The Brain Network Underpinning Novel Melody Creation

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Abstract

Musical improvisation offers an excellent experimental paradigm for the study of real-time human creativity. It involves moment-to-moment decision-making, monitoring of one's performance, and utilizing external feedback to spontaneously create new melodies or variations on a melody. Recent neuroimaging studies have begun to study the brain activity during musical improvisation, aiming to unlock the mystery of human creativity. What brain resources come together and how these are utilized during musical improvisation are not well understood. To help answer these questions, we recorded electroencephalography (EEG) signals from 19 experienced musicians while they played or imagined short isochronous learned melodies and improvised on those learned melodies. These four conditions (Play-Prelearned, Play-Improvised, Imagine-Prelearned, Imagine-Improvised) were randomly interspersed in a total of 300 trials per participant. From the sensor-level EEG, we found that there were power differences in the alpha (8–12 Hz) and beta (13–30 Hz) bands in separate clusters of frontal, parietal, temporal, and occipital electrodes. Using EEG source localization and dipole modeling methods for task-related signals, we identified the locations and network activities of five sources: the left superior frontal gyrus (L SFG), supplementary motor area (SMA), left inferior parietal lobule (L IPL), right dorsolateral prefrontal cortex, and right superior temporal gyrus. During improvisation, the network activity between L SFG, SMA, and L IPL was significantly less than during the prelearned conditions. Our results support the general idea that attenuated cognitive control facilitates the production of creative output.

Keywords: alpha; beta; brain networks; EEG; Granger causality; human creativity; musical improvisation

Introduction

HIGHLY CREATIVE PRODUCTS represent the pinnacle of human achievement, including scientific discoveries, musical symphonies, and inventions. The study of creativity has a long history and includes the analysis of creative people (Gardner, 2011), products (Amabile, 1996), and the processes used during creation (Simonton, 2010). Creative thought has only recently been investigated using neuroscientific methods, and the results have been conflicting due to the many diverse task paradigms used (Dietrich and Kanso, 2010). Tasks include various divergent thinking paradigms (Fink et al., 2009a) and studies in which the moment of insight during problem solving is investigated (Kounios et al., 2006). Dietrich and Kanso (2010) specifically argued that "only when the amorphous concept of creativity is subdivided into different types" would the field advance. One

such type of experimental creative paradigm is the study of products created in *real time where revision is not possible*. In this study, we studied musical improvisation as an example of this type of creative task. Musical improvisation has been used in several functional magnetic resonance imaging (fMRI) studies involving the contrast between brain responses recorded while playing fixed melodies (less creative) or improvised melodies (more creative) (Bengtsson et al., 2007; Berkowitz and Ansari, 2008; de Manzano et al., 2012a, 2012b; Limb and Braun, 2008). In this study, we conduct a controlled electroencephalography (EEG) study to advance our understanding of brain network oscillations and activity during musical improvisation.

One consistent finding in the EEG creativity literature is a change in alpha power (Fink et al., 2006, 2009a; Razumnikova et al., 2009). In one study of a real-time creative behavior, professional dancers were asked to imagine a very

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structured dance (less creative) and an improvisational dance (more creative) (Fink et al., 2009a). The more creative condition resulted in stronger alpha band synchronization in frontal and parietal regions, especially in the right hemisphere. These results align with some studies of creative problem solving not performed under real-time constraints where increased alpha synchronization has been observed in the creative condition compared to controls (Fink et al., 2006, 2009a; Lustenberger et al., 2015). However, other studies using that same paradigm have found a significant decrease (Razumnikova et al., 2009).

Simultaneous EEG and fMRI recordings show that increased alpha (~10 Hz) wave power is correlated with a decrease in the blood oxygenation level-dependent (BOLD) signal and may therefore represent deactivation (Goldman et al., 2002). It has been suggested that alpha waves represent a top–down inhibitory process attenuating brain regions not necessary for the current task (Klimesch, 2012; Klimesch et al., 2007). In a visual perception task, increased posterior alpha power was interpreted as attenuating the dorsal stream when the ventral stream was engaged in face recognition (Jokisch and Jensen, 2007). Similarly, alpha power increased in posterior and bilateral central areas with memory load in a working memory task, presumably because visual processing was inhibited (Jensen et al., 2002). Concerning creative tasks, Fink and Benedek (2014) argue that alpha band power is related to creative ideation and may reflect internally oriented attention in which external bottom–up stimulation is attenuated (Fink and Benedek, 2014), but it is unclear whether this explanation also applies to tasks performed under real-time constraints. In this study, we analyzed alpha power and cohesion during a musical task where participants played either prelearned or improvised melodies. Should the account of increased alpha power for a creative task also apply to real-time creative tasks, we would expect increased alpha power in the improvised condition (Fink et al., 2009a). However, should alpha power be more related to increased working memory demands (Jensen et al., 2002; Jokisch and Jensen, 2007), we would expect to see higher alpha power in the prelearned condition in which participants were asked to play or imagine one of four memorized melodies.

We used EEG source localization and dipole modeling methods for task-related signals to identify sources and network activities. One previous study used EEG to study network properties during performance of composed and improvised music (Wan et al., 2014). However, their goal was to investigate this contrast in an actual performance setting and included comparing both intrabrain and cross-brain networks in performers and listeners. Although arguably more ecologically valid, a performance setting introduces a number of possible confounds. They only had one (exp. 1) or three (exp. 2) musicians from which to construct intrabrain networks, the composed and improvised performances were not matched on tempo and note density, the EEG data were only collected with 10 or less channels, and the prefrontal cortex was not included in data acquisition and analysis. Nonetheless, it is interesting to note that they found an expanded distributed network during improvisation in the musicians.

Previous fMRI studies in which participants played a piano keyboard have identified differences in motor and prefrontal regions in response to the prelearned/improvised con-

trast using various musical tasks, although the results are inconclusive (Bengtsson et al., 2007; Berkowitz and Ansari, 2008, 2010; Limb and Braun, 2008). Berkowitz and Ansari (2008) identified a network involving the dorsal premotor cortex, the rostral cingulate zone, and the inferior frontal gyrus that was involved in both rhythmic and melodic improvisation. In another study, the same team compared activation in musicians and nonmusicians performing the same task and found that the right temporoparietal junction was deactivated during improvisation in the musician group only (Berkowitz and Ansari, 2010). Limb and Braun (2008) identified a different area that was deactivated during improvisation compared to the prelearned condition. They saw extensive deactivation of the dorsolateral prefrontal cortex (dlPFC) and lateral orbital regions accompanied by focal activation of the medial prefrontal cortex. They argued that the deactivation of the dlPFC facilitated creative responses by lessening top–down control. Opposite this view, de Manzano and Ullen (2012b) saw activation of the dlPFC during a more creative task and attributed this to the area actively being engaged in inhibiting habitual responses. In a study designed to resolve this contradiction, participants improvised either using defined pitch sets or expressing specific emotions (Pinho et al., 2015). They found improvisation using a defined pitch set resulted in activation of the dlPFC since subjects had to maintain available note choices in working memory. Opposite they saw deactivation of the dlPFC during the emotional improvisations as subjects presumably relied on implicit learned processes to create improvisations in which top–down control from dlPFC would be disadvantageous. Finally, de Manzano and Ullen (2012a) found that the presupplementary motor area (pre-SMA) is more active in both rhythmic and melodic improvisation compared to playing a given melody. Interestingly, functional connectivity between the pre-SMA and the cerebellum was higher during rhythmic improvisation only, indicating the pre-SMA may be particularly important for timing.

In this study, we were interested in the underlying creative process both for overt motor action and covert imagining. We therefore investigated the prelearned/improvised contrast using both a motor condition in which participants played a piano keyboard and performed a musical imagery task. It is well established that auditory perceptual regions are activated during internally generated covert auditory imagery. This phenomenon has been observed during internal auditory discrimination (Zatorre et al., 1996), auditory imagery of a musical score (Yumoto et al., 2005), and even during passive listening (Kraemer et al., 2005). In a study with advanced pianists, Meister et al. (2004) found a bilateral frontoparietal network was active during play. Much of this same network was also active during imagining of the music, with the exception of the contralateral primary motor cortex and bilateral posterior parietal cortex (Meister et al., 2004).

Based on previous fMRI research, we hypothesized that EEG source localization would identify a network involving frontal control regions and motor planning regions. We furthermore expected that cognitive control regions would show less connectivity to motor regions during played improvisation, thereby facilitating creative production. As improvisation has not previously been investigated using musical imagery, we did not form a prediction for those conditions.

Methods

Participants

Nineteen experienced musicians (16 male, 3 female; mean age = 25.5 years, standard deviation [SD] = 6.7 years) were exclusively recruited for this study. A criterion for participation, piano was either the participant's primary (5 participants) or secondary (14 participants) instrument. All participants demonstrated proficiency on the piano keyboard; however, their primary instruments included piano ($n=5$), guitar ($n=6$), voice ($n=3$), drums ($n=2$), bass guitar ($n=1$), bouzouki ($n=1$), and trumpet ($n=1$). Participants were also required to know how to read music. Experience on the piano typically began in early childhood; self-reported number of years experience on the piano (mean = 10.4 years, SD = 8.6 years) was noted, shown in Table 1. All participants had experience on their primary instrument for at least 2 years (mean = 14.3 years, SD = 6.6 years). Many of the participants were currently enrolled or had previous education in a University System School of Music ($n=8$), but not exclusively; average schooling years for all participants were 15.2 years (SD = 1.4 years). All participants were healthy with no self-reported neurological disorders. Eighteen participants were right handed and one was left handed in accordance with the Edinburgh handedness inventory. All participants gave written informed consent, following all guidelines approved by the Institutional Review Board of Georgia State University.

Experimental conditions

Before EEG recordings, participants were familiarized with the five conditions: Play-Prelearned, Play-Improvised, Imagine-Prelearned, Imagine-Improvised, and Rest. During the prelearned conditions participants were prompted to play or imagine one of four 8-quarter note melodies (CDEFGFED, CEGEFDBD, EECCFFDD, and GFECBCDF), which were memorized and rehearsed before the day of the experiment.

TABLE 1. THE TABLE LISTS THE AGE, THE PRIMARY MUSICAL INSTRUMENT, AND THE YEARS OF PLAYING (EXPERIENCE) OF THE PARTICIPANTS IN THE STUDY

Participant No.	Age (years)	Primary instrument	Years of playing
01	21	Piano	7
02	20	Piano	15
03	21	Piano	7
04	26	Piano	8
05	37	Bass guitar	20
06	25	Piano	2
07	22	Voice	6
08	23	Voice	5
09	28	Guitar	23
10	28	Drums	2
11	23	Drums	4
12	30	Guitar	4
13	24	Guitar	19
14	22	Guitar	14
15	43	Voice	28
16	33	Bouzouki	24
17	19	Guitar	11
18	24	Trumpet	13
19	25	Guitar	3

Participants were tested on competency upon arrival. Each melody was within a six-note range to minimize hand movement on the keyboard and not disrupt the EEG recording. During the Imagine-Prelearned condition, participants were instructed to imagine one of the four prelearned eight-quarter note melodies. These performances of memorized melodies presumably require little to no creativity. Results from these conditions could then be contrasted with the two improvised conditions: Play-Improvised and Imagine-Improvised, during which participants performed or imagined a spontaneously created melody within the same six-note range. During all of the conditions, except Rest, participants synchronized their piano playing and imagining with an auditory metronome playing every 0.7 sec. The improvised melodies therefore differed from the prelearned only with regard to the chosen pitches. For the Rest condition, participants were instructed to do nothing except listen to the metronome.

After the experimenter secured the EEG cap and familiarized the participant with the task, participants began a 10-trial practice run. Recordings from the practice run were used only to ensure that all the electrodes were online; no data from practice runs were used in analysis. The task was displayed on a computer monitor directly in front of the seated participant through a program written in the PsychToolbox extension in MATLAB. All trials began with the trial cue, lasting four metronome beats counting down to the performance phase. At the end of the countdown, the metronome continued and participants completed the cued task. All trials followed the same structure over time and were randomly selected from the five conditions. Each experiment was composed of 15 runs, with 20 randomized trials in each run. Participants were instructed to look at a fixation cross and try not to blink during the eight-count performance phase. They could blink during the four-count trial cue and countdown. Motor movement was limited to finger presses across six notes of the piano keyboard.

Data acquisition and preprocessing

Behavioral data were recorded using a MIDI interface with PsychToolbox in MATLAB. Specific key press and timing information was recorded and analyzed to determine participants' performance accuracy in reproducing the cued melodies and their synchronization with the metronome. Continuous EEG data were recorded using a 64-channel flexible cap and Brain Vision's actiCHamp System. A sampling rate of 1000 Hz and a DC amplifier were used.

Raw data were read in BrainVision Analyzer 2.0 software. EEG data were bandpass filtered of (0.1–70 Hz) and notch filtered to remove 60 Hz AC-line noise. Data from bad electrodes were discarded and replaced, when appropriate, by spatial interpolation of the recordings from the neighboring working electrodes. The preprocessed data from each run were then read in EEGLAB, combined to form a single data set for each participant, and then separated by each experimental condition based on behavioral trial sequences. Standard statistical procedures (Junghofer et al., 2000) were used to identify outlier trials and discard them from the subsequent analysis.

Data analysis

The analysis of the preprocessed EEG included the following main steps: (1) computation of grand average from EEG

trials, (2) EEG source reconstruction based on grand average of EEG trials and distributed dipole modeling, (3) reconstruction of single-trial source waveforms based on the identified sources and discrete dipole modeling, and (4) computation of spectral measures based on single-trial waveforms and the parametric spectral approach (Dhamala et al., 2008a). Details are provided below.

Sensor level power analysis

The EEG trials were collected from all participants, and the grand average waveforms were computed for each task condition. The peak amplitude values for the trials were calculated and tested to find out the electrode locations where the sensor level EEG signals differed significantly (t-tests, $p < 0.05$; with multiple comparison correction) between Play-Prelearned and Play-Improvised, and Imagine-Prelearned and Imagine-Improvised conditions. All the sensor level EEG trials were used to compute wavelet power to investigate when and how the power changes during prelearned and improvised musical conditions.

EEG source reconstruction

The grand average of EEG trials from four musical task conditions, Play-Prelearned, Play-Improvised, Imagine-Prelearned, and Imagine-Improvised, was used in the Brain Electrical Source Analysis Research software version 6.0 (www.besa.de) to reconstruct EEG sources. We used the minimum norm estimates (MNE) approach (Hamalainen and Ilmoniemi, 1994; Wang et al., 1992) with a depth-weighting scheme to find the localized sources generating the scalp potentials. The technique estimates the source activity without a priori assumptions about the sources' location and activity. The inverse problem is addressed by generating dipole solutions of the sensor data with the smallest amount of power for all dipole sources at each time point. Source activities are computed from the sensor data with the help of an inverse regularized estimation of the noise covariance matrix of the sensor data. Tikhonov regularization constant was set to 0.1 and applied to invert calculation. Spatial depth-weighting method was also used to compensate for the tendency of minimum-norm solution to favor superficial sources. Depth weighting for the mean norm of the recursive leadfields was applied using subspace correlation after single source scan ρ^2. The data with 15% lowest global field power are selected for noise estimation. The source activity of each

regional location is estimated as the root mean square of the sources' components. The source activity of evenly distributed regional sources is computed at 10% and 30% below the standard brain surface. The locations of the sources can be constrained to the cortical surface and their orientations can be restricted to be perpendicular to the local cortical surface (Dale and Sereno, 1993). In this study, we used the grand average sensor EEG data from all task conditions, subjects, and notes to find out the EEG sources.

We then used these EEG sources as nodes for subsequent spectral analysis of the network. For this, we used single-trial EEG data and obtained single-trial source waveforms by fitting dipoles at the peak activation locations of the localized sources with the dipole orientations given in Table 2. The source signals obtained from the single-trial EEG data were used in the spectral analysis of the network activity.

In this study, we calculated spectral measures: coherence and Granger causality (GC). Coherence is a measure of statistical interdependence between two oscillatory processes and is derived from the normalized cross-spectral density function. Coherence between neural processes reflects frequency-specific interareal synchrony between oscillatory neuronal processes. Spectral GC measures the directional causal influence from one oscillatory process to another (Ding et al., 2006; Geweke, 1982). These measures can be computed both by parametric and nonparametric methods (Dhamala et al., 2008a, 2008b). In this study, we applied the parametric method to single-trial EEG-source signals and computed network activity among the EEG sources of the observed scalp-recorded activity. The difficulty of finding an optimal model order in the parametric approach was circumvented by comparing power spectra from the nonparametric and parametric approaches at different model orders and choosing the model order yielding the lowest power difference (Adhikari et al., 2014; Dhamala et al., 2008a). We evaluated the patterns of causality spectra by using pairwise GC. We used the parametric spectral methods for all of these calculations. The thresholds for statistical significance were computed from surrogate data by using permutation tests and a gamma function fit (Blair and Karniski, 1993; Brovelli et al., 2004) under a null hypothesis of no interdependence at the significance level $p < 10^{-6}$.

Brain behavior relation

In the improvisation conditions, participants were asked to make up isochronous melodies using the same six pitches

TABLE 2. THE TABLE LISTS THE NAMES OF THE ELECTROENCEPHALOGRAPHY SOURCES WITH BRODMANN AREA, THEIR ANATOMICAL LOCATIONS IN TALAIRACH (MNI) COORDINATES, AND DIPOLE ORIENTATIONS

Region	Talairach (MNI) coordinates (mm) x, y, z	Diploe orientation (components) x, y, z
L SFG, BA 10	−18.0, 66.7, 7.0 (−18.2, 68.3, 11.2)	0.1, 1.0, 0.0
SMA, BA 6	0.0, 0.4, 65.3 (0, −2.9, 69.0)	0, 0.2, 1.0
L IPL, BA 40	−62.3, −31.6, 33.5 (−62.9, −34.3, 34.7)	−0.9, 0.2, 0.4
R middle frontal gyrus, dlPFC, BA 46	49.6, 42.9, 6.1 (50.1 43.9 9.0)	0.7, 0.7, 0.1
R STG, BA 22	65.9, −42.8, 6.5 (66.6, −44.4, 4.7)	0.9, −0.4, 0.1

In this study, sources are obtained using the minimum norm estimates approach.

BA, Brodmann area; dlPFC, dorsolateral prefrontal cortex; L IPL, left inferior parietal lobule; MNI, Montreal Neurological Institute; R STG, right superior temporal gyrus; SFG, superior frontal gyrus; SMA, supplementary motor area.

used in the prelearned condition. To evaluate those improvisations, we calculated the average Simonton's melodic originality score for each improvisation from the Play-Improvised conditions for each participant. This measure is based on second order pitch class distribution of western tonal music and has been derived from 15,618 classical music themes (Simonton, 1984, 1994). The melodic originality score is the inverse of averaged probability and scaled between 0 and 10; higher value indicates higher melodic originality. We computed coherence and GC spectra from the source waveforms for the Play-Improvised condition from all participants and extracted coherence and GC peak values to correlate with the melodic originality score. The relationship in the scatterplot was assessed by both Spearman's rank correlation and Pearson's correlation. A correlation was considered significant if the significance threshold was $p < 0.05$ for both results. The results are reported here in terms of Spearman's rank correlation. A positive correlation indicated that greater melodic originality related to higher network coherence or GC.

Results

Behavioral results

Performance accuracy and asynchrony scores were evaluated using the MIDI keyboard press data. Performance accuracy was measured by marking each individual trial (each eight-note performance) as either correct or failed. A failed trial received a score of 0, while a correct trial received a score of 1. Correct trials denote a perfect replication of the cued melody type with each note played in the correct order. Accuracy per participant ranged from 63.3% to 100% with average accuracy being 87.7% (SD = 11.7%). No feedback was given to participants indicating whether the played note sequence replicated the cued melody exactly. Asynchrony measured how well participants were able to synchronize their piano key presses to the metronome. Asynchrony was calculated as the difference between the metronome onset time and the key press time divided by the total time interval between metronome beats. An asynchrony score close to 0 represents a note played better in synchrony with the metronome; +1 represents a note played one full beat late, and −1 represents a note played one full beat early. Average asynchrony was −0.03, meaning the participants slightly anticipated the metronome.

Electrophysiological results

Group level average potentials. The average EEG waveforms were calculated from the trials from all participants for musical task conditions: Play-Improvised, Play-Prelearned, Imagine-Improvised, Imagine-Prelearned, and Rest separately. When the peak amplitude of the scalp recorded EEG signals from the trials was compared between prelearned and improvised conditions in musical play, the group of electrodes shaded by transparent red color (Fig. 1) showed statistically significant ($p < 0.05$, t-tests) difference. A similar comparison between prelearned and improvised conditions in imagery condition showed the group of electrodes shaded by transparent green color (Fig. 1) having the significant difference in peak amplitude ($p < 0.05$). This p-value is the corrected p-value for multiple comparison correction, when applied across 64 electrodes.

EEG sensor power spectra. Figure 2 shows the average power spectra for the groups of channels, which are marked in Figure 1. The displayed power spectra are for the left frontal, left central, bilateral parietal (more electrodes on left side), and bilateral parieto-occipital electrodes from top to bottom; left column is for Play-Improvised condition, whereas the right column is for Play-Prelearned condition (Fig. 2A). The z-score power (based on the baseline power from −500 to 0 ms) showed an increasing trend in alpha power from frontal to central, then to parietal, and even more to the parieto-occipital electrodes during Play-Improvised condition. The power increased significantly (z-score >3) starting from around 700 ms. Moreover, the average alpha (8–12 Hz) power was significantly higher ($p < 0.05$) during Play-Prelearned condition compared to Play-Improvised condition for all these electrode clusters, shown in Figure 2B. A statistically significant ($p < 0.05$) beta (13–30 Hz) power difference existed for frontal and parietal electrode clusters, but there was no gamma (30–70 Hz) power difference in these four electrode clusters (Fig. 2B). We found the similar power difference trends when average power calculation was done separately for five participants (pianist) who reported the piano as their primary musical instrument and five participants (nonpianist) who reported any other instrument except piano as their primary instrument. Neither of the electrode clusters (left frontocentral and
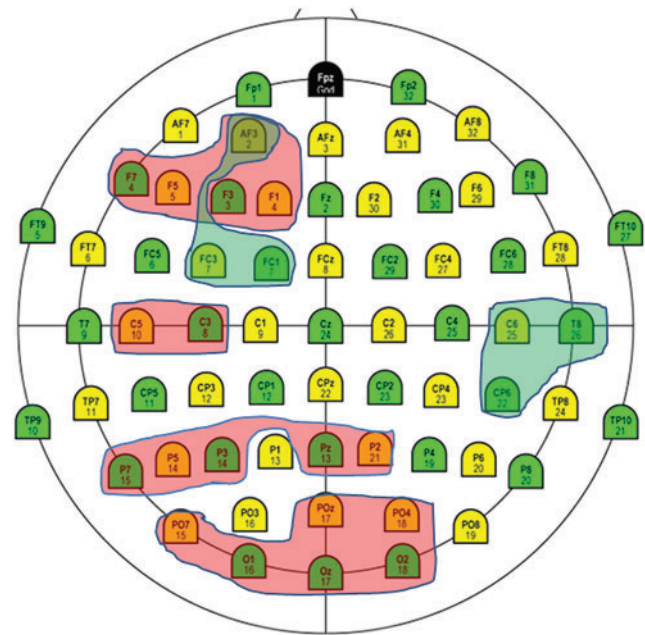

FIG. 1. The schematic represents a 64-channel EEG recording montage used in Brain Vision's actiCHamp System. The shaded regions covering two or more labeled electrodes show the locations in sensor space where peak amplitude of the trials differed significantly (t-tests, $p < 0.05$). Clusters shaded by red transparent color show where the peak amplitude between Play-Improvised and Play-Prelearned conditions increased and clusters by transparent green color show where peak amplitude differed between Imagine-Improvised and Imagine-Prelearned conditions. EEG, electroencephalography. Color images available online at www.liebertpub.com/brain
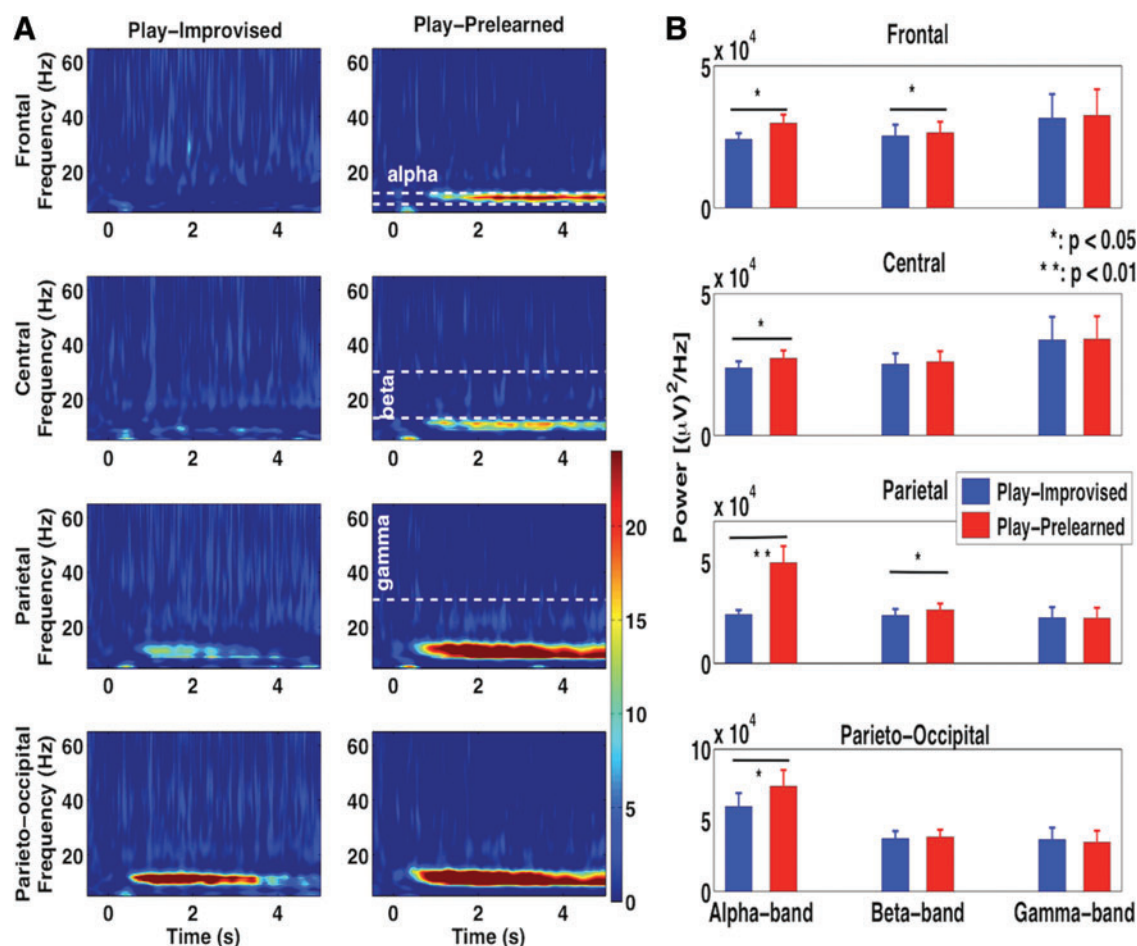
FIG. 2. Sensor level power spectra. Wavelet power (z-power) during Play-Improvised condition is shown in the first column and during Play-Prelearned condition in the second column **(A)**. Alpha power [first column **(B)**] is significantly higher during the prelearned condition compared to improvised condition. In this study, the results shown in rows the first to the fourth represent the average contribution of all the electrodes that lie on the frontal, central, parietal, and parieto-occipital cluster, respectively. Color images available online at www.liebertpub.com/brain

right central, shaded by transparent green color in Fig. 1) showed significant alpha power difference when the alpha power spectra from Imagine-Prelearned condition and Imagine-Improvised condition were compared (figure not shown). For these electrode clusters, we found no alpha power difference between Imagine-Prelearned condition and Imagine-Improvised condition for pianist and nonpianist.

EEG localized sources. The grand average EEG signals for all musical tasks were used in the MNE approach to reconstruct the inverse EEG solutions. The EEG sources were the left superior frontal gyrus (L SFG), SMA, left inferior parietal lobule (L IPL), dorsolateral prefrontal cortex (dlPFC), and right superior temporal gyrus (R STG; Fig. 3A–E). Table 1 lists the location (Talairach coordinates) of EEG sources; dipole orientations of the sources, names of region, and Brodmann area (BA) are in accordance to Talairach Client—Version 2.4.3 (www.talairach.org/client.html). The fitted dipoles at these anatomical locations and orientations explained ∼81% of the variance in the EEG signal for trials in all task conditions. We fitted the diploes in these

locations with their corresponding orientations (Fig. 3F) and computed the single trial source waveforms from single-trial EEG data that were then used in calculation of spectral measures.

GC spectra. We computed GC spectra to assess oscillatory network interactions among the five nodes of activity: SFG, SMA, IPL, dlPFC, and STG. The GC spectra were calculated separately for each condition. Significant causal connections (with maximum GC value) are shown in Figure 4. Both Play-Improvised and Play-Prelearned conditions had almost similar interaction patterns (Fig. 4A, B). The information flow was bidirectional between SFG and IPL, IPL and STG, and dlPFC and SMA and unidirectional from SFG to SMA and SMA to IPL in both cases. The stronger causal influences were from SFG to IPL and dlPFC to SMA; STG to IPL in improvised but equal in prelearned. In addition, significant causal influence from dlPFC to SFG plus bidirectional causal influences between dlPFC and IPL were found in Play-Prelearned. The interaction patterns were similar in both Imagine-Improvised and Imagine-Prelearned
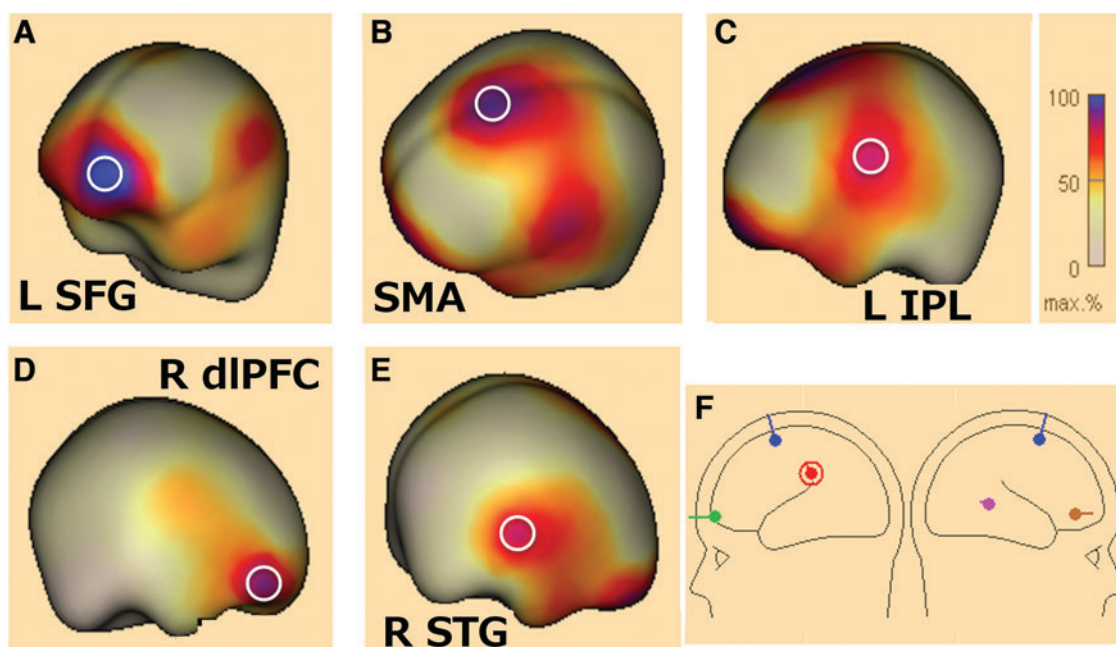
FIG. 3. Spatial profiles of the peak source-level electrophysiological activity. Cortical sources (**A–E**) are calculated using the MNE approach. The location and orientation of the fitted dipoles are given in (**F**). dlPFC, dorsolateral prefrontal cortex; IPL, inferior parietal lobule; L, left; MNE, minimum norm estimates; R, right, SFG, superior frontal gyrus; SMA, supplementary motor area; STG, superior temporal gyrus. Color images available online at www.liebertpub.com/brain

FIG. 4. Schematic representation of the GC network graph associated with Play-Improvised (**A**), Play-Prelearned (**B**), Imagine-Improvised (**C**), and Imagine-Prelearned (**D**) conditions. All the connections (causal influence strengths are represented by thickness of the line with arrow heads) shown are statistically significant for the threshold level at significance $p < 10^{-6}$ by permutation tests. For the schematic representation, network nodes (spherical ROIs of 10 mm radius, center coordinates' are given in Table 2) were overlaid on render brain and cut out for visualization of nodes, using MRIcron. GC, Granger causality; ROIs, regions of interest. Color images available online at www.liebertpub .com/brain
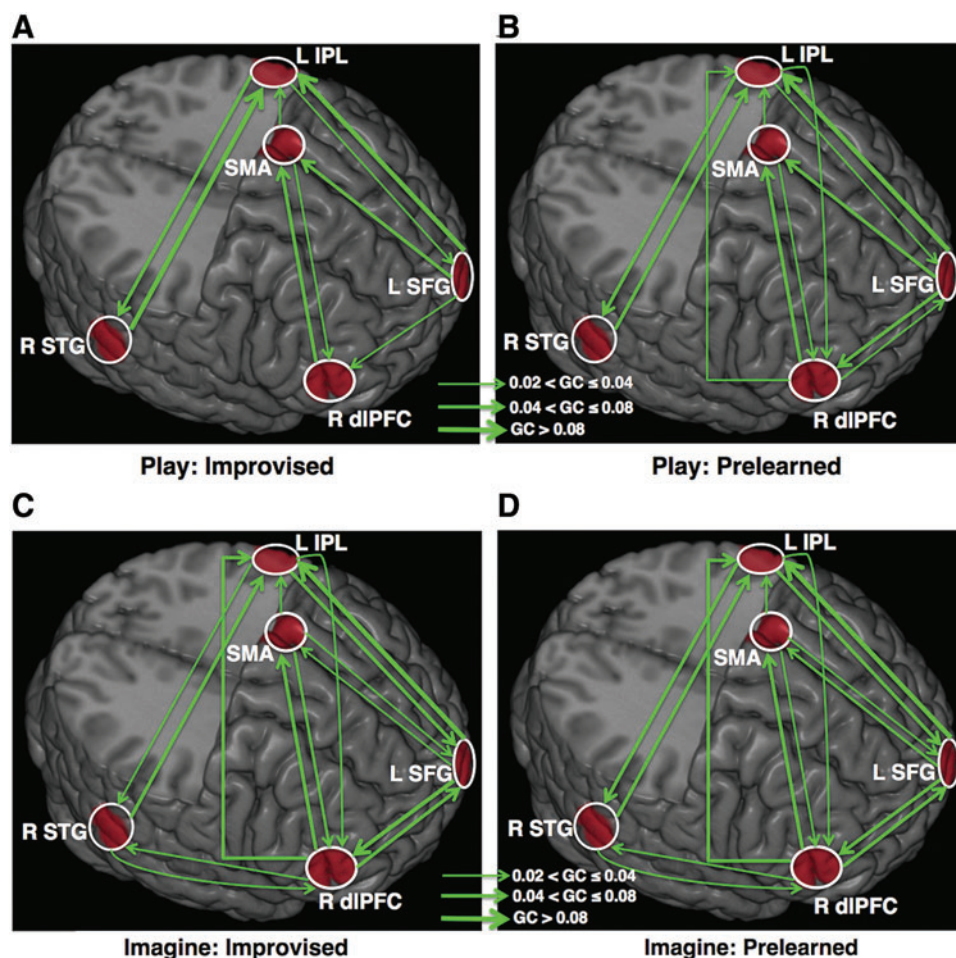
conditions (Fig. 4C, D). Bidirectional network interactions were found between SFG and IPL, SFG and SMA, SFG and dlPFC, IPL and STG, STG and dlPFC, and dlPFC and IPL. The stronger causal influences were found from SFG to IPL, dlPFC to SMA, and dlPFC to IPL than the other way around. The bidirectional causal interactions between dlPFC and STG, SFG and dlPFC are of equal strength. The causal influence was unidirectional from SMA to IPL. Considering these significant causal interaction directions (in the play condition and imagine condition), we computed integrated GC values (from 1.5 to 58 Hz) from individual participants to compare whether the overall causal interactions during improvised and prelearned conditions changed in musical play and imagine situations. Among these network sources, Play-Prelearned condition had significantly higher ($p<0.001$) causal interactions than Play-Improvised condition (Fig. 5A), whereas causal interactions did not differ significantly ($p<0.05$) between Imagine-Prelearned and Imagine-Improvised conditions (Fig. 5B). Among the significant causal interactions, common to both play and imagine conditions, the overall network interactions during Imagine-Prelearned and Imagine-Improvised were significantly higher ($p<0.001$) than Play-Prelearned and Play-Improvised (Fig. 5C).

We were also interested in seeing how the individual network interactions change during music play and imagine conditions. We used paired t-tests and compared the integrated GC values (improvised condition compared to prelearned condition) to evaluate the statistics of the change of the interactions. We found significantly decreased causal interactions from SFG to SMA, SMA to IPL, and IPL to SFG ($p<0.05$) during improvisation in the play condition as shown by a solid blue line with an arrowhead in Figure 6A. During the imagine condition, we found significantly decreased ($p<0.05$) causal interactions from SMA to dlPFC (shown by blue line with an arrowhead), whereas causal interaction was found significantly increased from SFG to dlPFC (shown by red line with an arrowhead) as in Figure 6B. Remaining interactions, which were significant from group level interactions during separate prelearned and improvised conditions in music play and imagine tasks (Fig. 4), were not significantly different when comparison was done between improvised and prelearned conditions. The dotted line with an arrowhead (red represents the increase in causal interactions and the blue represents the decrease in causal interactions) represents the statistically insignificant ($p>0.05$) change in causal influences as shown in Figure 6A and B.
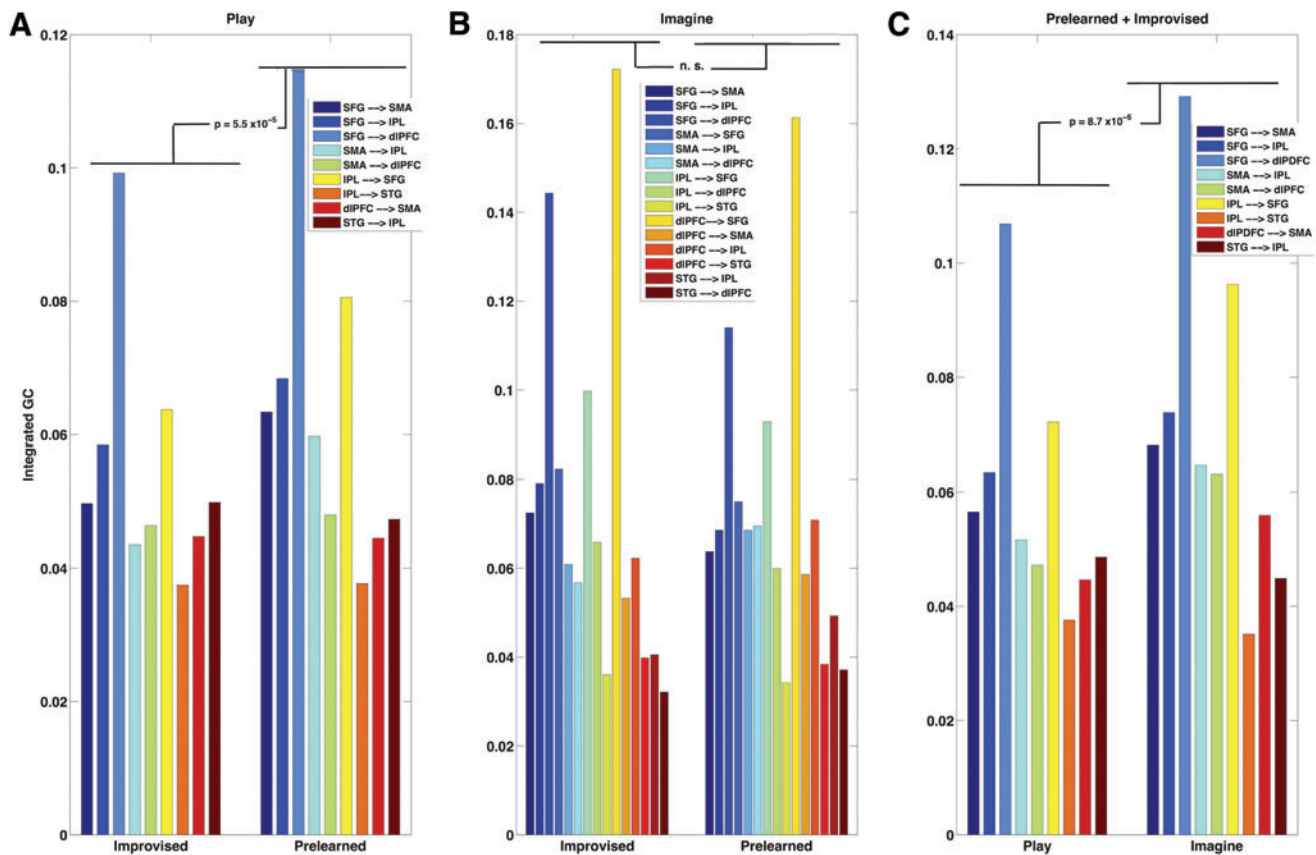

FIG. 5. Network activity comparison. Considering the causal influences for all significant connections during musical play (**A**), stronger network activity ($p<0.001$) was found for the prelearned condition than improvised condition. No difference in network activity was found between the prelearned condition and improvised condition under consideration of all significant causal connections during musical imagine conditions (**B**). Considering the causal influences for significant causal connections that are common for both musical play and imagine conditions, we found that the network activity was significantly higher ($p<0.001$) in musical imagine than musical play situations (**C**). Color images available online at www.liebertpub.com/brain
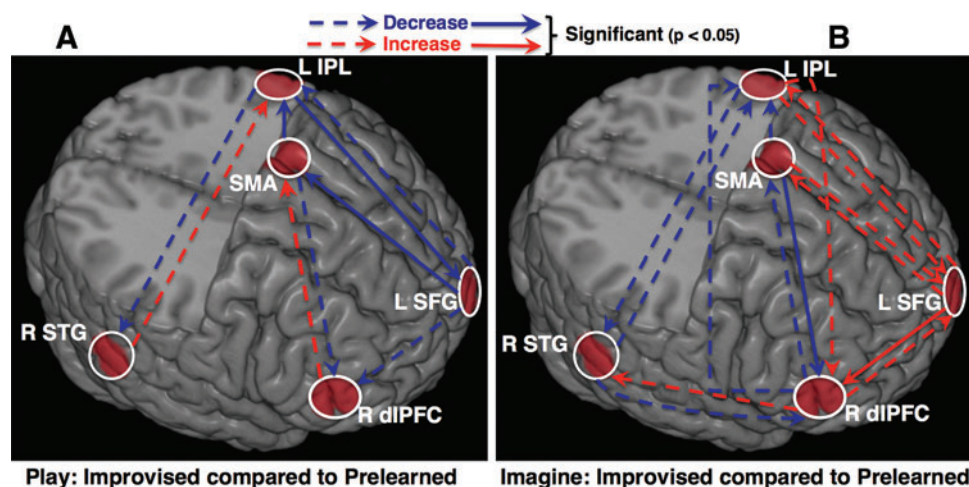
FIG. 6. Network modulation during play and imagine conditions. Network interactions during improvised compared to prelearned in musical play **(A)** and imagine **(B)** conditions. Lines with arrowhead (dotted plus solid) represent the significant causal connections among the four nodes in the network during Play-Improvised and Play-Prelearned conditions in **(A)** and Imagine-Improvised and Imagine-Prelearned condition in **(B)** from the spectral interdependency measures, as shown in Figure 4. In this study, solid lines with arrowhead represent the significant change ($p < 0.05$) in network interactions between nodes, while dotted lines with arrowhead represent for insignificant ($p > 0.05$) change. Red color represents the increase in causal strength, whereas blue color represents the decrease in causal strength. For the schematic representation, network nodes (spherical ROIs of 10 mm radius) were overlaid on render brain and cut out for their better visualization, using MRI-cron. Color images available online at www.liebertpub.com/brain

Brain behavior relation. Simonton's melodic originality score was correlated with spectral measures of network activity, coherence, and GC in Play-Improvised conditions (Fig. 7, only significant results are shown). The mean melodic originality score calculated from all improvisation conditions during music play from each participant was positively correlated ($p < 0.05$) with coherence for SFG-SMA, SFG-IPL, and SMA-IPL node pairs (first row, Fig. 7A–C).

Similarly, the melodic originality score was also negatively correlated with GC from SFG to SMA, IPL to SFG, and IPL to STG (second row, Fig. 7D–F).

Discussion

In this study, we investigated electrophysiological responses during musical improvisation using simple isochronous

FIG. 7. Relation between spectral measures and melodic originality score during Play-Improvised condition. Pairs of nodes showing significant positive correlations ($p < 0.05$) with coherence **(A–C)** and significant negative correlations ($p < 0.05$) with GC **(D–F)** are shown. Causal interactions SFG → SMA, IPL → SFG, and IPL → STG are negatively correlated ($p < 0.05$) to melodic originality score. Color images available online at www.liebertpub.com/brain
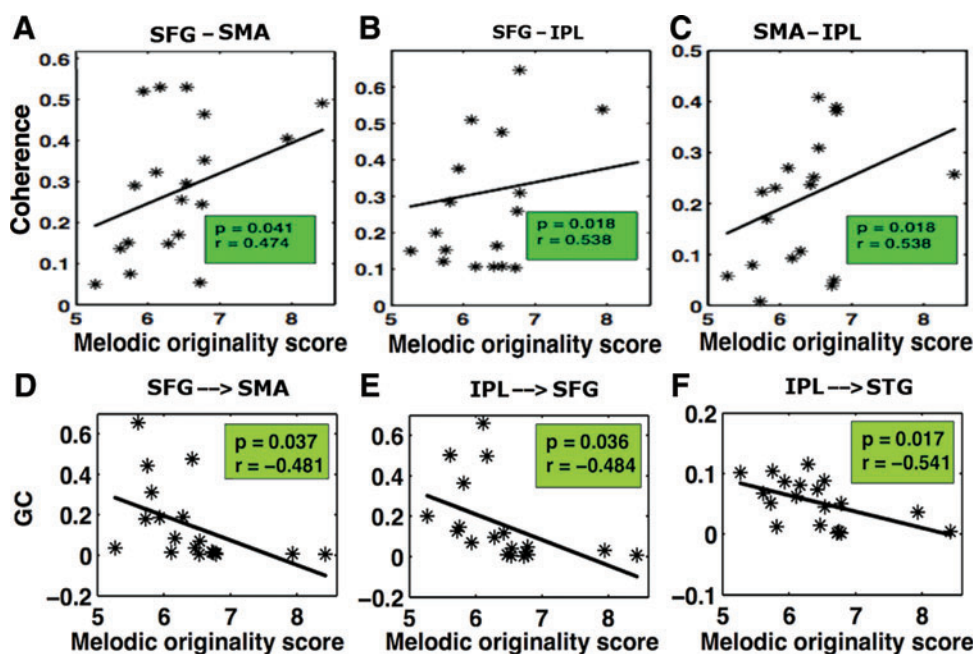
melodies that were either prelearned or improvised and either played on a piano keyboard or imagined. In the current paradigm, improvised and prelearned conditions both gave rise to similar motor actions, only the mode of creation was different. The neural correlates behind this difference were the focus of the current research. We found that the prelearned melodies elicited significantly stronger alpha waves in frontal, central, parietal, and parietal–occipital electrodes compared to improvisation in the play conditions. Using EEG sources we identified a network consisting of the L SFG, SMA, L IPL, R dlPFC, and R STG. In the play condition, a causal directional link was significantly decreased during improvisation from the SFG to the SMA to the IPL to the SFG compared to the prelearned. The connectivity strength of these links was also negatively correlated with the melodic complexity of the improvisations.

Music improvisation requires the performer to create a novel output under significant constraints. Specifically, tonal music improvisations typically must fit a given timing and harmonic structure (Berliner, 1994). The ability to improvise over complicated timing and harmonic structures therefore requires a high level of expertise (Limb and Braun, 2008; Pinho et al., 2014). These elements make music improvisation an ideal setting for the study of creative behavior that unfolds in real time. Previous research has suggested that expert improvisation relies partly on learned mechanisms for response selection without conscious mediation (Limb and Braun, 2008; Liu et al., 2012). Similar to expertise in other domains, conscious mediation may inhibit performance (Beilock and Gonso, 2008; Beilock et al., 2002; Ford et al., 2005). Specifically, a pattern of deactivation in the frontal areas has been suggested as central to expert improvisation (Limb and Braun, 2008; Liu et al., 2012) and the generation phase in other creative tasks (Liu et al., 2015). Our results align well with this research as we identified a network where top–down control is attenuated during improvisation. We discuss our results in detail below.

Contrasting event-related time frequency responses, we found significantly stronger alpha waves in the Play-Prelearned condition compared to Play-Improvisation. This appears to contradict previous research showing a link between stronger alpha waves and creative ideation (Fink and Benedek, 2014; Fink et al., 2009b; Lustenberger et al., 2015). However, this research was nearly exclusively done with creative tasks that did not involve response selection within a structured time constraint (Dietrich and Kanso, 2010). The one exception is a study in which stronger alpha waves were seen as advanced dancers imagined a creative dance (Fink et al., 2009a). Here the divergent results may simply be due to the imagery task. Indeed, we did not see a significant difference in alpha power in our Imagine-Prelearned Imagine-Improvised contrast. So why did we see such strong alpha power in the Play-Prelearned condition compared to Play-Improvisation? Stronger alpha waves have been linked to inhibition in which alpha power reflects attenuation of areas that could interfere with the task at hand (Klimesch et al., 2007). Here the Play-Prelearned task involved playing one of four memorized melodies necessitating suppression of the other three melodies. Similar to a visually presented working memory task (Jensen et al., 2002), this alpha band power increase appeared with a slight delay

(Fig. 2). It is possible that after about 1 sec, the motor sequence for the correct melody has been selected and confirmed by initial auditory and proprioceptive feedback (Baumann et al., 2007; Katahira et al., 2008). The alpha band increase could therefore reflect a top–down suppression of input from visual and auditory areas that could interfere with the melody performance already in progress. However, during the improvisation task, no such melody is specified and the participant may therefore incorporate feedback throughout the eight-note sequence. Nonetheless, this conclusion should be interpreted with caution as our results directly contradict the commonly referenced association between alpha waves and creativity. Indeed this literature argues that alpha waves cause attenuated top–down control, which facilitates creative ideation (Lustenberger et al., 2015). This explanation is in line with our network analysis in the current experiment, but does not appear to align with the observed changes in alpha power between conditions.

Beta oscillations are associated with alertness, active task engagement, and motor behavior (Neuper and Pfurtscheller, 2001). Previous studies showed beta waves are more synchronous during general consciousness (Teplan, 2002; William and Harry, 1985) and may be a useful measure of appropriate cognitive and emotional processes (Ray and Cole, 1985). Furthermore, beta activity was widely recognized to be linked with motor behavior and response inhibition, top–down signaling associated with selective attention (Gross et al., 2005), working memory (Tallon-Baudry et al., 2001), perception (Donner et al., 2007), or sensorimotor integration (Brovelli et al., 2004; Brown and Marsden, 2001; Witham and Baker, 2007). Considering its wide involvement, beta power increase during the prelearned condition may indicate an improvement in cerebral integrative and motor functions, further supporting the motor idling hypothesis (Pfurtscheller et al., 1996). As a beta frequency band is related to movement, we assumed that the frontal and parietal areas be associated with planning and execution of motor movements. Further research, in detail, will help explore the functional significance of beta activity in musical creativity.

Using EEG source localization, we identified a network consisting of the L SFG, SMA, L IPL, right dorsolateral prefrontal cortex (R dlPFC), and R STG. The SMA, including in particular the pre-SMA, has been implicated in several fMRI studies of musical improvisation (Beaty, 2015). The SMA is responsible for planning motor movements as evidenced by the readiness potential, which is present before the related movement is initiated (Cunnington et al., 2003). The area has specifically been implicated in internally selected actions designed to produce an effect on the external environment (Jenkins et al., 1994; Mueller et al., 2007). In addition to tasks that involve motor action, the area has been implicated in motor imagery (Cunnington et al., 2005) and is activated by musical recognition tasks that may involve covert vocalization (Halpern and Zatorre, 1999; Halpern et al., 2004). In a study of anticipatory musical imagery during silence just before a known melody, Leaver et al. (2009) found strong activations of premotor areas as well as rostral prefrontal cortex. Specifically in the current task, the SMA is probably involved in continuous monitoring of current and planned motor movements. Interestingly, new research suggests this monitoring function of the SMA

is stronger during spontaneous creation of a musically ambiguous emotional output, while a highly practiced overlearned output requires less monitoring (McPherson et al., 2016). Since participants in the current study included participants who were musicians but not necessarily pianists and not advanced improvisers, it is likely that our task mirrored more closely the ambiguous condition in McPherson et al. (2016). In other words, since the majority of the current participants were not pianists, the necessary movements were not overlearned and therefore required more engagement by the SMA.

The L IPL is part of the parietal association area and is commonly seen in fMRI studies involving musical improvisation (Beaty, 2015). Specifically, the area is probably involved in the interpretation of perceived somatosensory proprioceptive information from the contralateral hand used during the task. In addition, the area may also be involved in perception of auditory output. The IPL is likely involved in a feedback loop that also includes the R STG and is most likely related to perception of incoming auditory signals as participants depressed piano keys. Even when imagining music, activation is commonly observed in the auditory cortex within the STG (Meister et al., 2004; Zatorre et al., 1996). The right lateralization is commonly seen in pitch perception as opposed to left lateralization seen for speech input (Zatorre et al., 2007). In addition, the R STG has been linked to the storage of familiar melodies (Peretz et al., 2009).

Both frontal areas identified through source localization are likely involved in cognitive control in general (Hutcherson et al., 2012) and music improvisation tasks specifically (Limb and Braun, 2008; McPherson et al., 2016). This would include online evaluation of behaviors compared to overall goals both in nonmusic (Gerlach et al., 2011) and musical improvisation tasks (de Manzano and Ullen, 2012b). The R dlPFC in a network also including the SMA and the IPL may contain a working memory representation of the notes available for improvisation (Koelsch et al., 2009). Importantly, the same size pitch set was used in both the prelearned and improvised conditions. It is therefore likely that the changes observed in functional connectivity were due to the way the pitches were used. Furthermore, the size of the pitch sets during improvisation appears to have no influence on brain activity (de Manzano and Ullen, 2012b). The specific activity of the dlPFC in musical improvisation tasks appears to be modulated by whether or not improvisers were restricted to a defined pitch set during improvisation (Pinho et al., 2015).

The current research identified of a causal link from the L SFG to the SMA to the L IPL and back to the L SFG. The GC values were significantly higher combining all identified paths during the Play-Prelearned than Play-Improvisation (Fig. 5), specifically in the path going from L SFG to the SMA to the L IPL and back to the L SFG (Fig. 6A). This aligns well with previous research in which activation of frontal areas (Limb and Braun, 2008) was attenuated during improvisation. This was explained by the idea that top–down control may inhibit a creative process driven by bottom–up processes. However, other studies of musical improvisation saw conflicting results (Bengtsson et al., 2007; de Manzano and Ullen, 2012b). The only other EEG study to date that has compared networks between improvised and prelearned conditions also found increased connectivity during improvisation; however,

this study was not done in a controlled experimental setting (Wan et al., 2014). This discrepancy has recently been investigated in two studies where two types of improvisations were compared (McPherson et al., 2016; Pinho et al., 2015). In the current study, we wanted to return to a contrast that more specifically addressed the question of creative versus prelearned actions using the same pitch set for both conditions. The decrease of network activity in the Play-Improvisation condition supports the earlier work and the idea that spontaneous music creation is supported by bottom–up processes.

The contribution of the three areas in which significant decreases in GC values are seen could be interpreted as follows. During the initiation of a trial in which subjects are asked to play a memorized melody, they likely retrieve the melody from long-term memory and then maintain it in working memory. This process involves both frontal and motor areas (Koelsch et al., 2009). As they play, the melody in working memory is compared to the actual output involving a network controlled by frontal areas. In a trial in which participants are asked to play an improvisation using the same pitch set, the frontal control is less important (Limb and Braun, 2008). Although participants still perceive improvised melodies, these melodies do not have to fit a given representation in working memory.

One of the most intriguing findings in the current study relate to the correlations between GC values and the melodic complexity behavioral measure. The participants who played more varied improvisations appear to use less cognitive control as evidenced by significantly smaller GC values from SFG to SMA and from IPL back to SFG (Fig. 7). Since the coherence values show the opposite trend, it appears the causal influence is simply reversed. In other words, the information is coming from the SMA and going to the SFG in participants who play more varied improvisations. This could be because those participants rely on more bottom–up processes. These processes could be guided by learned musical rules and patterns for melody creation (Johnson-Laird, 2002; Norgaard, 2014).

We hypothesized that we would find similar results in the imagine conditions, which turned out not to be true. A comparison of overall integrated GC values for Imagine-Prelearned and Imagine-Improvise did not reveal a significant difference. There GC for connectivity from L SFG to R dlPFC was significantly higher in the imagine improvisation condition compared to the prelearned. This difference may simply be due to higher cognitive demand when imagining an improvised melody.

In the experimental questionnaire template, we did not ask the participants about their years of improvisation experience. Therefore, our manuscript lacked the information regarding improvisation experience of the participants.

In conclusion, the network identified here reveals the underpinnings of creative performance in a real-time musical improvisation task and involves regions that may function outside of the top–down control networks usually seen in traditional decision-making tasks (Dalley et al., 2011; Dosenbach et al., 2008; Gold and Shadlen, 2007; Heekeren et al., 2008). This is likely because individual notes in the current improvisation task were not chosen deliberately and align with the general idea of attenuation in top–down control during creative tasks (Limb and Braun, 2008;

López-González and Limb, 2012). Due to the time constraints, there simply was not time for participants to contemplate each note choice. Therefore, the network underpinning this task probably relies on bottom–up processes to control note choices using aesthetic rules that our advanced musician participants have internalized during a lifetime of music engagement.

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Author Disclosure Statement

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