Psychology of Aesthetics, Creativity, and the Arts

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Creative thinking is important for success in the fields of science, technology, engineering, and mathematics (STEM). Yet creativity in STEM is perhaps the most under-researched question in the creativity literature, with little known about the neurocognitive mechanisms supporting scientific creative thinking abilities, such as hypothesis generation. In the present functional magnetic resonance imaging study, undergraduate STEM majors ($n = 47$) completed a scientific hypothesis generation task (thinking of novel/plausible explanations for hypothetical scenarios) and a control task (thinking of synonyms to replace a word in a hypothetical scenario). Multivariate pattern analysis identified a whole-brain network supporting hypothesis generation, including hubs of the default (posterior cingulate cortex [PCC]), salience (right anterior insula [AI]), and semantic control (left inferior frontal gyrus [IFG]) networks. Using these network hubs as seed regions, we found increased between-network functional connectivity during hypothesis generation, including stronger coupling between semantic control (IFG) and posterior default regions (PCC and bilateral angular gyrus) and stronger coupling between salience (AI) and default regions, alongside weaker within-network functional connectivity. Our results indicate that scientific creative thinking involves increased cooperation among the default, salience, and control networks—similar to creative thinking in other domains—potentially reflecting a coordination of spontaneous/generative and controlled/evaluative processes to construct original explanations for scientific phenomena.

Keywords: creativity, default mode network, functional connectivity, scientific creativity, semantic control network

Creativity is among the most valuable skills for success in the 21st century, particularly as artificial intelligence automates many technical jobs (Amabile, 2020). Understanding how people think creatively, and how creativity can be cultivated in fields of science, technology, engineering, and mathematics (STEM), is thus a priority for modern education.

Cognitive neuroscience can provide a window into creative thought processes, from the process of producing artworks to the process of generating novel scientific hypotheses, by identifying mechanisms that govern the production of new and effective ideas. Past research on "domain-general" creative thinking, that is, creativity that does not require expert knowledge and skills, has consistently implicated three large-scale brain networks: the default, salience, and executive control networks (Beaty et al., 2016, 2019). These three networks are thought to dynamically interact to support the generation and evaluation of new ideas. Less is known, however, about whether these same networks support *domain-specific* creative thinking, particularly in STEM, which is among the most under-researched domains in the creativity literature.

The present study sought to address this gap by examining brain network connectivity associated with scientific creative thinking. Using functional magnetic resonance imaging (fMRI), we scanned undergraduate STEM majors as they engaged in hypothesis generation—a common form of scientific creative thinking requiring the production of original explanations for scientific phenomena—and employed multivariate functional connectivity analysis to identify brain networks associated with this scientific thought process. By studying the brain basis of scientific creative thinking, we aimed to provide insights for educational interventions aimed at fostering creativity in STEM education.

Creativity and Functional Brain Networks

Researchers often distinguish between domain-general creativity and domain-specific creativity. Domain-general creativity has been operationalized as a person's ability to generate original ideas, and it does not require expert knowledge of a field (e.g., visual art or engineering); domain-general creativity is commonly assessed with verbal divergent thinking tasks, such as the alternate uses task (AUT)—which involves thinking of original uses for objects—among other word association tasks (e.g., Acar & Runco, 2019; Forthmann et al., 2019; Silvia et al., 2008). Domain-specific creativity benefits from expert knowledge and skills within a given field (e.g., a scientist knowing how to design an original and effective experiment); domain-specific

creativity is measured in a variety of ways, depending on the domain, with common tasks requiring people to come up with a variety of ideas related to a common problem in their field (e.g., science students generating a range of hypotheses to explain an observed phenomenon; Aschauer et al., 2022). Notably, the extent to which domain-general cognitive abilities and traits contribute to domain-specific creative performance is a matter of continuing debate in the creativity literature (Baer, 2015; Kaufman et al., 2016; van Broekhoven et al., 2020).

Neuroscience research has explored the neural mechanisms of both domain-general and domain-specific creativity. Within creativity neuroscience, researchers are increasingly examining the role of large-scale functional brain networks, such as the executive control network (ECN), the default (mode) network (DMN), and the salience network (SN). The executive network consists of lateral prefrontal (e.g., dorsolateral prefrontal cortex) and anterior inferior parietal regions (e.g., inferior parietal sulcus); the executive network contributes to cognitive control functions, such as response inhibition and goal maintenance (Seeley et al., 2007). The default network consists of cortical midline (e.g., posterior cingulate), lateral temporal (e.g., middle temporal gyrus), and lateral parietal regions (e.g., angular gyrus); the default network contributes to a range of cognitive processes involving memory and imagination, such as episodic retrieval or mental simulation (Smallwood et al., 2021). The SN is comprised of bilateral insulae and anterior cingulate cortex; the SN detects behaviorally relevant information, and it plays a mediating role in switching between the executive and default networks (Sridharan et al., 2008).

Creative thinking is consistently associated with the interaction (i.e., functional connectivity) of the executive, default, and salience networks (Beaty et al., 2016, 2019; Jung et al., 2013; Lloyd-Cox et al., 2022). Functional connectivity of these networks is hypothesized to reflect the interaction of idea generation and idea evaluation processes in the brain: the default network is posited to support the generation of candidate ideas via memory retrieval and mental simulation; the executive network may support the evaluation of ideas through inhibition (of common ideas) and selection (of original ideas); and the SN may switch between these generative (default) and evaluative (executive) processes (Jung et al., 2013). This network neuroscience theory of creativity is consistent with classic dual-process models of the creative process that emphasize iterative processes of idea generation and idea evaluation (Sowden et al., 2015; Ward, 2015).

Domain-general creativity has been associated with functional connectivity of the executive, default, and salience networks. For example, in a study of divergent thinking, Beaty et al. (2015) reported functional connectivity between regions within these three networks during the performance on the AUT. This pattern of network connectivity was replicated in subsequent studies by Shi et al. (2018) and Beaty et al. (2021), who also found that the strength of connectivity between the executive and default networks correlated with creative task performance at the individual level. Additional evidence from individual differences research has found that people who produce more original ideas on domain-general creativity tasks (e.g., AUT) show stronger functional connectivity between the executive and default networks (Huo et al., 2022; Ovando-Tellez et al., 2022; Zhuang et al., 2021). Evidence for a causal role of specific network regions in domain-general creative thinking comes from neuromodulation studies, such as Shofty et al. (2022), who used direct cortical stimulation of default network

regions in neurosurgical patients, finding that it increased the number of ideas that participants produced on the AUT (i.e., fluency).

Regarding domain-specific creativity, network neuroscience research has focused exclusively on artistic creativity, with no such work on scientific creativity. However, artistic creativity has also implicated the executive, default, and salience networks (Vartanian, 2022). In a study of visual artists, for example, Ellamil et al. (2012) reported functional connectivity between default, executive, and SN regions when artists creatively elaborated on sketches (compared to an initial stage of idea generation). In a similar vein, Liu et al. (2015) reported increased functional connectivity between executive and default networks when poets elaborated on poetry, and Meyer et al. (2019) found stronger resting connectivity within the default network of artists associated with mental simulation, thus further implicating these networks in domain-specific artistic creativity.

Scientific Creativity

Compared to artistic creativity, scientific creativity has been substantially understudied, potentially due in part to popular associations of science with technical modes of thinking rather than with creativity, which is more commonly associated with arts. Yet creativity is critical for success in scientific domains, such as generating novel hypotheses, flexibly connecting information from diverse sources, and solving ill-defined problems (Daker et al., 2022). Psychologists have studied some aspects of scientific creativity, such as behavioral correlates of scientific productivity (e.g., intelligence, personality; Barron & Harrington, 1981; Sternberg et al., 2020) and cognitive processes relevant for scientific thinking (e.g., analogical reasoning, hypothesis generation; Sak & Ayas, 2013; Sanchez-Ruiz et al., 2013). However, very few neuroimaging studies have examined neural correlates of STEM creativity (cf. A. Anderson et al., 2022; Wertz, Chohan, Flores, & Jung, 2020; Wertz, Chohan, Ramey, et al., 2020), and to the best of our knowledge, no research has assessed functional brain network activity during scientific creative thinking.

In two recent studies, Wertz and colleagues explored the structural brain correlates of STEM creativity (Wertz, Chohan, Flores, & Jung, 2020; Wertz, Chohan, Ramey, et al., 2020). Wertz, Chohan, Flores, and Jung (2020) examined correlations between creative achievement and brain structure in a large sample of young adults, using the Creative Achievement Questionnaire (CAQ) to assess artistic and scientific creativity. Higher CAQ scores were associated with decreased structural measures across multiple areas of the brain, including regions within the ECN and DMN. Wertz, Chohan, Ramey, et al. (2020) focused on divergent thinking ability in a STEM sample, using a composite measure of three divergent thinking tasks. The results showed that decreased fractional anisotropy (FA) was correlated with higher scores on divergent thinking tasks, with reduced FA found within white matter pathways partially overlapping ECN and DMN, including the right uncinate fasciculus and the left cingulum gyrus. Overall, these studies provide insights into structural brain correlates of STEM creativity and point to the potential involvement of ECN and DMN.

There are reasons to suspect that scientific creative thinking would recruit different brain systems than artistic creativity. For example, in a recent fMRI meta-analysis of artistic creativity, Chen et al. (2020) found domain-specific neural activity patterns across different

artistic domains (i.e., musical, visual, and literary creativity; see also Sacheli et al., 2022). However, the meta-analysis also showed common engagement of frontal and motor control regions for all three domains, pointing to a domain-general executive system supporting creative performance across a range of creative practices.

Neuroimaging studies directly comparing artists and scientists also suggest both commonalities and differences in brain activity and connectivity. Recently, A. Anderson et al. (2022) conducted a graph theory analysis of brain networks of eminent artists and scientists during the performance on domain-general creativity tasks (e.g., AUT), finding more "random" network patterns in both artists and scientists (compared to an intelligence-matched control group); notably, the results corresponded to whole-brain networks, and no differences were found for specific networks (e.g., default network). Contrasting differences in brain activity (not connectivity) between expert and nonexpert during domain-general divergent and convergent creative thinking has also showed both commonalities and differences in regional activity (Chrysikou et al., 2020; Japardi et al., 2018).

Behavioral studies also suggest both general and specific cognitive abilities and personality traits relevant for artistic and scientific creativity (Feist, 1998; Merseal et al., 2023). For example, in a large sample of college students with different majors in the arts and sciences, van Broekhoven et al. (2020) found that divergent thinking was a "domain-general prerequisite" for creativity. Thus, despite mixed evidence regarding the cognitive and brain systems supporting creative thinking across domains, evidence indicates scientific creative thinking may recruit similar neurocognitive mechanisms as domain-general creative thinking.

The Present Research

In the present research, we aimed to provide insight into brain networks associated with scientific creative thinking. We focused on a cognitive process that is central to scientific creative thinking: hypothesis generation. The ability to generate original hypotheses to explain scientific phenomena is common to all STEM disciplines, from chemistry to physics to neuroscience. Hypothesis generation can be considered a creative thought process to the extent that it requires constructing novel and plausible explanations to open-ended scientific problems. Behavioral studies in educational settings have demonstrated the importance of hypothesis generation to academic achievement and STEM creativity (Aschauer et al., 2022; Hu & Adey, 2002; Sak & Ayas, 2013). Moreover, teaching students how to generate original hypotheses is a component of modern STEM curricula that aim to foster scientific creative thinking skills (Haim & Aschauer, 2022).

Although no prior study has examined brain network connectivity associated with open-ended hypothesis generation, a few studies have assessed univariate brain activity during closed-ended hypothesis generation (convergent thinking; Kwon et al., 2009). For example, in a longitudinal study, Kwon et al. (2009) found that following 2 months of training undergraduates how to generate accurate hypotheses (with a single/correct solution), brain activity increased within the left inferior frontal gyrus (IFG) of the ECN, as well as the anterior cingulate cortex of the SN (compared to a control group; Lee & Kwon, 2012). Other studies have examined cognitive processes relevant to scientific creative thinking, such as analogical transfer and abductive reasoning (H. Zhang et al., 2014).

Understanding how creativity operates in such knowledge-rich and domain-specific contexts—and how it differs (or not) from domain-general creativity—is central to educational interventions aimed at fostering creativity (Yang et al., 2022).

Here, we aimed to uncover functional brain networks supporting scientific hypothesis generation. Using fMRI, we scanned a sample of STEM undergraduate students ($n = 47$) during performance of a hypothesis generation task, and conducted a series of functional connectivity analyses, including (a) a data-driven multivariate pattern analysis (MVPA) to identify networks of interest and (b) a seed-based connectivity analysis to map functional connectivity of these networks during hypothesis generation. Given prior work implicating the default, salience, and executive networks in both domain-general creative thinking and domain-general artistic performance (Beaty et al., 2016, 2019; Ellamil et al., 2012; Liu et al., 2015), we hypothesized that hypothesis generation would be characterized by a similar pattern of network connectivity, potentially reflecting the coordination of generative and evaluative processes to construct novel and plausible scientific explanations.

Method

Participants

Data were collected as part of a larger project on the neuroscience and measurement of scientific creative thinking. The full sample of participants consisted of 51 undergraduate students from Pennsylvania State University. We specifically recruited students majoring in STEM (broadly defined), given the focus of the study on scientific creativity. Students were recruited from large introductory science courses (chemistry and biology), as well as through a mass screening database including STEM students enrolled in introductory psychology; students were invited to participate via email if they had a declared STEM major. They completed consent forms and received $50 for their participation, in addition to a coffee mug with their anatomical brain scan. Four participants were excluded, including one for an incidental finding, one for excessive motion, one for hardware failure, and one for terminating the scan early, yielding a final sample of 47 participants (28 females, 16 males, three genders not reported; mean age = 19.33, age range: 18–32). All participants were right-handed, native English speakers, with normal or corrected-to-normal vision, and they reported no history of cognitive impairment, neurological issues, or drugs affecting the central nervous system. The study procedure was approved by the Pennsylvania State University Institutional Review Board.

fMRI Task Procedures

Participants completed two tasks during fMRI in an event-related design: (a) a Hypothesis Generation Task and (b) a Synonym Control Task. Each task included 24 items. The Appendix lists all items from both tasks.

The *Hypothesis Generation Task* presented participants with an environment (e.g., "island") and a scenario/phenomenon occurring within this environment ("all flowers are the same color"). Participants were asked to think of a novel and scientifically plausible hypothesis to explain the scenario (e.g., "bees only pollinate certain colored plants" or "all other flowers are eaten by animals" or "the color helps them camouflage in the environment"). If they produced a hypothesis before the end of the trial, they were encouraged

to think of an even more original response (cf. Beaty et al., 2015, 2018; Benedek et al., 2014).

The *Synonym Control Task* was designed to mirror the task structure of the Hypothesis Generation Task (including scientific terminology of items). However, instead of showing an environment, participants were shown a verb (e.g., "refracted") and a scenario/phenomenon that includes this verb ("light is refracted by strong magnetic or gravitational fields"). Participants were asked to think of a synonym to replace the verb. If they produced a synonym before the end of the trial, they were encouraged to think of an even more appropriate response. Synonym generation has been used in prior work as a control task to compare against creative tasks (e.g., Benedek et al., 2014). Both the synonym and hypothesis tasks require participants to self-generate a response. Critically, the hypothesis task required creative thinking, and the synonym tasks did not.

Figure 1 shows the fMRI task paradigm. A block began with a pre-cue fixation (5 s), followed by a conditioned cue (hypothesis or synonym). Then, the trial presented (a) a jittered fixation cross (3–5 s), (b) a thinking period displaying the stimulus (environment/verb at the top, and scenario/phenomenon at the bottom, depending on condition; 15 s), and (c) a verbal response phase, where participants spoke their response into an MRI-compatible microphone (5 s; cf., Beaty et al., 2018; Benedek et al., 2014). Verbal responses were collected for a separate study on individual differences.

The two tasks were presented in eight blocks of six trials (three hypotheses and three synonyms) in an ABBAABBA/BAABBAAB fashion (task order was counterbalanced across participants). Prior to the fMRI session, participants received instructions and completed several practice trials. The fMRI sequence consisted of (a) a 10-min resting-state scan, (b) two runs of the hypothesis and synonym tasks, (c) a T1 scan, and (d) an unrelated task.

MRI Data Acquisition and Preprocessing

Whole-brain imaging was performed on a 3T Siemens Magnetom Prisma Fit MRI system (Siemens Medical Systems) using a 64-channel head coil. Multislice T2*-weighted functional images were acquired using a multiband gradient-echo echo-planar imaging sequence (repetition time = 900 ms, echo time = 30.2 ms, flip angle = 53°, 60 axial slices, 2.4 × 2.4 × 2.4, distance factor 0%, field of view = 222 × 222 mm, multiband factor = 5). The first two volumes were discarded to allow for T1 equilibration effects. Visual stimuli

were presented using E-Prime and viewed through a mirror attached to the head coil. In addition to functional imaging, a high-resolution T1 scan was acquired for anatomic normalization. Preprocessing of the anatomical and functional data was performed using *fMRIPrep*1.4rc1 (Esteban et al., 2019).
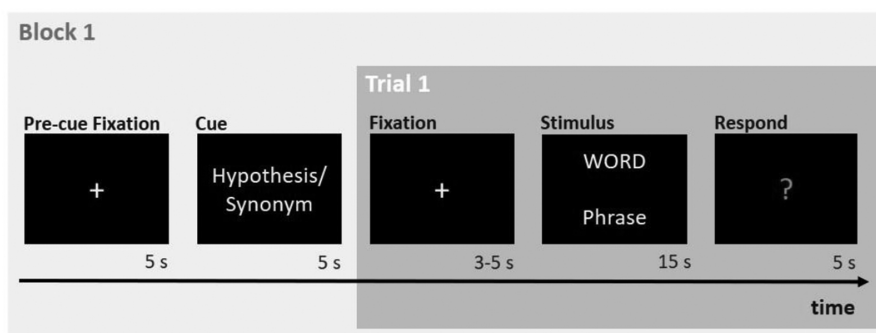
Anatomical Data Preprocessing

The T1-weighted (T1w) image was skull-stripped and corrected for intensity nonuniformity using Advanced Normalization Tools (ANTs v.2.2.0; Avants et al., 2008). Brain tissue segmentation of cerebrospinal fluid (CSF), white matter (WM), and gray matter (GM) was performed on the brain-extracted T1w using FMRIB's Automated Segmentation Tool in FMRIB Software Library (FSL) v.5.0.9 (Y. Zhang et al., 2001). Brain surfaces were reconstructed using FreeSurfer v.6.0.1 (Dale et al., 1999), and the brain mask estimated previously was refined with a custom variation of Mindboggle (Klein et al., 2017). Volume-based spatial normalization to one standard space (MNI152NLin2009cAsym; Fonov et al., 2009) was performed through nonlinear registration with ANTs, using brain-extracted versions of both T1w reference and the T1w template.

Functional Data Preprocessing

For each Blood Oxygenation Level Dependent (BOLD) run per subject, first, a reference volume and its skull-stripped version were generated using a custom methodology of *fMRIPrep*. The BOLD reference was then coregistered to the T1w reference FreeSurfer, which implements boundary-based registration (Greve & Fischl, 2009). Coregistration was configured with nine degrees of freedom to account for distortions remaining in the BOLD reference. Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using FSL (Jenkinson et al., 2002). BOLD runs were slice-time corrected using Analysis of Functional NeuroImages (AFNI; Cox & Hyde, 1997). The BOLD time series were then resampled into Montreal Neurological Institute (MNI) space using ANTs. Framewise displacement and three region-wise global signals extracted from CSF, the WM, and the whole-brain masks, respectively, were also computed as confound regressors (Power et al., 2014; Satterthwaite et al., 2013).

Figure 1
An Overview of the fMRI Task Paradigm

Note. fMRI = functional magnetic resonance imaging.

Functional Connectivity Analysis

Functional connectivity was assessed using the functional connectivity (CONN) toolbox in MATLAB (Whitfield-Gabrieli & Nieto-Castanon, 2012). The analysis included two main steps: (a) whole-brain functional connectivity analysis (i.e., MVPA) to identify voxel clusters (regions of interest) associated with hypothesis generation (focusing on clusters within the DMN, ECN, and SN), and (b) seed-based functional connectivity analysis, using the regions from the whole-brain analysis, to map connectivity patterns with the rest of the brain.

MVPA was used for the whole-brain connectivity analysis (Beaty et al., 2015, 2017; Nieto-Castanon, 2022). MVPA, as implemented in CONN, is a data-driven method for identifying voxel clusters (i.e., regions of interest) that show task-related differences in functional connectivity (instead of using a predefined anatomical atlas). Here, MVPA was employed to uncover voxel clusters associated with hypothesis generation. MVPA uses a searchlight procedure (cf. Kriegeskorte et al., 2006) to characterize the entire multivariate connectivity pattern for each voxel with the rest of the brain. Then, a data reduction procedure is employed to characterize the fMRI data as low-dimensional "eigenpatterns," similar to principal components in principal component analysis. Finally, a multivariate general linear model (GLM) F test is used to assess differences between conditions. This process is completed for all voxels in the brain. To summarize, the MVPA: (a) computes functional connectivity for each voxel (with the rest of the whole brain); (b) generates eigenpattern scores capturing spatial features across participants; and (c) conducts group-level functional connectivity analysis (entering the eigenpatterns into GLM). The first four eigenpatterns (components) were entered into the GLM, consistent with past work (Beaty et al., 2015, 2017; Nieto-Castanon, 2022).

For the MVPA, voxel-level results were considered significant at a threshold of $p < .001$ (uncorrected), and clusters were significant at $p < .001$ (false discovery corrected) threshold.

For the seed-to-voxel analysis, voxel-level results were considered significant at a threshold of $p < .001$ (uncorrected), and clusters were significant at $p < .05$ (false discovery corrected).

Results

Multivariate Pattern Analysis

We began by conducting whole-brain functional connectivity analysis (via MVPA) to identify regions associated with hypothesis generation. The MVPA yielded 14 voxel clusters that showed connectivity differences during the hypothesis or synonym conditions (see Table 1 and Figure 2). The largest cluster ($k = 330$) was within the left lateral frontal cortex, corresponding to the left IFG of the semantic/ECN. Importantly, the whole-brain network also included core hubs within the default network (posterior cingulate cortex and precuneus) and SN (right anterior insula). Additional clusters outside the networks of interest are listed in Table 1, including a cluster ($k = 212$) within the superior frontal gyrus (corresponding to the pre-supplementary motor area [SMA]). In sum, the whole-brain MVPA yielded regions within the default, salience, and control networks that showed connectivity differences during hypothesis generation.

Seed-to-Voxel Analysis

Next, we conducted a series of post hoc seed-to-voxel functional connectivity analyses using the regions of interest from the MVPA: left IFG,

Table 1

MVPA Task Effects for Hypothesis and Synonym Generation

Region	BA	x	y	z	Voxels
Inferior frontal gyrus	44	−50	24	22	330
Superior frontal gyrus	8	−2	16	48	212
Supplementary motor area	6	−40	−2	34	145
Inferior frontal gyrus	47	−46	22	−6	115
Precuneus	7	8	−72	36	51
Posterior cingulate	30	2	−48	20	36
Middle temporal gyrus	21	−48	−44	2	31
Middle temporal gyrus	21	−58	−34	2	25
Supramarginal gyrus	40	62	−44	32	24
Anterior insula	13	32	28	−2	19
Posterior cingulate cortex	31	0	−42	48	16
Precuneus	7	−8	−74	32	15
Lateral occipital cortex	39	−34	−58	48	14
Primary visual cortex	17	2	−90	2	14

Note. Regions were identified based on MNI coordinates using the Bioimage Suite and CONN Toolbox. Bolded regions were included in the seed-to-voxel analysis as regions of interest based on their network affiliation (default, salience, control). MVPA = multivariate pattern analysis; BA = Brodmann area; MNI = Montreal Neurological Institute.
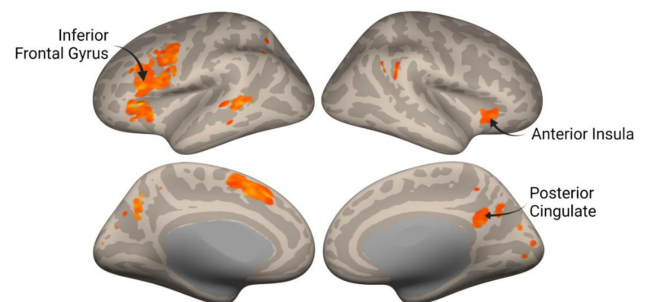
right anterior insula, and posterior cingulate. The three clusters were extracted to form binary masks, using the entire cluster from the MVPA as seed region. Then, the average BOLD time series were correlated with all other voxels in the brain—separately, for each of the three regions—and contrasts were computed for hypothesis generation > synonym generation ($p < .05$, family-wise error-corrected cluster size).

The first analysis focused on the left IFG of the semantic control network during hypothesis generation. Results showed widespread connectivity differences for the left IFG during hypothesis generation (see Table 2 and Figure 3). Critically, the left IFG showed stronger connectivity during hypothesis generation with posterior regions of the default network, including the angular gyrus (bilaterally), posterior cingulate, precuneus, parahippocampal cortex, and lateral temporal cortex. The reverse contrast (synonym generation > hypothesis generation) yielded stronger connectivity of the left IFG with other control-related regions, as well as clusters within the lateral occipital cortex.

Next, we assessed functional connectivity of the posterior cingulate of the default network during hypothesis generation. We found stronger connectivity of the posterior cingulate with two clusters

Figure 2

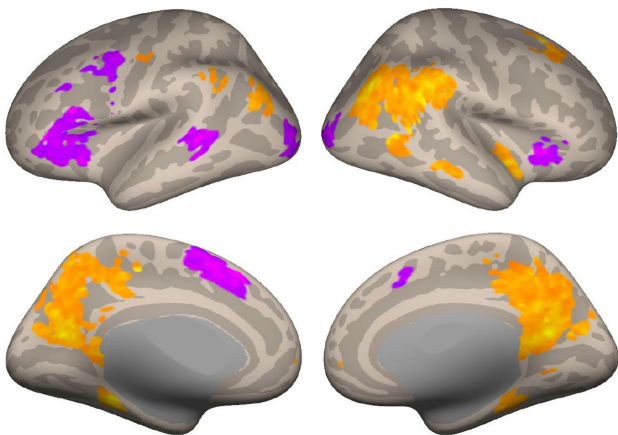*Whole-Brain MVPA for Hypothesis and Synonym Generation*

Note. Regions of interest for the seed-to-voxel functional connectivity analyses are labeled. MVPA = multivariate pattern analysis. See the online article for the color version of the figure.

Table 2

Seed-to-Voxel Functional Connectivity for the Left Inferior Frontal Gyrus

Region	BA	x	y	z	Voxels
Hypothesis > synonym					
Posterior cingulate cortex	23	14	−54	20	1,843
Angular gyrus	39	42	−70	38	1,396
Lateral occipital cortex	19	−36	−86	32	169
Frontal eye fields	8	22	26	38	78
Angular gyrus	NA	−56	−58	42	77
Fusiform cortex	NA	−34	−38	−14	62
Middle temporal gyrus	21	62	−16	−12	55
Parahippocampal gyrus	36	34	−32	−16	42
Superior temporal gyrus	22	42	−8	−12	41
Cingulate gyrus	30	−8	−46	8	33
Frontal eye fields	8	22	22	50	28
Fusiform gyrus	37	54	−54	0	24
Fusiform gyrus	37	66	−50	0	22
Dorsal anterior cingulate	32	−2	50	0	21
Primary somatosensory cortex	1	−40	−20	38	20
Synonym > hypothesis					
Inferior frontal gyrus	47	−48	22	−10	611
Supplementary motor area	6	−2	14	50	372
Cerebellum	NA	12	−80	−18	196
Middle frontal gyrus	NA	−44	2	60	173
Occipital pole	18	−28	−90	−6	126
Occipital pole	18	26	−90	6	97
Middle temporal gyrus	21	−48	−42	2	87
Insula	13	32	26	−4	52

Note. Regions were identified based on MNI coordinates using the Bioimage Suite and CONN Toolbox. BA = Brodmann area; regions labeled NA were not defined in the Bioimage Suite; NA = not applicable; MNI = Montreal Neurological Institute.

within left frontal regions, corresponding to the left IFG, overlapping with the left anterior insula. The posterior cingulate was also more strongly connected to a frontal midline cluster within the superior frontal gyrus/pre-SMA. The reverse contrast showed a pattern of within-

Figure 3

Seed-to-Voxel Functional Connectivity for the Left Inferior Frontal Gyrus Cluster (Hypothesis > Synonym)

Note. Warmer colors indicate stronger connectivity for hypothesis generation; cooler colors indicate stronger connectivity for synonym generation. See the online article for the color version of the figure.

network connectivity, with the posterior cingulate more connected to other default network regions, among others (see Table 3 and Figure 4).

Finally, we examined the connectivity of the right anterior insula of the SN during hypothesis generation. Consistent with the two previous analyses, the right anterior insula displayed widespread connectivity with posterior regions of the default network, with the largest clusters corresponding to the right angular gyrus ($k = 937$) and the precuneus/posterior cingulate ($k = 258$; see Table 4 and Figure 5). The reverse contrast largely mirrored the prior patterns for synonym generation, with the right anterior insula exhibiting connectivity with other control-related areas (e.g., left IFG and pre-SMA), among several other regions.

Discussion

Despite the importance of creativity to STEM success, scientific creativity is among the least well-understood topics in the creativity literature, particularly the brain basis of scientific creative thinking. The present study provides novel insight into the brain networks supporting a canonical form of scientific creative thinking: hypothesis generation. Undergraduate STEM majors were asked to generate novel and plausible scientific hypotheses to hypothetical scenarios. Whole-brain functional connectivity analyses yielded several voxel clusters corresponding to key hubs within the default (posterior cingulate), salience (right anterior insula), and semantic control (left IFG) networks. Seed-based connectivity analyses, using these network hubs as seeds, found increased between-network connectivity during hypothesis generation (compared to a semantic control condition). The findings suggest that scientific creative thinking recruits similar brain systems as domain-general creative thinking, potentially reflecting a coordination between generative and evaluative cognitive processes to construct original explanations for scientific phenomena.
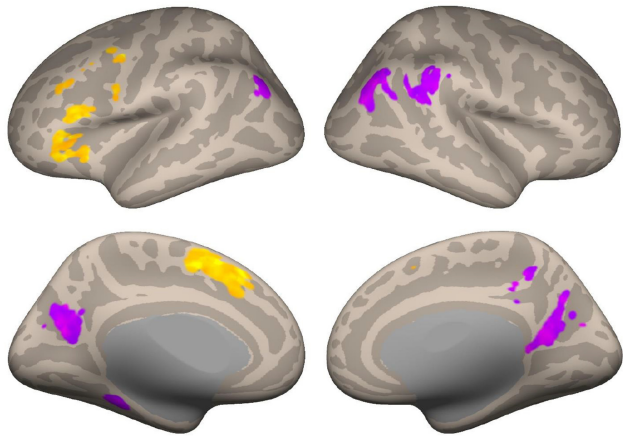
Seed-based connectivity analysis showed stronger functional connectivity between the left IFG and posterior regions within the default network, including the posterior cingulate and bilateral angular gyri. The left IFG is associated with goal-directed retrieval from

Table 3

Seed-to-Voxel Functional Connectivity Analysis for the Posterior Cingulate

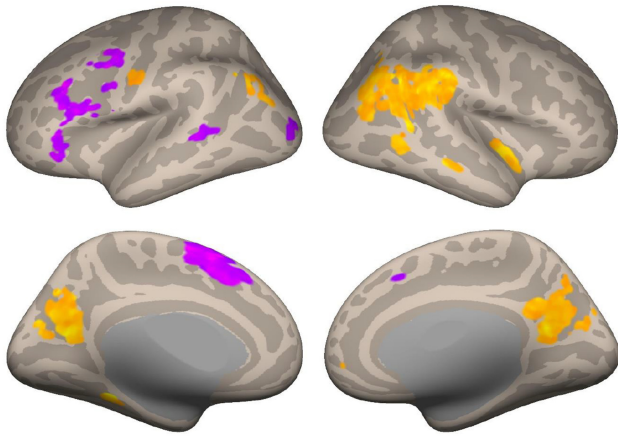| Region	BA	x	y	z	Voxels
Hypothesis > synonym					
Supplementary motor area	6	−2	12	48	239
Inferior frontal gyrus	44	−56	22	26	176
Inferior frontal gyrus	47	−44	24	−4	164
Supplementary motor area	6	−50	4	50	30
Supplementary motor area	6	−44	−2	60	25
Cerebellum	NA	10	−78	−22	20
Synonym > hypothesis					
Supramarginal gyrus	40	60	−44	42	179
Angular gyrus	39	44	−72	30	163
Posterior cingulate cortex	23	18	−54	18	124
Precuneus	18	−20	−62	22	114
Lateral occipital cortex	NA	−50	−74	34	68
Posterior cingulate cortex	31	10	−38	48	50
Parahippocampal gyrus	36	−32	−38	−12	20

Note. Regions were identified based on MNI coordinates using the Bioimage Suite and CONN Toolbox. BA = Brodmann area; regions labeled NA were not defined in the Bioimage Suite; NA = not applicable; MNI = Montreal Neurological Institute.

Figure 4

Seed-to-Voxel Functional Connectivity for the Posterior Cingulate Cluster (Hypothesis > Synonym)

Note. Warmer colors indicate stronger connectivity for hypothesis generation; cooler colors indicate stronger connectivity for synonym generation. See the online article for the color version of the figure.

Figure 5

Seed-to-Voxel Functional Connectivity for the Right Anterior Insula Cluster (Hypothesis > Synonym)

Note. Warmer colors indicate stronger connectivity for hypothesis generation; cooler colors indicate stronger connectivity for synonym generation. See the online article for the color version of the figure.

long-term memory (Vatansever et al., 2021), inhibition of task-irrelevant information (Thompson-Schill et al., 1999), and selection of items among competing alternatives (Moss et al., 2005). Prior fMRI studies on divergent thinking have consistently

Table 4

Seed-to-Voxel Functional Connectivity Analysis for the Right Anterior Insula (Hypothesis > Synonym)

Region	BA	x	y	z	Voxels
Angular gyrus	39	44	−66	30	937
Posterior cingulate cortex	23	14	−54	20	258
Secondary visual cortex	18	−14	−58	18	173
Posterior cingulate cortex	31	10	−54	30	47
Superior temporal gyrus	22	42	−10	−10	33
Medial temporal gyrus	21	60	−24	−10	27
Fusiform gyrus	37	62	−54	−4	21
Angular gyrus	39	−44	−68	42	23
Angular gyrus	39	−38	−78	38	20
Supplementary motor area	6	−52	−8	26	20
Dorsal anterior cingulate cortex	32	0	48	−2	20
Fusiform gyrus	37	−32	−42	−10	20
Somatosensory association cortex	7	6	−78	38	19
Synonym > hypothesis					
Supplementary motor area	6	−2	20	66	337
Inferior frontal gyrus	44	−46	20	24	162
Supplementary motor area	6	−48	2	54	95
Inferior frontal gyrus	47	−50	22	−10	95
Cerebellum	NA	32	−56	−30	39
Inferior frontal gyrus	44	−58	14	6	25
Cerebellum	NA	32	−66	−28	25
Secondary visual cortex	18	−22	−94	8	24
Medial temporal gyrus	21	−48	−42	2	19
Cerebellum	NA	30	−60	−52	19
Lateral occipital cortex	NA	−46	−80	24	19

Note. Regions were identified based on MNI coordinates using the Bioimage Suite and CONN Toolbox. BA = Brodmann area; regions labeled NA were not defined in the Bioimage Suite; NA = not applicable; MNI = Montreal Neurological Institute.

implicated the left IFG (Cogdell-Brooke et al., 2020). For example, Madore et al. (2019) found that the left IFG showed increased functional connectivity with regions of the default network during divergent thinking following an episodic specificity induction—brief training in recalling details of recent experiences—suggesting that one process supported by IFG–default coupling may be the goal-directed retrieval of episodic information from long-term memory. In the context of the current findings, one possibility is that hypothesis generation similarly requires selectively searching long-term memory, or constructing a mental simulation requiring imagery about the hypothetical situation.

Another possible mechanism of control–default coupling during hypothesis generation is response inhibition. Studies have reported frontal control of memory activation in the context of suppressing unwanted memories (M. C. Anderson et al., 2004) and other prepotent, task-irrelevant responses from memory (Forstmann et al., 2008). Beaty et al. (2017) conducted a word association study, where participants first studied a noun–verb association, and in a separate condition, were asked to think of a new and creative association to the noun—presumably requiring the suppression of the original association to think of something new. Functional connectivity was reported between a left ECN and anterior regions of the default network (compared to a control condition that did not require response inhibition). Likewise, in the hypothesis generation task of the present study, participants are asked to think of novel explanations of scientific phenomena (e.g., "The water in one lake is warmer than the water in the other, despite getting the same amount of sunlight—why might this be?"), which may require inhibiting easy or simple accounts (e.g., "One lake is in a cold location and one lake is in a hot location."). Thus, functional connectivity between executive and default regions during hypothesis generation may indicate the suppression of unoriginal ideas when attempting to think creatively.

Functional connectivity of control and default networks may also reflect goal maintenance. In our study, participants were instructed to "be creative," requiring them to maintain the goal of coming up with

a novel—and scientifically plausible—explanation of the given phenomenon. Prior work on divergent thinking has found that such "be creative" instructions invoke executive control mechanisms (Beaty & Kenett, 2023; Nusbaum et al., 2014). At the behavioral level, such instructions typically cause participants to be more discerning in their responses by outputting fewer ideas, but more original ideas. In this context, goal maintenance may also play an important role in successful performance on the hypothesis generation task, to the extent that participants had to maintain the goal of generating an original explanation, and to avoid saying the first thing that came to mind, which may also invoke inhibitory control (as noted above). Notably, however, we did not include a control condition without "be creative" instructions, so whether control–default coupling reflects goal maintenance remains to be explored in future work.

Strengths, Limitations, and Future Directions

The present study provides the first network neuroscience investigation of scientific creative thinking. Our study was strengthened by a relatively large sample of STEM undergraduate students, as well as a strong representation across STEM disciplines (e.g., engineering, chemistry, and the life sciences). Critically, the present study provides initial evidence that a fundamental process in scientific thinking—hypothesis generation—may rely on similar neurocognitive mechanisms to "domain-general" creative thinking.

One limitation of our study is that we did not distinguish between STEM subfields (e.g., chemistry and biology). This was due in part to the modest expertise of our student population (i.e., subfield differences may not emerge until later in STEM education). Recently, van Broekhoven et al. (2020) reported small differences in divergent thinking across "micro-domains" in undergraduate engineering students. Although the study was correlational, one possibility is that educational differences across STEM subfields may lead to differences in creative thinking (or hypothesis generation, more specifically). Therefore, future studies should explicitly investigate differences between STEM domains (and micro-domains) that may result from different pedagogical practices. Another limitation relates to the unbalanced gender ratio in this study, which should be considered in light of past work on sex differences in brain network connectivity (Ryman et al., 2014; Silberstein & Camfield, 2021).

More broadly, educational neuroscience research should investigate how STEM education impacts brain network development (Cortes et al., 2022), and whether specific pedagogical practices—for example, "flex-based learning" (Haim & Aschauer, 2022)—promote creative thinking and a corresponding strengthening of brain connectivity, particularly within the default, salience, and control networks. Prior work has indicated that domain-specific expertise (e.g., in music) affects brain network dynamics during creative activities, such that executive control contributions decrease in experts, allowing for less effortful idea generation (e.g., Pinho et al., 2014). Using longitudinal study designs, network-level interactions could be assessed at the beginning and end of educational interventions intended to foster STEM learning and creative thinking. Future research should also continue to explore the relationship between domain-general (e.g., divergent thinking) and domain-specific creative thinking (e.g., hypothesis generation). Our findings indicate that similar functional brain networks contribute to both domain-general and domain-specific creative thinking, suggesting that—to the

extent that creative thinking skills can be improved through education—cultivating creativity in one domain may have a broader impact on the neurocognitive system supporting creative thinking.

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(Appendix follows)

Appendix

Table A1

fMRI Items for the Hypothesis Task

Environment	Situation
Desert	The climate shifts from extremely dry to very humid.
Large city	Foxes are observed in metropolitan areas.
Zoo	Two species of animals begin attempting to cross-breed.
Small village	All community members are nocturnal.
Earth	The moon appears brighter and brighter over the course of a year.
Ocean	A certain kind of seaweed is always found near especially clear water.
Ocean floor	Crabs become highly overpopulated in the ecosystem.
Beach	The ocean has gradually been receding from the shoreline for years.
Highway	A highway is busiest during the middle of the night.
Large city	Water pipes burst and all electricity goes out.
Forest	A species of bird starts making nests using materials from other birds' nests.
New planet	A device that works on Earth does not work.
Island	All flowers are the same color.
Abandoned building	Filled with plants, even though it receives no direct sunlight.
Hospital	Doctors notice that babies are being born with larger ears.
Corporation	Productivity increases after employees visit a museum.
Earth	A natural disaster wipes out all animals except humans and giraffes.
Pond	Lily pads appear earlier in the spring but also disappear earlier.
Island	All flowers are the same color.
Abandoned building	Filled with plants, even though it receives no direct sunlight.
Hospital	Doctors notice that babies are being born with larger ears.
Corporation	Productivity increases after employees visit a museum.
Earth	A natural disaster wipes out all animals except humans and giraffes.

Note. fMRI = functional magnetic resonance imaging.

Table A2

fMRI Items for the Synonym Task

Word to replace	Situation
Use	Humans become allergic to all animal products and can no longer use them.
Grown	All fruits and vegetables grown are nonperishable.
Refracted	Light is refracted by strong magnetic or gravitational fields.
Crumble	All of the clothes products start to crumble after being worn once.
Sleep	All community members sleep during the day and go out at night.
Allow	Wearable devices allow people to turn off physical pain.
Received	Emails took 2 days to be sent and received.
Notice	Astronauts 1 day notice a massive increase in gravity near Earth.
Mutating	All species on the ground level begin mutating extra limbs.
Eating	Carnivorous predators begin exclusively eating plants.
Evolve	As humans evolve, they need more calcium to survive.
Taught	Schoolchildren are no longer taught math.
Stain	You get a stain on your shirt from a new type of synthetic oil.
Claim	Passengers claim that sodas taste better after takeoff.
Spills	A company spills radioactive waste and decimates the environment.
Removed	One day students discover that all of the books have their words removed.
Vanished	All transportation suddenly vanished from the world.
Seek	Natural processes begin to seek randomness instead of equilibrium.
New	A new drug is created that has the ability to cure cancer.
Produced	All paper was removed from the world and no more could be produced.
Transportation	All transportation suddenly vanished from the world.
Access	Humanity had access to an unlimited, free energy source.
Longer	Ice is no longer less dense than water.
Future	In the future humans can no longer live above water.

Note. fMRI = functional magnetic resonance imaging.