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Frontopolar Activity and Connectivity Support Dynamic Conscious Augmentation of Creative State

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Abstract: No ability is more valued in the modern innovation-fueled economy than thinking creatively on demand, and the "thinking cap" capacity to augment state creativity (i.e., to try and succeed at thinking more creatively) is of broad importance for education and a rich mental life. Although brain-based creativity research has focused on static individual differences in trait creativity, less is known about changes in creative *state* within an individual. How does the brain augment state creativity when creative thinking is required? Can augmented creative state be consciously engaged and disengaged dynamically across time? Using a novel "thin slice" creativity paradigm in 55 fMRI participants performing verb-generation, we successfully cued large, conscious, short-duration increases in state creativity, indexed quantitatively by a measure of semantic distance derived via latent semantic analysis. A region of left frontopolar cortex, previously associated with creative integration of semantic information, exhibited increased activity and functional connectivity to anterior cingulate gyrus and right frontopolar cortex during cued augmentation of state creativity. Individual differences in the extent of increased activity in this region predicted individual differences in the extent to which participants were able to successfully augment state creative performance after accounting for trait creativity and intelligence. *Hum Brain Mapp 36:923–934, 2015.* © 2014 Wiley Periodicals, Inc.

Key words: state creativity; verb generation; frontopolar cortex; semantic distance; fMRI

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INTRODUCTION

Some people are more creative than others, so creativity is a trait [Guilford, 1950]. But even the most creative people are not always being creative, and even generally uncreative people experience occasional moments of creativity, so creativity is also a state [Gilchrist and Taft, 1972; O'Hara and Sternberg, 2001]. Trait creativity has thus far been the primary focus of creativity research. For instance, Guilford's influential theoretical framework [Guilford, 1950, 1967], and the prominent Torrance Tests of Creative Thinking [Goff and Torrance, 2002] are based on measurement of creativity as a stable trait quality, similar to IQ. Far less well understood, though no less important, is state creativity. Across several decades, the human capacity to consciously augment creativity has been demonstrated in multiple cognitive domains,

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[Chen et al., 2005; Gilchrist and Taft, 1972; Green et al., 2012a; Harrington, 1975; Howard-Jones et al., 2005; Niu and Sternberg, 2001; O'Hara and Sternberg, 2001; Seger et al., 2000]. However, very little is known about the neural mechanisms that support "thinking cap" augmentation of creative state (one exception may be work on the neural bases of musical improvisation [Limb and Braun, 2008; Liu et al., 2012]). This is particularly surprising because mechanisms that make creativity dynamic within an individual are likely to be critical for enabling current efforts in science [Harrison et al., 2012; NSF, 2011], education [NSF, 2013], and industry [IBM, 2010] to improve creative thinking and augment creative output [Holyoak and Thagard, 1995; Sternberg and Lubart, 1991; Vartanian, 2013].

At the cognitive level, an important remaining question is whether a person can engage and disengage augmented state creativity dynamically across time. To address this question, we have extensively validated a measure of "thin slice creativity" [Prabhakaran et al., 2013], a variant of the classical verb-generation paradigm [Petersen et al., 1989], devised to be compatible with neuroimaging and to elicit engagement of augmented state creativity over brief, discrete durations. Rigorous investigation of creativity requires tasks that are suitable for quantified psychometrics but also sufficiently open-ended to be construct-valid assays of creativity (i.e., they must allow freedom for divergent production). Accordingly, thin slice creativity task allows open-ended real time responding, and performance can be measured using a quantitative index of "semantic distance," derived via latent semantic analysis [LSA; Dumais, 2004; Landauer et al., 1998], a reliable and construct-valid measure of creativity [Forster and Dunbar, 2009; Green et al., 2010, 2012b; Prabhakaran et al., 2013; Wolfe and Goldman, 2003].

Here, using the thin slice creativity task, an explicit creativity cue successfully elicited repeated conscious engagement and disengagement of augmentated state creativity during fMRI, yielding a large effect on creative performance and enabling direct investigation of neural activity associated with augmented creative state. We hypothesized that augmenting creativity would place greater demand on neural circuitry within frontopolar cortex that supports creative integration across semantic distance [Gonen-Yaacovi et al., 2013; Green et al., 2010, 2012b; Ramnani and Owen, 2004]. Thus, we specifically interrogated activity in frontopolar cortex as a predictor of state creativity. Participants also performed a battery of trait creativity and intelligence measures outside the scanner, allowing us to examine neural mechanisms of state creativity in the context of trait creativity and intelligence. To test our central, a priori hypothesis, a series of analyses was conducted to evaluate whether increased frontopolar activity during the creativity cue predicted augmented creative performance, accounting for trait intelligence and creativity variables, participant demographics, and activity in other brain regions.

MATERIALS AND METHODS

Participants

Sixty-three healthy, right-handed native English speakers with no history of mental illness or psychoactive drug use, provided informed consent and participation in behavioral and fMRI sessions. All procedures received institutional review board (IRB) approval prior to the study. Data from eight participants were removed from analyses due to technical problems with the voice-recording microphone and/or presentation software that resulted in inaccurate or missing response timing data (seven participants) or errant execution of the scan acquisition procedure (one participant), such that 55 participants (31 male; mean age = 22.5 ± SD = 4.78 years) were included in our analyses. Power calculation indicated a required sample size of 54 to achieve 95% power to detect an estimated effect size of 0.5 (based on our prior behavioral data; [Prabhakaran et al., 2013]) for the effect of a creativity cue on semantic distance via a two-tailed within-subjects *t*-test. Exceeding this minimum sample size by 15% provided a buffer against technical problems associated with our somewhat complex in-scanner voice-recording method, as well as ordinary issues with data usability in fMRI research.

fMRI Data Acquisition and Analysis

Scanning was performed on a 3-T Allegra System (Siemens, Erlangen, Germany) to collect whole-brain T2*-weighted blood-oxygen-level dependent (BOLD) functional images (asymmetric spin-echo echo-planar sequence; whole-brain repetition time, TR = 2,000 ms; echo time = 25 ms; field of view = 256 mm; flip angle = 80°; matrix = 64×64; axial slices 4 mm thick). Sequential whole-brain volumes (32 contiguous slices) were collected during two event-related functional runs. 36 task trials were presented during each functional run. Each trial ended when a voice response was received, which triggered the PsyScope [Cohen et al., 1993] presentation script to continue. Voice responses were recorded using a noise-cancelling optical microphone system (Phon-Or, Israel) mounted to the head coil such that it could be situated 20–40 mm from participants' lips. Responses were transcribed by an experimenter for subsequent LSA semantic distance calculation. "Jitter" was interleaved between trials, across a range from 250 to 4,250 ms in steps of 2,000 ms (1 TR). The scanning run began with an unanalyzed fixation period equal to 3 TRs, which allowed the scanner to reach steady state.

fMRI data processing was performed using fMRI expert analysis tool Version 5.98, part of FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl. The following pre-statistics processing was applied: motion correction using MCFLIRT; spatial smoothing using a Gaussian kernel of FWHM 5 mm; grand-mean intensity normalization of the entire 4D dataset by a single multiplicative factor; high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma = 50.0 s). Registration to high resolution structural and, subsequently, standard space images was performed using FLIRT. At the individual subjects level, a design matrix was fit to each subject's data as part of a general linear model with each condition (Cued and Uncued) modeled as events with a specified duration (i.e., the time from stimulus onset to onset of the voice response) convolved with a canonical hemodynamic response function. Higher-level analysis was performed using FLAME. Z (Gaussianised T/F) statistic images were thresholded using a relatively conservative exploratory threshold of $P < 0.0001_{\text{uncorrected}}$.

fMRI Task

On each trial of the thin slice creativity verb-generation task, participants were presented with a noun on a computer screen and asked to say a verb that was related to the noun in any way. For example, given the noun prompt, "Yarn," participants generated spoken responses including "Sew" (relatively uncreative) and "Bleat" (relatively creative). Of the 72 nouns presented across the two fMRI runs, half (36) were shown in green (Cued condition) and the other half in purple (Uncued condition). For nouns presented in the cue color, participants were instructed to "think creatively when generating a verb response." Conditions were interleaved such that two trials of each condition were followed by two trials of the other condition. This design allowed us to investigate acute engagement of state creativity while minimizing set shifting and executive attention demands (e.g., from unpredictable or surprising shifts), which were not the intended targets of investigation. Validating the effectiveness of this design, we found that trials representing the shifts between Cued and Uncued conditions (i.e., the first trial of a pair of Cued or Uncued trials) did not differ from the trials that occurred after (i.e., the second trial of a pair) with respect to semantic distance or response time (RT) (all P for both Cued and Uncued trials > 0.3).

By design, the two word lists used for Cued and Uncued trials, respectively did not differ in terms of their average constraint $t(70) = 0.35$, $P = 0.73$, where constraint refers to the extent to which the noun is associated with a single common verb associate [Barch et al., 2000]. Constraint level was based on normative pilot data from testing in an independent sample (verb responses were obtained for each noun from 62 to 85 adults as part of a larger set of verb generation stimuli; no creativity cue manipulation was used in this pilot testing; see [Prabhakaran et al., 2013]). For example, the noun prompt, "Pie," was relatively high-constraint because more than 75% of pilot participants generated the same verb response, "Eat," whereas the noun prompt, "Dirt," was relatively low constraint because no single verb response accounted for as much as 25% of responses. Cued and Uncued words also did not differ from each other on number of letters, $t(70) = 1.18$, $P = .244$. Item order and condition assignment of words were held constant across subjects to eliminate these factors as between-subjects variables because of our strong interest in individual differences in state creativity augmentation. Given our ability to control for word properties, especially constraint, the introduction of a potential between-subjects confound was judged to represent an unnecessary cost. Supporting this design, we found that reversing condition assignment and cue color of the word list in two additional, modestly powered behaviorally tested university student groups (Cue color green group: $N = 32$, 15 male, mean age $= 20.1 \pm \text{SD} = 2.65$ years; Cue color purple group: $N = 34$, 18 male, mean age $= 20.4 \pm \text{SD} = 3.02$ years) had no effect on Overall, Cued, Uncued, or Δ Semantic Distance (all $P \geq 0.9$).

For each noun, participants were given 8 seconds to indicate their verb response by speaking aloud, with voice responses recorded by the customized head coil-mounted microphone. We derived RT as the latency until the start of the spoken response (the verb).

Calculation of Semantic Distance via Latent Semantic Analysis

Participants' verb responses were transcribed from the digital voice recordings. A quantified measure of the semantic distance between each verb and its noun prompt was calculated via LSA [Dumais, 2004; Landauer et al., 1998], a highly reliable measure with low measurement error and good construct validity [Forster and Dunbar, 2009; Green et al., 2010, 2012b; Landauer et al., 1998; Prabhakaran et al., 2013; Wolfe and Goldman, 2003]. LSA is a method for quantifying the similarity between words based on statistical analyses of a large corpus of text (see lsa.colorado.edu for additional details). We have previously used LSA to obtain a quantifiable measure of creativity in verb-generation and analogical reasoning, delineating a continuum of semantic distance between within-domain (less creative) and cross-domain (more creative) analogical reasoning [Green et al., 2006, 2008, 2010, 2012a, 2012b; Prabhakaran et al., 2013].

We used the topic space of "general reading up to first year college (300 factors)" and term-to-term comparison type. Technically, this measure of semantic similarity corresponds to the cosine of the angle between vectors corresponding (in our usage) to a noun and a verb within a given semantic space, which is derived through analyses of all of the contexts in which the word tends to be present or absent in that topic space [Landauer et al., 1998]. To provide a measure of semantic distance (i.e., the inverse of semantic similarity), LSA-derived semantic similarity values were subtracted from 1 (i.e., semantic distance = 1—semantic similarity from LSA). Thus, the higher the semantic distance value between two words, the less proximate their meanings in semantic space. Note that semantic distance is not a measure of the unusualness of the verb, but rather of the unusualness of the verb in the context of the given noun; the noun is the same for all participants, but the verbs can vary. LSA values provide a highly reliable measure of noun–verb semantic distance, one with low measurement error and good construct validity [Forster and Dunbar, 2009; Green et al., 2010, 2012b; Landauer et al., 1998; Prabhakaran et al., 2013; Wolfe and Goldman, 2003]. Verb responses were excluded from the analysis if they were not in the LSA database (1% of responses), or not recorded by the voice-recording system (0.7% of responses). No more than five responses were excluded for any individual participant based on these exclusion criteria. Transcribed verb responses were not available from one participant.

The validity of LSA as a measure of creativity has been demonstrated both conceptually and empirically. At the conceptual level, LSA provides an index of the difference between the context usage meanings of words. Thus, LSA-derived semantic distance measures semantic divergence [Bossomaier et al., 2009; Landauer et al., 1998], which is a core component of creativity [Mayer, 1999]. Bossomaier et al. [2009] detail the conceptual and practical utility of corpus analysis tools such as LSA for the measurement of creativity, and empirical studies have demonstrated the validity of LSA as a creativity measure. Forster and Dunbar [2009] successfully validated LSA-derived semantic distance as a method for scoring the classical uses of objects creativity measure, and argue that LSA actually provides a better model of underlying semantic originality than traditional human-rated methods. Our own prior work has also demonstrated that LSA-derived semantic distance closely matches creativity ratings assigned by human raters for creative analogy stimuli [Green et al., 2012b].

Likewise, considerable research has demonstrated the reliability of the LSA measure for evaluating semantic distance in complex human language usage. As reviewed by Wolfe and Goldman [2003], there is substantial evidence to support the notion that the reliability of LSA is as good as human raters when asked to perform the same judgments. These authors consider studies that have used LSA for assessing a broad range of human-generated responses on complex cognitive tasks, including rating the quality of essays and summaries [Foltz et al., 2000; Kintsch et al., 2000], differentiating among texts on the basis of internal coherence [Foltz et al., 1998], measuring a readers' conceptual understanding of a topic [Wolfe et al., 1998], and reasoning about conflicting accounts of historical events [Wolfe and Goldman, 2003].

Trait Creativity and Intelligence Measures

Outside of the scanner, participants performed behavioral tasks to measure trait creativity and intelligence. Trait creativity measures were Verbal and Figural items from the Torrance Test of Creative Thinking [Goff and Torrance, 2002], The Creative Achievement Questionnaire [Carson et al., 2005], and a test of creative story-writing. Trait intelligence measures were abbreviated versions of the Wechsler Adult Intelligence Scale [Wechsler, 2008], including verbal and performance IQ measures, and Raven's Advanced Progressive Matrices [Raven, 1965]. Administration and scoring of these tasks was as described in [Prabhakaran et al., 2013]. Data were available for a minimum of 49 participants for each task.

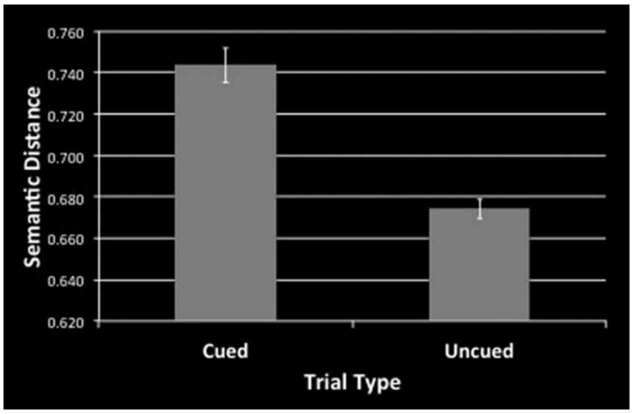

Figure 1.

Behavioral performance on verb generation task by trial type (Cued, Uncued) measured by LSA-derived semantic distance. Participants generated verbs that were more semantically distant from noun prompts on Cued trials ($P < 0.001$). Error bars represent one standard error of the mean.

RESULTS

Behavioral

Participants generated verbs that were more semantically distant from noun prompts when they were cued to think creatively (i.e., Cued trials; LSA semantic distance value = 0.74 ± SD = 0.06) than when they were not (i.e., Uncued trials; LSA semantic distance value = 0.67 ± SD = 0.03), $t\ (53) = 7.56$, $P < 0.001$. Thus the effect of the cue represents an increase of more than two full standard deviations above Uncued performance (Fig. 1). Response times were also longer on Cued trials (4529 ± SD = 1,021 ms) than Uncued trials (3521 ± SD = 649 ms), $t\ (54) = 9.42$, $P < 0.001$. We have previously reported the results of trait creativity and intelligence measures administered to a large group of behaviorally tested participants [Prabhakaran et al., 2013] of which the current study's fMRI sample was a subset. Here, we focus on the relationship of these behavioral measures to the brain imaging data collected in this subset. No sex differences were observed for age ($P = 0.461$), I.Q. ($P = 0.871$), or any measure of trait intelligence or creativity (all $P > 0.09$).

TABLE I. Descriptive statistics for behavioral measures

	Average	Std. deviation	Range	*N*
Δ Semantic Distance	0.07	0.07	−0.05 to 0.24	54
Cued semantic distance	0.74	0.06	0.62 to 0.89	54
Uncued semantic distance	0.67	0.03	0.57 to 0.76	54
log CAQ total	1.24	0.45	0 to 2.01	49
Torrance (verbal)	2.11	7.07	−12.25 to 20.42	48
Torrance (figural)	7.63	6.51	−13.89 to 17.78	51
Story-writing composite	0.61	4.27	−8.62 to 9.30	49
Raven's accuracy	0.74	0.19	0.25 to 1.00	51
WAIS total DQ	128.04	10.23	107.5 to 143.5	49
WAIS verbal DQ	127.03	9.90	105.5 to 143.0	49
WAIS performance DQ	124.21	11.53	91.59 to 144.87	49

Scores for story-writing, and for Torrance verbal and figural measures are expressed as sums of *z*-scores.

Descriptive statistics and first order correlations are provided for all behavioral measures in Table I and Supporting Information Table I.

fMRI

To determine the effect of the creativity cue on brain activity, independent of reaction time, we performed a whole-brain contrast of Cued > Uncued verb-generation, representing cue-related changes, including response time as a regressor of no interest in the design matrix. This contrast revealed activity in frontopolar cortex as well as anterior cingulate cortex (ACC), angular gyrus, posterior cingulate gyrus, bilateral inferior frontal gyrus (IFG), and left-lateralized dorsolateral prefrontal cortex (Fig. 2; Table II). The emergence of frontopolar activity after inclusion of response time as a regressor of no interest in the design matrix is consistent with previous evidence that specific task demands (in this case state creativity augmentation), rather than time-on-task or difficulty *per se*, account for frontopolar recruitment [Christoff et al., 2001; Geake and Hansen, 2005]. The opposite contrast (Uncued > Cued) identified relatively few clusters of activity, with above-threshold peaks in bilateral precentral gyrus and putamen. We predicted that left medial frontopolar cortex would contribute to augmenting creative state. We have identified activity associated with creative analogical reasoning in this region in two prior studies, and found that this activity increases as analogies become more creative [Green et al., 2010, 2012b]. Consistent with our prediction, the global maximum of activation for the Cued > Uncued contrast (Montreal Neurological Institute (MNI) co-ordinates: $x = -4$, $y = 46$, $z = 28$; survived whole-brain voxel-wise correction at $P < 0.0001$) was in a large cluster of activity in dorsal medial prefrontal cortex, including frontopolar cortex, which overlapped the functional peaks identified in our two prior studies of creative analogical reasoning.

The frontopolar peak identified in the Cued > Uncued contrast remained significant when this contrast was re-run with individual differences in absolute semantic distance modeled as a covariate of no interest in the design matrix. Thus, although frontopolar activity was related to individual differences in semantic distance increases, as described below, performance effects (measured by absolute semantic distance) did not account for the Cue-related state effects observed in frontopolar cortex. This analysis was performed to further distinguish state effects from trait effects; trait effects are more likely to be associated with individual differences in absolute semantic distance rather than individual differences in dynamic augmentation of semantic distance.

To further elucidate the within-subject changes associated with augmented creative state, we conducted a within-subjects contrast of more versus less creative responses. Median splits were performed for each participant's responses in each run of the verb-generation task based on the LSA-derived semantic distances for their verb responses. First-level design matrices were set up for each run to contrast the above-median half of responses with the below-median half. Individual subjects data were then combined at the group level to generate the contrast

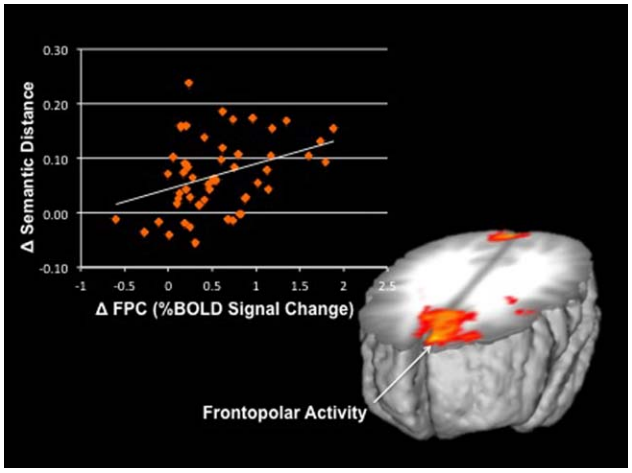

Figure 2.

Brain image: Results of the whole-brain Cued > Uncued contrast, thresholded at $P < 0.0001$. This axial view ($z = 28$) displays activity in frontopolar cortex. *Scatter plot*: Activity for the Cued > Uncued contrast extracted from the frontopolar ROI and plotted against Δ Semantic Distance for verb-generation responses in Cued versus Uncued trials. Cue-related increases in frontopolar cortex predicted increases in semantic distance of verb-generation. These data indicate that individuals who were more able to increase frontopolar activity on cue were more able to augment state creativity. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

TABLE II. Whole-brain Cued > Uncued contrast

			MNI co-ordinates			
Anatomical region	BA	z	x	y	z	Voxels
Left medial frontal gyrus (frontopolar)	9/10	6.62	−4	46	28	3308
Right cerebellar uvula	NA	6.57	30	−82	−32	5697
Anterior cingulate gyrus	32	6.46	−2	36	22	236
Right inferior frontal gyrus	47	6.37	34	22	−12	489
Right thalamus	NA	6.06	2	−12	10	188
Right occipital cuneus	18	5.79	12	−82	16	379
Left posterior cingulate	30	5.5	−22	−68	4	43
Right caudate body	NA	5.44	16	−10	22	85
Left inferior frontal gyrus	9	5.39	−54	22	24	199
Left middle frontal gyrus	6	5.27	−40	6	46	43
Left middle temporal gyrus	21	5.27	−58	−50	−4	22
Left inferior frontal gyrus	45	5.24	−60	20	0	189
Left caudate body	NA	5.21	−16	−2	22	79
Left middle frontal gyrus	10	5.2	−36	58	4	30
Right lingual gyrus	19	5.18	18	−62	−2	43
Left occipital cuneus	18	5.07	−16	−92	22	38
Right parahippocampal gyrus	19	4.92	36	−46	−4	20
Left claustrum	19	4.62	−30	18	−8	85

of more creative versus less creative responses. The results of this contrast (exploratory whole-brain threshold $P < 0.0001_{\text{uncorrected}}$) were similar to those of the Cued > Uncued contrast, which was also a within-subjects contrast. This is consistent with the finding that Cued responses were more creative than Uncued responses. The more creative versus less creative contrast yielded activity highly overlapping with the activity found in the Cued versus Uncued contrast, including in frontopolar cortex, anterior cingulate, bilateral IFG, posterior cingulate, parahippocampal gyrus, bilateral occipital cuneus, and cerebellum. This analysis provides additional confidence that within-subjects state creativity effects are associated with activity in the regions we have identified.

Region of Interest Analysis

To test the prediction that augmentation of frontopolar activity supports state augmentation of creative performance, we defined a region of interest (ROI) within left-sided frontopolar cortex as a 10 mm radius sphere, centered on the peak voxel of the frontopolar cluster identified in the Cued > Uncued contrast. This frontopolar ROI was selected based on several converging justifications. At a theoretical level, we predicted that augmenting creativity would place greater demand on neural circuitry in frontopolar cortex, which supports creative integration across semantic distance. This prediction was based on a recent meta-analysis of the creativity brain-imaging literature [Gonen-Yaacovi et al., 2013], as well as an influential model of frontopolar function, based on cytoarchitecture and neuroimaging, which indicates frontopolar cortex an integrator of information during abstract thinking [Ramnani and Owen, 2004]. Semantic distance was the key measure of creativity in this study and the only two extant neuroimaging studies that have investigated semantic distance have identified frontopolar cortex activity as a key indicator of individual differences [Green et al., 2010, 2012b]. Thus, our strongest a priori prediction for this study was that frontopolar cortex proximate to the functional peaks identified in these two studies (which were quite proximate to each other) would contribute to individual differences in state augmentation of creativity as measured by increased semantic distance. The cluster selected as the ROI overlapped both of the frontopolar functional peaks identified in these two prior investigations of semantic distance. The selected ROI was centered on the *global maximum* of activation for the Cued > Uncued group contrast, the primary analysis of cued creative state augmentation. The activity observed in the present study is also overlapping with medial prefrontal activity identified during creative improvisation in rap artists and jazz musicians [Limb and Braun, 2008; Liu et al., 2012], indicating that when artists deliberately engage a creative state for novel generation of words and music, this frontopolar region is strongly engaged. It is important to note that creativity is a broad and multifaceted construct. Although the present study draws hypotheses from the prior literature most relevant to our paradigm and research questions, it does not reflect all forms of creativity or all prior brain-based creativity findings.

We regressed cue-related change in semantic distance for each participant (referred to as Δ Semantic Distance; the result of subtracting each participant's average LSA-derived semantic distance values for Uncued trials from their average semantic distance values for Cued trials) on activity extracted from the frontopolar ROI for the Cued > Uncued contrast (referred to as Δ frontopolar cortex (FPC); measured as percent signal change). Consistent with our prediction, Δ FPC was significantly associated with Δ Semantic Distance ($r = 0.40$, $P = 0.003$; Fig. 2). Recall that the individual differences investigated in this analysis are individual differences in amount of *within-subject* state augmentation of creativity between Cued and Uncued performance (i.e., Δ Semantic Distance is a within-subject difference score). This difference thus reflects dynamic, transiently cued changes in level of creativity across time within an individual (i.e., state).

To determine whether the ability to augment state creativity was specifically due to greater capacity to augment recruitment of frontopolar cortex, rather than trait cognitive abilities, we repeated the regression, including our trait ability measures of creativity and intelligence as regressors. Consistent with our main prediction, Δ FPC was a significant predictor of Δ Semantic Distance even after accounting for all trait creativity measures [$\beta = 0.48$, $t(45) = 3.72$, $P = 0.001$] and all trait intelligence measures [$\beta = 0.42$, $t(47) = 3.03$, $P = 0.004$]. An exploratory sequence of multiple regressions was conducted with each trait ability measure individually, and all possible sets of trait ability measures, regressed alongside Δ FPC. Δ FPC was significantly predictive of Δ Semantic Distance in each of these models (all $P < 0.01_{\text{uncorrected}}$).

To test the anatomical specificity of the cue-related frontopolar effect on Δ Semantic Distance, we extracted activity for the Cued > Uncued contrast from an unthresholded Harvard–Oxford Cortical Atlas region containing all voxels in frontopolar cortex. This larger frontopolar ROI showed a nonsignificant, trend-level association with Δ Semantic Distance [$\beta = 0.221$, $t(53) = 1.63$, $P = 0.109$]. Including the activity in the larger frontopolar ROI in the regression with our 10 mm frontopolar ROI, the 10 mm ROI remained significantly predictive of Δ Semantic Distance [$\beta = 0.49$, $t(53) = 2.70$, $P = 0.009$], while the larger ROI was no longer significantly predictive [$\beta = -0.13$, $t(53) = -0.70$, $P = 0.489$]. These findings indicate a high degree of anatomical specificity for state creativity-related activity in dorsal medial frontopolar cortex, consistent with evidence that this region of frontopolar cortex reliably demonstrates association with semantic distance processing [Green et al., 2010, 2012b] and extemporaneous musical improvisation [Limb and Braun, 2008; Liu et al., 2012].

Post hoc ROI analyses were performed to test whether changes in frontopolar activity were more strongly associated with individual differences in augmented state creativity than changes in other regions identified in the Cued > Uncued contrast. Activity for the Cued > Uncued contrast was extracted from 10 mm radius spheres centered on each functional peak (Table II). Significant associations with Δ Semantic Distance were found at $\alpha = 0.05_{\text{uncorrected}}$ for anterior cingulate ($r = 0.28$), cerebellar uvula ($r = 0.29$), right parahippocampal gyrus ($r = 0.30$), and left claustrum ($r = 0.35$), indicating that these regions contributed to individual differences in state creativity augmentation. However, these associations were weaker than the association between Δ FPC and Δ Semantic Distance, and Δ FPC remained significantly predictive of Δ Semantic Distance even after regressors for these additional regions were included alongside Δ FPC [$\beta = 0.621$, $t(53) = 2.27$, $P = 0.028$]. None of the additional regions remained significantly predictive of Δ Semantic Distance in this model (i.e., after accounting for the effect of Δ FPC).

To determine the extent to which the effect of the creativity cue on frontopolar cortex was due to increasing frontopolar activity in the Cued condition and/or decreasing frontopolar activity in the Uncued condition, we regressed Δ FPC on frontopolar ROI activity extracted for Cued > Rest and Uncued > Rest contrasts. Activity for both contrasts showed significant effects on Δ FPC (both $P < 0.001$), with Cued > Rest showing a positive association ($\beta = 1.60$), and Uncued > Rest showing a negative association ($\beta = -1.84$). Thus, it appears that Δ FPC is due to both lower activity for Uncued generation and higher activity for Cued generation. Given the relationship between Δ FPC and Δ Semantic Distance, this may indicate not only that greater ability to recruit frontopolar cortex on cue supports greater increases in state creativity, but also that individuals who have greater ability to augment state creativity do not have to tax frontopolar cortex as heavily to generate Uncued verbs. To test this hypothesis, we regressed Δ Semantic Distance on frontopolar activity for Cued > Rest and Uncued > Rest. This analysis revealed that both regressors were significantly predictive of Δ Semantic Distance (both $P < 0.01$), with Cued > Rest again showing a positive association ($\beta = 0.80$), and Uncued > Rest again showing a negative association ($\beta = -0.71$).

Analysis of Sex and IQ Range

Including sex as a nominal covariate in our regression model along with the trait measure covariates did not substantially alter the effect of Δ FPC on Δ Semantic Distance, $\beta = 0.48$, $t(45) = 3.42$, $P = 0.002$. Sex was not significantly associated with Δ Semantic Distance in this model [$\beta = 0.02$; $P = 0.823$]. Additionally, separate regression models for males [$\beta = 0.60$, $t(23) = 2.81$, $P = 0.013$] and females [$\beta = 0.51$, $t(21) = 2.18$, $P = 0.047$] revealed that both sexes showed an effect of Δ FPC on Δ Semantic Distance.

We additionally performed a set of analyses to determine the effect of high IQs and IQ range on our data. These analyses converge to demonstrate that the high IQs and somewhat truncated range of our full sample are unlikely to present significant issues for the interpretability of our findings. First, we performed a median split of our sample by total IQ score. We then examined regression models for both the upper half and lower half of our IQ

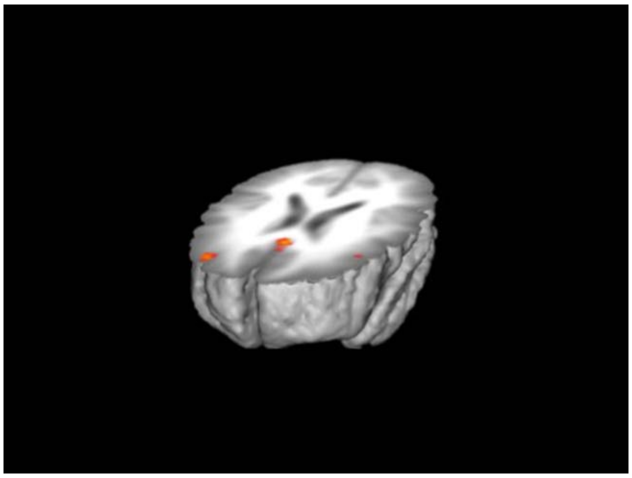

Figure 3.

Results of the whole-brain PPI functional connectivity analysis, thresholded at $P < 0.0001$, showing regions that exhibit increased connectivity with the frontopolar seed region on Cued versus Uncued trials ($z = 24$). A significant cue-related increase in connectivity to the frontopolar ROI was found in anterior cingulate gyrus, as well as a region within right frontopolar cortex. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

range, including all trait creativity and intelligence covariates in the model. These analyses showed that the effect of primary interest (i.e., the effect of Δ FPC on Δ Semantic Distance) was significant in both the lower [$\beta = 0.70$, $t(23) = 4.05$, $P = 0.001$] and upper [$\beta = 0.60$, $t(21) = 2.19$, $P = 0.047$] halves of our IQ median split. These analyses show that the effect of Δ FPC on Δ Semantic Distance is at least as strong, and appears to be stronger, in the lower half of our IQ range, indicating our effect is not driven by extreme high IQs in our sample that are unrepresentative of the general population. Further, we performed an analysis in which subjects in the two middle quartiles of our IQ range were excluded. This yielded a standard deviation of 13.9 (12.8 verbal, 15.3 performance), which is substantially greater than the standard deviation of 10.23 (9.9 verbal, 11.53 performance) for the full sample. Running the full regression model with the middle IQ quartiles excluded again yielded a significant effect of Δ FPC on Δ Semantic Distance [$\beta = 0.49$, $t(21) = 2.51$ $P = 0.026$].

Functional Connectivity Analysis

Functional connectivity analyses were performed using the frontopolar ROI as a seed region. To identify whether the creativity cue led to increased connectivity with frontopolar cortex, we performed a psycho-physical interaction (PPI) analysis in FSL. A psychological "A − B" regressor represented the contrast of Cued > Uncued trials, a physiological regressor represented the extracted averaged timecourse within the 10 mm-radius ROI, and a PPI regressor represented the interaction of the first two regressors. In addition, a psychological "A + B" regressor was included to account for variance shared by Cued and Uncued trials. This analysis (Fig. 3) revealed that the creativity cue led to increased connectivity between frontopolar cortex and ACC (BA 24; Talairach co-ordinates of peak voxel: $x = 0$, $y = 32$, $z = 26$; z-value for peak voxel = 3.90), as well as a region of right frontopolar cortex (BA 10; Talairach co-ordinates of peak voxel: $x = 32$, $y = 50$, $z = 24$; z-value for peak voxel = 3.89). By comparison, a basic functional connectivity analysis, using the extracted timecourse for the frontopolar ROI to predict activity across the whole brain on all trials (not including the PPI regressor or the A + B regressor), revealed a more widely distributed network of regions, largely overlapping those identified in the Cued > Uncued contrast, including in bilateral inferior prefrontal cortex.

DISCUSSION

This study investigated a valuable and commonly experienced but poorly understood phenomenon: augmented state creativity. The findings indicate increased recruitment of frontopolar cortex as a mechanism for deliberate and acute augmentation of creative state, and demonstrate that augmented creative state can be dynamically engaged and disengaged across time. The large effect size elicited by our simple and direct creativity cue extends previous evidence that creativity cues can augment creative state [Chen et al., 2005; Gilchrist and Taft, 1972; Green et al., 2012a; Harrington, 1975; Howard-Jones et al., 2005; Niu and Sternberg, 2001; O'Hara and Sternberg, 2001; Seger et al., 2000; Shalley, 1991]. However, with a few exceptions [Benedek et al., 2013], most neuroimaging studies of creativity rely on relatively broad performance metrics, such as reaction time or the number of responses, rather than directly capturing creative production [Fink et al., 2007]. Prior brain-imaging studies of creative generation have reported frontopolar activity, among other activity [Green et al., 2012b; Howard-Jones et al., 2005; Seger et al., 2000]. Green et al. [2012b] found that activity in left frontopolar cortex parametrically varied with increasing semantic distance during covert generation of analogical solutions. However, these studies did not obtain actual creative responses during neuroimaging [Green et al., 2012b; Howard-Jones et al., 2005; Seger et al., 2000], so it has not been possible to directly relate changes in activity to changes in a performance measure of creative production. In addition, the studies by Seger et al. [2000] and Howard-Jones et al. [2005] were limited by small fMRI samples of 7 and 8 participants, respectively. Other studies have investigated passive evaluation of creative stimuli, and have also implicated left frontopolar cortex [Green et al., 2010; Rutter et al., 2012].

The present study points to a fruitful avenue for the growing literature on frontopolar cortical function (for reviews, see [Gilbert et al., 2006; Gonen-Yaacovi et al., 2013; Ramnani and Owen, 2004]). Previous studies have implicated frontopolar activity in creative responding [Green et al., 2012b; Howard-Jones et al., 2005; Seger et al., 2000], and in analogical mapping, a process that often requires integrating ostensibly dissimilar semantic representations [Green et al., 2008, 2010, 2012b; Holyoak and Thagard, 1995]. We have previously found that frontopolar cortex is preferentially recruited for the relational integration component of analogical reasoning as compared to other component processes that contribute to analogy [Green et al., 2006], and that increasing frontopolar recruitment reflects increasing semantic distance in evaluating complete analogies [Green et al., 2010] and solving incomplete analogies [Green et al., 2012b]. Critically, the present findings demonstrate that frontopolar cortex activity can be increased as an active mechanism for the conscious effort to augment creative thinking, rather than simply reflecting receptive processing of stimuli that present varying levels of semantic distance. This mechanism in frontopolar cortex may be analogous to augmented activation in sensory cortices in the conscious effort to heighten attention and improve processing of information in a specified modality [Hopfinger et al., 2000; Porro et al., 2002; Ruff and Driver, 2006].

Interpretation of the present findings is informed by the cognitive-anatomical architecture of prefrontal function proposed by Ramnani and Owen [2004]. Within this architecture, frontopolar cortex is specialized for integrating information, including pieces of information with disparate cortical representations, which is a crucial operation for semantically distant verb-generation in response to prompt nouns. Increasing frontopolar cortical activity in the present investigation may reflect increasing computational demand on neuronal circuitry in frontopolar cortex as semantic distance increases, as we have previously posited [Green et al., 2010, 2012b]. Our data are also broadly consistent with previous empirical neurocognitive models placing anterior prefrontal cortex at the peak of a caudal-to-rostral progression or hierarchy in complex cognition [Badre and Wagner, 2004; Christoff and Gabrieli, 2000], and with evidence that, among patients with frontotemporal dementia, creative ability depends on the integrity of frontopolar cortex [de Souza et al., 2010].

The relatively medial locus of peak frontopolar activity in this present study may indicate preferential recruitment of medial frontopolar cortex during the conscious effort to think creatively. This may account for the involvement of medial frontopolar regions during extemporaneous musical improvisation [Limb and Braun, 2008; Liu et al., 2012], and is consistent with prior evidence that medial frontopolar cortex is involved in making, and preparing to make, decisions among abstract alternatives (in this case deciding among candidate verbs abstractly related to the noun prompts) [Hampton and O'Doherty, 2007; Haynes et al., 2007; Soon et al., 2013]. The seminal work of Beeman, Kounios and colleagues (e.g., [Jung-Beeman et al., 2004]) has associated left-sided anterior medial prefrontal activity, proximate to the frontopolar activity we identified, with insight in creative problem solving. Our study did not find the right-sided superior temporal activity observed by those authors, which may reflect the distinction between active, conscious augmentation of creative state and the somewhat less conscious mechanism by which insights arise, or other differences in task characteristics.

A co-ordinate-based meta-analysis of the neuroimaging creativity literature, using activation likelihood estimation, identified medial frontopolar cortex, where frontopolar activity was observed in the present study, as a point of strong convergence among studies of unusualness generation [Gonen-Yaacovi et al., 2013]. Dividing creativity tasks into categories of unusualness generation and integration, the meta-analysis suggested that medial frontopolar cortex supports the formation of connections between semantically distant representations in both unusualness generation (as in the present task), and integration (e.g., in creative analogical reasoning).

In addition to frontopolar cortex, the creativity cue elicited responses in frontal regions including ACC and bilateral IFG. The ACC finding is consistent with a proposed role of ACC in conscious switching and maintenance of mental states, including resolution of conflict between competing states (for review, see [Tang et al., 2012]). Anterior cingulate activity is also a consistent finding in verb-generation [Barch et al., 2000], and generating novel uses of objects [Abdullaev and Posner, 1997], and is reliably related to the executive processes of response conflict and response selection (i.e., choosing which verb to say from among competing alternatives) [Barch et al., 2000]. Increasing ACC activity on creativity cue trials may reflect the consideration of a greater number of possible responses, and is likely to reflect the inhibition of the first response that comes to mind to select a more creative response [Braver et al., 2001].

Activity in bilateral IFG is also likely to reflect increasing selection demand as a component of the deliberate effort to augmented state creativity. IFG is reliably associated with tasks that require choosing among words or objects along some semantic dimension (e.g., color, size, expense, similarity) [Badre et al., 2005]. Across studies, IFG has been preferentially recruited for higher versus lower selection demand conditions, indicating that increasing activity in IFG supports a task-general selection process (i.e., identifying the best alternative amid ambiguity or competition [Badre et al., 2005] and top-down inhibition of prepotent responding [Aron et al., 2014; Hampshire et al., 2010]. The involvement of left IFG also likely reflects increased semantic elaboration [Kapur et al., 1994] as participants sought to elaborate from the prompt nouns and their prepotent associations to find nonobvious semantic associations.

The finding of more posterior cortical involvement in the present study, especially posterior cingulate and cuneus, accords with the parietofrontal integration theory of intelligence [P-FIT; Jung and Haier, 2007], an empirical review-based account of the combined involvement of posterior and anterior regions in complex cognitive function. Notably, recent evidence indicates that the P-FIT model is applicable to creativity [Jung et al., 2010].

The finding of cerebellar involvement is generally consistent with recent models of cerebellum as a co-ordinator of mental operations that instantiate high-level cognition (for review, see [Ito, 2008]), and creativity in particular [Chavez-Eakle et al., 2007]. Parahippocampal recruitment has also been implicated in creative performance [Chavez-Eakle et al., 2007] and verb-generation [Crescentini et al., 2010]. Increased claustrum activity is associated with a heightened state of "in-the-zone" performance in athletes [Ferrell et al., 2006], which may share properties with heightened creative state.

Functional connectivity analyses revealed that, while frontopolar cortex participates in a broad network of functional connectivity during verb-generation, the creativity cue alters this network in a regionally specific way, especially leading to greater connectivity with ACC. This finding further underscores the importance of ACC function for deliberately augmenting creative state. In addition to a general role in conscious switching and maintenance of mental states [Tang et al., 2012], ACC contributes to monitoring and resolving competition among semantic noun–verb connections [Braver et al., 2001]. The integrative function of frontopolar cortex is likely to support the formulation of these connections [Gonen-Yaacovi et al., 2013; Green et al., 2010, 2012b; Ramnani and Owen, 2004], requiring ongoing communication between frontopolar cortex and ACC. We hypothesize that the need for this communication increases under the Cued condition because bias toward prepotent verb associates is inhibited, leading to an expanded set of possible connections to be monitored [Braver et al., 2001].

The observed cue-related increase in functional connectivity with right frontopolar cortex is also likely to support inhibition of prepotent, uncreative responses based on similar involvement of this region in previous creativity research [Gonen-Yaacovi et al., 2013]. The fact that frontopolar cortex increases activity during the creativity cue, but shows limited, focal increases in connectivity, suggests that augmenting creativity depends more on augmenting integrative function within frontopolar cortex than on increasing the already-high levels of communication between frontopolar cortex and other task-relevant regions (e.g., language areas in IFG).

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