECN and DMN and/or the semantic system might exert bidirectional control
over each other as cycles of generation-evaluation are performed before an eventual response is produced (hypothosis 2). According to this second possibility there would be feedback loops such that selections made by the ECN might result in additional rounds of generation by the DMN and/or the semantic system until an optimal solution is found (see Vartanian, 2011). We used DCM to test these two possibilities based on fMRI data collected from participants engaged in a divergent thinking task. To determine whether unidirectional or bidirectional control is unique to divergent thinking, as a control condition we investigated the same effects involving the same regions in the context of retrieval from long-term memory (see Fink et al., 2009). In other words, we were motivated to determine whether the pattern of effective connectivity characterizing the interaction between ECN and DMN and/or the semantic system is unique to divergent thinking, or whether it generalizes to another psychological process (e.g., recall from long-term memory). Conducting this control analysis is essential for determining the generalizability of the reported findings beyond divergent thinking.

At the outset of the planned DCM analyses it is important to point out that whereas the discussion above has centered on the interaction between networks in the service of creative cognition (e.g., ECN, DMN, semantic network), our own analyses will instead focus on specific nodes (i.e., brain regions) of interest instead. In particular, we will test hypotheses regarding the causal effects that certain nodes exert on other nodes. As such, any inference drawn from the study will be based on the nodes and their specific functions, rather than the larger networks that they are embedded in. We believe that such focal analyses that test causal hypotheses with DCM are
complementary to network-based approaches, and allow one to test the relationship between specific nodes of theoretical interest embedded within larger networks, rather than the interactions of the networks themselves.

2. Method

2.1 Participants

The participants were 44 neurologically healthy right-handed volunteers (31 males, 13 females) with normal or corrected-to-normal vision recruited from Canada’s Department of National Defence (DND). Handedness was assessed using a standard self-report questionnaire (Oldfield, 1971). No participant reported color blindness. The participants ranged from 20 to 56 years of age (M = 35.47 ± 11.3 years). The protocol for the study was approved by the Human Research Ethics Committee of Defence Research and Development Canada, and by the Research Ethics Board of Sunnybrook Health Sciences Centre.

2.2 Materials and procedures

The participants completed the Alternate Uses Task (AUT) in the fMRI scanner. The AUT is a classic divergent thinking task from the creativity literature (Guilford, 1967). The scanner version of the AUT was modeled after Fink et al. (2009). The task was presented in two blocks (i.e., uses and characteristics), the order of which was counterbalanced across participants. Each of the 20 trials in the uses block had the same structure. During the generation phase participants were presented with the name of a common object (e.g., knife) and instructed to think of as many uses for it as possible for 12000 ms. In this phase the name of the object appeared in black ink. The response
phase followed immediately afterwards during which participants were given 3000 ms to enter the number of generated uses. In this phase the name of the object appeared in green. This color change acted as a prompt to enter the response as quickly as possible. This was followed by an inter-trial interval (ITI) varying randomly between 4,000-6,000 ms. Each trial in the characteristics block had an identical structure, except that participants were instructed not to generate uses, but instead to recall from long-term memory physical features characteristic of the object. For example, possible physical features for “knife” could be solid, sharp, metallic, etc. For both generating uses as well as recalling characteristics the participants were limited to entering a maximum of five uses and/or characteristics as their uppermost response, where each response button corresponded to the number of generated uses or recalled characteristics within a 12-second time window (e.g., response “3” on a generation trial indicated that three uses were generated on that trial by the participant).

The decision not to ask participants to vocalize responses in the fMRI scanner was taken in order to minimize movement artifacts. However, in order to verify that the participants had indeed engaged in divergent thinking as instructed, immediately after exiting the scanner they were presented (at random) with one of two lists that included five objects drawn from the scanner trials, and asked to generate uses for them under standard paper-and-pencil laboratory conditions that involved a 3-minute time limit per object (Vartanian et al., 2007, 2009). This enabled us to ensure that participants’ performed the task as instructed, and that their responses were appropriate. In addition, we were able to score responses on (a) fluency (i.e., number of generated
uses), (b) originality (i.e., statistical infrequency of responses), and (c) flexibility (i.e., number of conceptual categories). Finally, this procedure also enabled us to conduct a manipulation check to ensure that the 12-second limit for generating uses or recalling characteristics was not too restrictive in the course of the fMRI acquisition run.

2.3 Image acquisition

A 3-Tesla MR scanner with an 8-channel head coil (Discovery MR750, 22.0 software, GE Healthcare, Waukesha, WI) was used to acquire T1 anatomical volume images (.86 .86 1.0 mm voxels). For functional imaging, T2*-weighted gradient echo spiral-in/out acquisitions were used to produce 26 contiguous 5 mm thick axial slices (repetition time [TR] = 2000 ms; echo time [TE] = 30 ms; flip angle [FA] = 70°; field of view [FOV] = 200 mm; 64 × 64 matrix; voxel dimensions = 3.1 × 3.1 × 5.0 mm), positioned to cover the whole brain. The first five volumes were discarded to allow for T1 equilibration effects. The number of volumes acquired was 418.

2.4 Statistical analysis

Data were analyzed using Statistical Parametric Mapping (SPM8) (www.filion.ucl.ac.uk/spm/). Head movement was less than 2 mm in all cases. All functional volumes were spatially realigned to the first volume. Given that the volumes were acquired using a descending sequence with short TR, slice timing to correct for variation in acquisition time followed realignment (Huettel et al., 2004). A mean image created from realigned volumes was spatially normalized to the MNI EPI brain template using nonlinear basis functions. Voxel size after normalization was the SPM8 default,
namely $2 \times 2 \times 2$ (mm). The derived spatial transformation was applied to the realigned T2* volumes, and spatially smoothed with an 8 mm full-width at half-maximum (FWHM) isotropic Gaussian kernel. Time series across each voxel were high-pass filtered with a cut-off of 128 s, using cosine functions to remove section-specific low frequency drifts in the BOLD signal. Condition effects at each voxel were estimated according to the general linear model (GLM) and regionally specific effects compared using linear contrasts. The BOLD signal was modeled as a box-car, convolved with a canonical hemodynamic response function. Using a random-effects analysis, in the 2nd level the reported activations survived voxel-level intensity threshold of $p < .05$, corrected for multiple comparisons using the Bonferroni family-wise error (FWE), as well as a cluster-level significance of $p < .001$ (uncorrected for multiple comparisons).

Using an event-related design, in the 1st level we specified regressors corresponding to (1) the generation phase (coupled with the parameter indicating number of uses or characteristics generated—depending on the condition: uses or characteristics), (2) response phase, (3) motor response, (4) and ITI (rest). Typically the critical contrast in previous studies that have used Fink et al.’s (2009) design has involved the generating uses–recalling characteristics contrast. The decision to focus on that contrast has been motivated by the search for neural correlates that are specific to divergent thinking over and above recall from long-term memory. Here however we focused on the generating uses–ITI (rest) contrast for conducting our focal DCM, in order to be able to use the recalling characteristics–ITI (rest) contrast as our control condition (see Introduction). The generating uses–ITI (rest) contrast was conducted by
assigning a weight of “1” to the regressor corresponding to the generating uses phase and a weight of “−1” to the regressor corresponding to the ITI (rest) phase (a weight of “0” was assigned to all other regressors). In turn, the recalling characteristics–ITI (rest) contrast was conducted by assigning a weight of “1” to the regressor corresponding to the recalling characteristics phase and a weight of “−1” to the regressor corresponding to the ITI (rest) phase (a weight of “0” was assigned to all other regressors). These two contrasts will form the focus of our DCM analyses. In addition to the aforementioned two contrasts that formed the basis for our subsequent DCM analyses, we also ran the standard generating uses recalling characteristics contrast to enable a comparison of our own results with previously published reports using the same basic trial structure (e.g., Fink et al., 2009). The results are reported in Table 1.

2.5 Dynamic Causal modeling (DCM)

As noted by Daunizeau et al. (2011), DCM is an analytic technique for examining changes in the functional integration of brain regions as a result of experimental manipulations as well as endogenous brain activity. The focus of DCM is effective connectivity—defined as the causal effects that elements within a system exert on one another. A key feature of DCMs is that they are causal in accordance with control theory, such that they can describe how changes in the neural dynamics of one element cause changes in the neural dynamics of another element within the system, as a function of experimental manipulations as well as endogenous brain activity (Stephan et al., 2010). In addition, they are Bayesian in all respects, in the sense that each parameter in the model is constrained by a prior distribution, and informed by empirical knowledge
about the range of possible values as well as mathematical considerations. Importantly, Bayesian inversion provides posterior probabilities as well as an approximation to the log model evidence, enabling one to compare alternative models (i.e., hypotheses).

3. Results

3.1 Behavioural results

On average, across 20 trials of each kind completed within the fMRI scanner, participants reported fewer uses \((M = 3.59, SD = .67)\) than characteristics \((M = 3.87, SD = .72)\), \(t(40) = 2.83, p = .007, d = .40\).

For data generated outside of the fMRI scanner, we first checked the responses for appropriateness and then scored them for fluency, originality, and flexibility. Fluency was calculated by averaging the number of responses generated across the five prompts. Originality was calculated based on the “uniqueness scoring” method, according to which a response generated by only a single person within the sample is given a score of “1,” with all other responses receiving a score of “0” (see Wallach & Kogan, 1965). Examples of original responses included ‘cut out letters for threatening note’ for newspaper, ‘a heat pad for hot drinks’ for map, and ‘a small clothes line for drying stockings’ for necklace, among others. A participant’s overall originality score was computed by summing unique responses across the five prompts. Finally, flexibility was calculated by computing the number of conceptual categories that responses to each prompt fell into, and then averaging the number of categories across the five prompts. For flexibility two independent judges discussed the intended scoring procedure in detail in advance, and then binned all responses into various agreed-upon categories;
the correlations between the ratings by the two judges was high ($r[108] = .93, p < .001$), and their inter-rater reliability can be considered “substantial”: $Kappa = .65$ (Cohen, 1960; McHugh, 2012). The distributions for fluency, originality and flexibility are depicted in Appendix 2. Separate Kolmogorov-Smirnov tests demonstrated that the distributions did not deviate from normality ($p > .05$ in all three cases). The correlations between fluency and originality ($r[41] = .78, p < .001$), fluency and flexibility ($r[41] = .83, p < .001$), and flexibility and originality ($r[41] = .78, p < .001$) were all positive and statistically significant.

Importantly for us, outside of the fMRI scanner, the average number of uses (i.e., fluency) that participants generated within a 3-minute time window (i.e., 15 longer than the time allowed in the fMRI scanner) was 8.62 ($SD = 2.98$, range = 4.80 and 15.80). As such, it is unlikely that given only 12 seconds to generate responses per item in the fMRI scanner, a maximal response option of 5 would have limited their generative potential, although that possibility cannot be ruled out entirely.

3.2 Neural results

Generating uses and recalling characteristics were correlated with brain activation in distributed sets of regions (Tables 2-3). Our analytic approach involved comparing our two models (i.e., hypothesis 1 vs. hypothesis 2)—separately for generating uses and recalling characteristics. In other words, we intended to see the relative viability of hypothesis 1 vs. hypothesis 2 for each task (i.e., generating uses vs. recalling characteristics). Our choice of regions for selection in the DCM was motivated by five considerations. First, the regions needed to have survived our thresholds for
statistical significance (i.e., be listed in Tables 2 and 3). Recall that in all cases our
threshold for statistical significance was a voxel-level intensity threshold of $p < .05$
(corrected for multiple comparisons using the Bonferroni FWE correction), as well as a
cluster-level significance of $p < .001$ (uncorrected for multiple comparisons). Second, for
reasons of interpretive simplicity, we opted to include a single region that fell within the
ECN, the semantic system, and the DMN (unless the same structure was activated
bilaterally in which case both locations in the two hemispheres were taken into
account). Third, the specific regions that were selected as falling within the ECN, the
DMN and/or semantic system needed to have been activated in previous studies of
creativity. As a result of our third consideration for the ECN our focus fell on the
dorsolateral and ventrolateral aspects of PFC in particular (see Boccia et al., 2015;
Gonen-Yaacovi et al., 2013; Wu et al., 2015), whereas for the semantic system and the
DMN our focus fell on regions that fall within the temporal lobes and the DMN
respectively (see Abraham 2014; Zabelina & Andrews-Hanna, 2016). Fourth, the same
regions needed to have been activated for both generating uses and recalling
characteristics in order to make the models corresponding to the control condition
identical in structure to the focal condition. Fifth, in cases where more than a single
region met the above four criteria (e.g., more than one region within the PFC was
activated), then the region with the higher Z-score was selected. As can be seen in
Tables 2-3, based on the aforementioned criteria we selected the right inferior gyrus
(IFG) to represent a structure that resides within the ECN, the right middle temporal
gyrus (MTG) to represent a structure that resides within the semantic network, and the
bilateral inferior parietal lobule (IPL) as structures that resides within the DMN. The models that were tested in relation to the IFG-MTG relationship are depicted in Figure 1, whereas the models that were tested in relation to the IFG-IPL relationship are depicted in Figure 2. Appendix 3 depicts the volumes of interest (VOI) that were created in SPM8 as part of the DCM procedures.

Here it is important to note that by selecting a region as residing within a network, we are not implying that the same region is not associated with any other network. For example, although the IFG is implicated in both intelligence and executive functions (Jung & Haier, 2007) and has been associated with the ECN (also referred to as the frontoparietal control network), it has also been shown to be involved in semantic processes, especially the selection and controlled retrieval of information from memory (for review see Thompson-Schill, 2003). More specifically, the contribution of IFG to semantic processing appears to be in the form of the cognitive control it exerts on the contents of the semantic system (Badre & Wagner, 2007), and it is in this sense that we are interested in its relationship with MTG in the context of divergent thinking. In other words, we suspect that IFG likely exerts control over MTG to ensure that the contents retrieved from the latter meet the task demands of divergent thinking. As such, it is the specific functional role of the IFG as a cognitive control structure that is more relevant to testing our hypothesis, rather than the networks within which it resides per se. Similarly, although we selected the IPL due to its association with the DMN (Ingelström & Graziano, 2017), we are not making the claim that its contribution is exclusive to the DMN.
In accordance with best practice guidelines (see Stephan et al., 2010), we have noted all the steps taken in the preparation of our DCMs in Appendix 1. Importantly, the critical difference between the two models was whether the association between IFG and MTG or IPL was unidirectional (i.e., from IFG to MTG or IPL) vs. bidirectional. In addition, the instruction to engage in generating uses was hypothesized to exert its effects on IFG, MTG and IPL, consistent with what is known about bottom-up as well as top-down processes that govern divergent thinking (Beaty et al., 2014; Benedek et al., 2014). We tested separate models for MTG and bilateral IPL to be able to make separate inferences about the ways in which IFG might control and be controlled by MTG and bilateral IPL.

We conducted two separate sets of analyses to test our focal hypotheses. The first set of analyses centered on tests of effective connectivity involving IFG and MTG (Figure 1). The second set of analyses centered on tests of effective connectivity involving IFG and bilateral IPL (Figure 2). For generating uses, the posterior probabilities as well as the approximations to the log model evidence for hypothesis 1 vs. hypothesis 2 in terms of the relationship between IFG and MTG are depicted in Figure 3. As can be seen, regardless of whether one focuses on the posterior probabilities or the approximations to the log model evidence, the data are more consistent with hypothesis 1 than with hypothesis 2. In turn, when we shift our focus to the relationship between IFG and IPL, examination of both posterior probabilities and the approximations to the log model evidence also indicate that the data are more
consistent with hypothesis 1 than with hypothesis 2, although in this case the evidence is weaker than was the case for the IFG-MTG relationship (Figure 4).

Interestingly, an altogether different pattern emerges regarding our control condition (i.e., recalling characteristics). Specifically, when the focus is on the relationship between IFG and MTG, as was the case for generating uses, both posterior probabilities as well the approximations to the log model evidence indicate that the data are more consistent with hypothesis 1 than with hypothesis 2 (Figure 5). In contrast, when we shift our focus to the relationship between IFG and IPL, both types of evidence indicate that the data are more consistent with hypothesis 2 than with hypothesis 1 (Figure 6). In other words, whereas the unidirectional nature of the effect of IFG on MTG does not vary as a function of the task under consideration, it does appear to vary when we examine the IFG-IPL link.

4. Discussion

There is already substantial evidence to indicate that regions within the ECN and the DMN and/or the semantic system cooperate in the service of creativity (Abraham, 2014; Jung et al., 2013; for review see Beaty et al., 2016). The involvement of regions within these systems in support of creativity is consistent with a large body of theoretical models and empirical findings according to which both bottom-up and top-down processes contribute to creative cognition (Benedek et al., 2014; Kenett et al., 2014; Mednick, 1962). In addition, and despite some differences, this body of evidence is consistent with the idea that creative thinking is supported by a two-step process, according to which creative ideas emerge when an initial blind variation (i.e.,
generation) step is followed by a secondary selective retention stage (Campbell, 1960; Eysenck, 1993; Simonton, 1999). The novel contribution of the present work has been to use DCM to compare two models based on two competing hypotheses involving the nature of the relationship between regions that fall within the ECN and the DMN and/or the semantic system. Specifically, we found that the relationship is more accurately characterized as unidirectional than bidirectional. In terms of our understanding of the creative process, these findings suggest that the IFG controls activation in the MTG during divergent thinking, rather than being also controlled by the MTG via a feedback loop. Conceptually, this is consistent with a model wherein the IFG prunes the ideas generated by MTG to produce responses that meet task demands. Importantly, our results are silent regarding the temporal progression and dynamics of the proposed model. In other words, we were not able to test directly whether the generation of candidate ideas within the MTG or bilateral IPL takes temporal precedence over the control processes exerted by IFG. It remains to be seen whether IFG exerts sustained control over the generation process from the outset, or whether the engagement of control mechanisms increases as one progresses toward task completion (i.e., response generation). However, as noted earlier, Beaty et al. (2015) have shown that the coupling between ECN and the PCC—a core hub of the DMN—was stronger in the later phases of divergent thinking, precisely when one would expect ECN to exert control over DMN activity prior to response generation. As such, it would appear that a natural extension of the work described here would be to examine effective connectivity in the context of divergent thinking within windows of time.
The DCM results provided stronger support for the unidirectional model of IFG control in regards to MTG than bilateral IPL. As noted earlier, it is well known that IFG contributes to the selection and controlled retrieval of semantic information from memory (Thompson-Schill, 2003), as well as cognitive control of memory (Badre & Wagner, 2007). Indeed, the link between MTG and the PFC (including IFG) was highlighted in a detailed analysis of the N400 event-related potential (ERP)—a waveform that is sensitive to semantic violations—indicating that this region of the temporal cortex (and adjacent areas) “mediate the long-term storage of and access to information associated with lexical representations...This ‘lexical’ information serves as input to higher-order semantic processes” (Lau et al., 2008, p. 923). This body of work is consistent with a tight linkage between IFG and MTG during semantic processing, as well as with theoretical models of the interplay between cognitive control regions and the semantic system (Abraham, 2014). Our observation of a similar effect in relation to our control task (i.e., recalling characteristics) suggests that IFG’s unidirectional control of brain activation in MTG in the context of the present study might represent specific examples of a more general effect across many tasks. In contrast, the observation of a weaker unidirectional effect involving bilateral IPL in the case of generating uses coupled with the observation of a bidirectional effect involving bilateral IPL in the case of recalling characteristics suggests that the functional link between IFG and bilateral IPL might be more variable and sensitive to contextual and task demands than is the functional link between IFG and MTG.
The behavioural data demonstrated that output was greater for recalling characteristics than generating uses. This suggests that it is easier to retrieve relevant content from memory than it is to generate uses in relation to the same prompts. This difference in difficulty must be taken into consideration in relation to the DCM findings. Specifically, differences in the pattern of findings in relation to the IFG-IPL connectivity as a function of recalling characteristics vs. generating uses might be due to differences in task difficulty.

Inside the fMRI scanner our participants were given only twelve seconds to generate uses for various prompts. On average, this led to the production of 3.59 uses ($SD = .67$). Analyses of our post-scan behavioural data demonstrated that even when they were given 3 minutes (i.e., 15 longer than the time allowed in the fMRI scanner) for generating uses, on average they produced 8.62 uses ($SD = 2.98$). This suggests that it is unlikely that they would have been able to produce >5 responses within 12 seconds in the fMRI scanner, and as such the 5-option format did not constrain their performance. However, we do know that whereas initial responses generated in AUT tend to be drawn from memory, it is the later responses that are more likely to be creative—known as the “serial-order effect” (Beaty & Silvia, 2012; Gilhooly et al., 2007). Therefore, it is possible that the responses generated in the fMRI scanner in a short window of time might not reflect cognition in relation to truly creative output, and might instead foster fluency rather than novel and useful output per se.

The DCMs conducted in this manuscript were based on contrasts that compared each of our two experimental conditions separately to rest. We employed this analytic
approach to enable us to include a control condition in our analysis. However, care must be taken in interpreting such results because rest states can be associated with spontaneous thought (e.g., mind wandering) known to engage the DMN. For example, Andreasen et al. (1995) used positron emission tomography (PET) to examine regions of the brain that were activated during resting state in which participants were allowed to let their minds wander freely. They found activations in multiple regions of association cortex, including frontal, temporal and parietal, as well as the retrosplenial cingulate—regions that form components of the DMN. Partly for this reason, researchers who examine the neural correlates of divergent thinking using variants of Fink et al.’s (2009) AUT design typically conduct the generating uses recalling characteristics to isolate brain activity associated with divergent thinking. In the present study that contrast resulted in multiple areas of activation along the cingulate gyrus—including PCC as well as the anterior cingulate cortex (ACC). Although in Fink et al.’s (2009) original study that contrast resulted exclusively in activation in the angular gyrus, many studies since then have isolated the PCC as a key contributor to divergent thinking as well. This is true both in terms of studies that have reported the results of the generating uses recalling characteristics specifically (e.g., Mayseless et al., 2015), as well as studies that have explored the interactions between different brain networks based on divergent thinking tasks using the same experimental design (see Beaty et al., 2016). Future studies aiming to apply DCM analysis to divergent thinking would do well to utilize designs that enable contrasts that use task-based contrasts rather than rest conditions.
There are several important caveats for interpreting our findings. First, although we treated the IFG, MTG and IPL as residing within the ECN, the semantic system and DMN respectively, we are in no way implying that these regions reside within or contribute exclusively to those networks. As noted earlier, it was the specific functional roles of the regions that were more relevant to testing our hypothesis, rather than the networks within which they reside. Second, and related to the first point, we have only tested for the causal effects of specific regions on each other, rather than the causal effects of networks on each other. As such, whether the larger systems exhibit a similar pattern of control over each other remains to be tested in future studies. Third, in the case of IFG and MTG, the results involving our control condition (i.e., recall from long-term memory) demonstrated that the unidirectional control that characterizes that relationship is not unique to divergent thinking, but also applies to at least one other cognitive process. This is consistent with the idea that creative cognition likely draws on modes of control within the brain that are generally true across cognitive tasks rather than unique to creativity. However, in the case of IFG and IPL, our results demonstrated that the IFG and IPL likely exhibit bidirectional control over each other. This suggests that in some cases engagement in divergent thinking might alter the effective connectivity patterns of activated regions.

4.1 Limitations

There are several limitations that must be highlighted in our approach. First and foremost, the choice of our specific VOIs for inclusion in our DCMs was based on our own set of five criteria. Clearly, one might have selected other regions based on a
different set of principled criteria. Second, for reasons of simplicity, we opted to include only a single region (unilaterally or bilaterally) within each model. Clearly, models with multiple regions representing each system are likely more realistic and can be tested in the future. Third, given that we only tested one control case (i.e., recall from long-term memory), we cannot infer that the unidirectional nature of the IFG-MTG relationship is universally valid in other contexts. For example, there are cases where creative cognition has been shown to in fact benefit from a state of diminished cognitive control—achieved through cathodal (inhibitory) transcranial direct current stimulation (tDCS) of left PFC (Chrysikou et al., 2013). As such, it would be very interesting to test DCMs within tasks and contexts where the a priori theoretical assumptions for optimal creative cognition differ from the model(s) tested here. Fourth, DCM’s tests of goodness of fit (i.e., posterior probabilities or the approximations to the log model evidence) are relative, not absolute (see Stephan et al., 2010). Comparisons of other models might exhibit different patterns of relative fitness. Fifth, the relationship that we have exhibited was obtained based on using the AUT as our measure of divergent thinking. It has yet to be demonstrated whether other measures of divergent thinking and/or creativity will exhibit the same relationship. Finally, due to the makeup of our sample we did not explore sex differences in the DCMs under consideration, although that could form a focus of study in future investigations into this question (see Abraham et al., 2014).

5. Conclusion
We applied DCM to fMRI data collected during a divergent thinking task to compare two competing hypotheses: According to hypothesis 1, during divergent thinking the IFG exerts unidirectional control over the MTG and bilateral IPL, whereas according to hypothesis 2 the regions exert bidirectional control over each other (in the form of a feedback loop). Our data were consistent with the former hypothesis, highlighting potential causal pathways that could underlie the neural bases of divergent thinking.

Acknowledgments

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References


Table 1. Regions exhibiting greater activation for generating uses recalling characteristics.

<table>
<thead>
<tr>
<th>Region</th>
<th>BA</th>
<th>Coordinates</th>
<th>Z-score</th>
<th>Cluster size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cingulate gyrus (PCC)*</td>
<td>31</td>
<td>28, 34, 42</td>
<td>4.62</td>
<td>226</td>
</tr>
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<td>Cingulate gyrus (PCC)</td>
<td>31</td>
<td>24, 26, 42</td>
<td>4.11</td>
<td>96</td>
</tr>
<tr>
<td>Cingulate gyrus (PCC)</td>
<td>31</td>
<td>24, 48, 22</td>
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<td>153</td>
</tr>
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<td>Superior parietal lobule</td>
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<td>22, 68, 46</td>
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<td>Cingulate gyrus (ACC)</td>
<td>32</td>
<td>22, 20, 26</td>
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<td>Caudate</td>
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<td>20, 24, 22</td>
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<td>23</td>
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<td>Precuneus</td>
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<td>26, 54, 40</td>
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<td>23</td>
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<td>13</td>
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<tr>
<td>Cingulate gyrus</td>
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<td>20, 14, 32</td>
<td>3.24</td>
<td>5</td>
</tr>
<tr>
<td>Postcentral gyrus</td>
<td>2</td>
<td>56, 20, 40</td>
<td>3.20</td>
<td>4</td>
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<tr>
<td>Cingulate gyrus</td>
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<td>22, 16, 24</td>
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<td>Middle occipital gyrus</td>
<td>19</td>
<td>30, 94, 26</td>
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</table>

Notes. Because the coordinates within this table are presented purely for comparative purposes with previous studies that used varying threshold for reporting results (e.g., voxel- or cluster-level significance involving FDR, FWE, or no correction for multiple comparisons), we have opted to list all activations where voxel-level significance was $p < .001$ (uncorrected for multiple comparisons). Regions are designated in MNI coordinates. BA = Brodmann Area; ACC = anterior cingulate cortex; PCC = Posterior cingulate cortex; * reflects the only area that would have survived the threshold set for the DCM (Dynamic Causal Modeling) analyses elsewhere in this manuscript (i.e., $p < .05$ corrected for multiple comparisons using the Bonferroni family-wise error [FEW] correction, as well as a cluster-level significance of $p < .001$ [uncorrected for multiple comparisons]).
Table 2. Regions exhibiting greater activation for generating uses ITI (rest).

<table>
<thead>
<tr>
<th>Region</th>
<th>BA</th>
<th>Coordinates</th>
<th>Z-score</th>
<th>Cluster size</th>
</tr>
</thead>
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<tr>
<td>Cerebellum</td>
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<td>22, 52, 22</td>
<td>7.05</td>
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<tr>
<td>Inferior parietal lobule</td>
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<td>48, 28, 44</td>
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<td>Inferior frontal gyrus</td>
<td>9</td>
<td>58, 10, 24</td>
<td>6.57</td>
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<tr>
<td>Inferior parietal lobule</td>
<td>40</td>
<td>60, 40, 26</td>
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<td>1460</td>
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<td>Insula</td>
<td>13</td>
<td>46, 2, 4</td>
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<td>Inferior temporal gyrus</td>
<td>37</td>
<td>56, 70, 2</td>
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<td>797</td>
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<td>Cerebellar tonsil</td>
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<td>26, 46, 36</td>
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<td>696</td>
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<tr>
<td>Middle temporal gyrus</td>
<td>21/22</td>
<td>54, 22, 12</td>
<td>5.68</td>
<td>79</td>
</tr>
<tr>
<td>Superior frontal gyrus</td>
<td>9</td>
<td>28, 44, 26</td>
<td>5.40</td>
<td>118</td>
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<tr>
<td>Cerebellum</td>
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<td>0, 64, 20</td>
<td>5.11</td>
<td>101</td>
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</tbody>
</table>

Notes. ITI = inter-trial interval; Regions are designated in MNI coordinates; BA = Brodmann Area.
Table 3. Regions exhibiting greater activation for recalling characteristics ITI (rest).

<table>
<thead>
<tr>
<th>Region</th>
<th>BA</th>
<th>Coordinates</th>
<th>Z-score</th>
<th>Cluster size</th>
</tr>
</thead>
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<tr>
<td>Cerebellum</td>
<td>24, 54, 18</td>
<td>6.90</td>
<td>4269</td>
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<tr>
<td>Medial frontal gyrus</td>
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<td>4, 4, 52</td>
<td>6.49</td>
<td>775</td>
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<tr>
<td>Inferior parietal lobule</td>
<td>40</td>
<td>54, 22, 26</td>
<td>6.45</td>
<td>286</td>
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<tr>
<td>Inferior parietal lobule</td>
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<td>56, 38, 28</td>
<td>6.15</td>
<td>606</td>
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<tr>
<td>Inferior parietal lobule</td>
<td>40</td>
<td>46, 30, 50</td>
<td>6.12</td>
<td>336</td>
</tr>
<tr>
<td>Lentiform nucleus</td>
<td>28, 2, 2</td>
<td>5.82</td>
<td>684</td>
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<td>Thalamus</td>
<td>12, 16, 0</td>
<td>5.71</td>
<td>129</td>
<td></td>
</tr>
<tr>
<td>Thalamus</td>
<td>12, 20, 0</td>
<td>5.69</td>
<td>547</td>
<td></td>
</tr>
<tr>
<td>Inferior frontal gyrus</td>
<td>8</td>
<td>56, 8, 26</td>
<td>5.68</td>
<td>76</td>
</tr>
<tr>
<td>Middle frontal gyrus</td>
<td>8</td>
<td>36, 38, 32</td>
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<td>142</td>
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<tr>
<td>Middle temporal gyrus</td>
<td>21/22</td>
<td>58, 26, 10</td>
<td>5.36</td>
<td>116</td>
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<tr>
<td>Inferior temporal gyrus</td>
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<td>44, 70, 2</td>
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<tr>
<td>Precentral gyrus</td>
<td>6</td>
<td>32, 8, 52</td>
<td>5.22</td>
<td>75</td>
</tr>
</tbody>
</table>

Notes. ITI = inter-trial interval; Regions are designated in MNI coordinates; BA = Brodmann Area.
Figure 1. The two models under consideration for DCM involving IFG and MTG.

Model (hypothesis) 1

Model (hypothesis) 2

Notes. DCM = Dynamic Causal modeling; IFG = inferior frontal gyrus; MTG = middle temporal gyrus. Red arrows indicate intrinsic connections (i.e., direction of control) within the models.
Figure 2. The two models under consideration for DCM involving IFG and bilateral IPL.

Notes. DCM = Dynamic Causal modeling; IFG = inferior frontal gyrus; IPL = inferior parietal lobule (L = left, R = right). Red arrows indicate intrinsic connections (i.e., direction of control) within the models.
**Figure 3.** Approximations to the log model evidence and posterior probabilities in relation to Model 1 vs. Model 2 involving IFG and MTG for generating uses.

*Notes. RFX = Random effects; IFG = inferior frontal gyrus; MTG = middle temporal gyrus.*
Figure 4. Approximations to the log model evidence and posterior probabilities in relation to Model 1 vs. Model 2 involving IFG and MTG for recalling characteristics.

Notes. RFX = Random effects; IFG = inferior frontal gyrus; MTG = middle temporal gyrus.
Figure 5. Approximations to the log model evidence and posterior probabilities in relation to Model 1 vs. Model 2 involving IFG and bilateral IPL for generating uses.

Notes. RFX = Random effects; IFG = inferior frontal gyrus; IPL = inferior parietal lobule.
Figure 6. Approximations to the log model evidence and posterior probabilities in relation to Model 1 vs. Model 2 involving IFG and bilateral IPL for recalling characteristics.

Notes. RFX = Random effects; IFG = inferior frontal gyrus; IPL = inferior parietal lobule.
Appendix 1

The following represent the details of the DCM analytic choices for testing the two models. When specifying the DCM we extracted time series for VOI (IFG and MTG) within the contrasts of interest based on spheres with a radius of 10 mm centered around the voxel of choice (see Tables 1-2). In turn:

1. Slice timing = 2,
2. Echo time (TE) = 0.03,
3. Modulating effects = bilinear,
4. States per region = one,
5. Stochastic effects = no,
6. Centre input = no,
7. Intrinsic connection: IFG to MTG (Model 1), IFG to MTG and MTG to IFG (Model 2),
8. Effects on regions and connections: Effects on both regions (IFG and MTG); no effect on connections between regions.
Appendix 2

Distribution of fluency scores based on AUT data collected post-scan.

Notes. AUT = Alternate Uses Test.
Distribution of originality scores based on AUT data collected post-scan.

Notes. AUT = Alternate Uses Test.
Distribution of flexibility scores based on AUT data collected post-scan.

Notes. AUT = Alternate Uses Test.
Appendix 3

These images illustrate the volumes of interest (VOI) that were created for the Dynamic Causal Modeling (DCM) analyses within SPM8.

<table>
<thead>
<tr>
<th>IFG</th>
<th>MTG</th>
<th>IPL (right)</th>
<th>IPL (left)</th>
</tr>
</thead>
<tbody>
<tr>
<td><img src="image1.png" alt="Image" /></td>
<td><img src="image2.png" alt="Image" /></td>
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</tr>
<tr>
<td><img src="image9.png" alt="Image" /></td>
<td><img src="image10.png" alt="Image" /></td>
<td><img src="image11.png" alt="Image" /></td>
<td><img src="image12.png" alt="Image" /></td>
</tr>
</tbody>
</table>

Notes. From top to bottom row, the images are depicted in the coronal, axial and sagittal orientations respectively.
Highlights:

- IFG controls brain activation in MTG during divergent thinking.
- IFG also controls brain activation in MTG during recall from memory.
- IFG’s control over MTG activation appears to be task-invariant.
- IFG exerts weaker control over IPL during divergent thinking.
- IFG and IPL exert bidirectional control over one another during recall from memory.