

Cortical Regions Involved in the Generation of Musical Structures during Improvisation in Pianists Sara L. Bengtsson¹, Miha'ly Cs'kszentmiha'lyi², and Fredrik Ull'e'n¹

Abstract & Studies on simple pseudorandom motor and cognitive tasks have shown that the dorsolateral prefrontal cortex and rostral premotor areas are involved in free response selection. We used functional magnetic resonance imaging to investigate whether these brain regions are also involved in free generation of responses in a more complex creative behavior: musical improvisation. Eleven professional pianists participated in the study. In one condition, *Improvise*, the pianist improvised on the basis of a visually displayed melody. In the control condition, *Reproduce*, the participant reproduced his previous improvisation from memory. Participants were able to reproduce their improvisations with a high level of accuracy, and the contrast *Improvise* versus *Reproduce* was thus essentially matched in terms of motor output and sensory feedback. However, the *Improvise* condition required storage in memory of the improvisation. We therefore also included a condition *FreeImp*, where the pianist improvised but was instructed not to memorize his performance. To locate brain regions involved in musical creation, we investigated the activations in the *Improvise*–*Reproduce* contrast that were also present in *FreeImp* contrasted with a baseline rest condition. Activated brain regions included the right dorsolateral prefrontal cortex, the presupplementary motor area, the rostral portion of the dorsal premotor cortex, and the left posterior part of the superior temporal gyrus. We suggest that these regions are part of a network involved in musical creation, and discuss their possible functional roles.

INTRODUCTION Creative behaviors and creative individuals fascinate scientists and laymen alike, and studies of creativity have a long history in psychology (see, e.g., Simonton, 1999; Sternberg, 1999; Csikszentmihalyi, 1997; Eysenck, 1995). A precise, generally agreed-upon definition of what constitutes a creative behavior has been difficult to arrive at, however, although two characteristics seem central: Creative acts are novel or original and, qualified judges will agree that they constitute valuable contributions to the field (Sternberg, 1999). The novelty aspect is critical, and tests designed to measure creative ability typically require divergent thinking, as opposed to the convergent problem-solving abilities measured by traditional intelligence tests. Convergent problems have a single answer. Divergent tasks have a large number of possible solutions, and the free generation and selection of alternatives among these possibilities are fundamental processes in creative behavior (Campbell, 1960). Although psychological research has provided valuable information on both creativity as a trait and the characteristics of divergent thinking, little is still known about the brain mechanisms underlying creative behaviors. A few neuroimaging studies have investigated more complex verbal tasks involving divergent thinking, such as story generation (Howard-Jones, Blakemore, Samuel, Summers, & Claxton, 2005), sentence completion (Nathaniel-James & Frith, 2002), generation of unusual verbs in response to nouns (Seger, Desmond, Glover, & Gabrieli, 2000), and the Brick test of unusual uses of objects (Carlsson, Wendt, & Risberg, 2000). These studies generally show an activation of cortical association areas, in particular, the prefrontal cortex, during divergent thinking. Interestingly, there appears to be a tendency for the right prefrontal cortex to be particularly involved (Howard-Jones et al., 2005; Carlsson et al., 2000; Seger et al., 2000; Abdullaev & Posner, 1997). A major difficulty in the investigation of more complex actions, however, is obviously to isolate the neurocognitive components responsible for controlling different aspects of the behavior. A systematic investigation of neural processes underlying free selection has been performed using simpler model behaviors, as a part of studies of willed action. Willed actions involve “free” choice as well as attention, conscious awareness, and intentionality (Jahanshahi & Frith, 1998). By studying tasks such as finger or hand movements (Lau, Rogers, Ramnani, & Passingham, 2004; Frith, 2000; Playford et al., 1992; Deiber et al., 1991) or number generation (Jahanshahi, Dirnberger, Fuller, & Frith, 2000), and by comparing pseudorandom

generation of responses with stereotyped actions, a number of 1 Karolinska Institutet, Stockholm, Sweden, 2 Claremont Graduate University D 2007 Massachusetts Institute of Technology Journal of Cognitive Neuroscience 19:5, pp. 830–842 cortical regions involved in free selection have been characterized. These include the dorsolateral prefrontal cortex (DLPFC), medial and lateral premotor areas, and the anterior cingulate cortex. This approach has enabled an elegant analysis of the various processes involved in free selection, such as attention to action, working memory, suppression of stereotype responses, and selection per se (Lau et al., 2004; Nathaniel-James & Frith, 2002; Desmond, Gabrieli, & Glover, 1998). However, an interesting question is whether the brain regions involved in free selection in simple willed actions are also utilized in more complex behaviors that could qualify as ecologically valid examples of creativity. In the present study, we investigated this issue using musical improvisation in professional pianists as a model. Improvisation arguably satisfies the demands of a prototypical creative behavior. It involves freely generated choices, but these must be adapted to ongoing performance, and monitored through auditory and somatosensory feedback, as well as to an overall aesthetic goal (Pressing, 1988). It is simple enough, however, to allow an experimental design where the neural processes involved in the free generation of musical structures can be separated from those involved in the sequential organization and programming of the movements (i.e., piano playing), and the processing of movement feedback. To achieve this, we used one condition, *Improvise*, where the pianist improvised on the basis of a visually displayed melody. In the control condition, *Reproduce*, the participant reproduced his previous improvisation from memory. The critical contrast, *Improvise–Reproduce*, was thus matched in terms of motor output and sensory feedback. Because the *Improvise* condition required storage of the improvisation in memory, we also included a third condition, *FreeImp*, where the pianist improvised but was instructed not to memorize his performance. To find brain regions involved in music generation, but not in memorization or motor programming, we examined which activations in the *Improvise–Reproduce* contrast were also present in a conjunction analysis between *Improvise–Reproduce* and *FreeImp–Rest*. Activity in the *Improvise–Reproduce* contrast was regressed on a measure of improvisation complexity in order to localize brain regions with a higher level of activity during the generation of more complex musical structures. Finally, differences in brain activity between *FreeImp* and *Improvise* were evaluated by contrasting these two conditions in brain regions that were active in *Improvise–Reproduce*.

METHODS

Participants Eleven professional Swedish concert pianists took part in the study. All participants were men, healthy, righthanded (Oldfield, 1971), and had a Master's degree in the performing arts (piano) from the Royal Academy of Music in Stockholm. They were between 23 and 41 years old, with a mean age of 32.0 ± 6.0 years, and had started playing the piano between 4 and 8 years old (mean 5.7 ± 1.4 years). The experimental procedures were ethically approved by the Karolinska Hospital Ethical Committee (Dn 02-194) and were undertaken with the understanding and written consent of the participants. Experimental Setup Magnetic resonance (MR) imaging recordings were conducted on a 1.5-T scanner (Signa Horizon Echospeed, General Electric Medical Systems). During the functional magnetic resonance imaging (fMRI) scans, the participants played with their right hand on a small piano keyboard, especially designed for usage in an MR environment (LUMItouch, Inc.). The keyboard had one octave of 12 authentic keys (from F to E), and was connected to a PC computer through a fiber-optic cable. During scanning, the participant's performance on the keyboard was recorded on the PC, using the E-Prime software (Psychological Software Tools, Inc.). Auditory feedback from the piano was provided to the participant through headphones. The pianists were lying in a supine position, with the arm supported so that the keyboard could be played by moving the fingers and the wrist without arm movements. A plastic bite bar was used to restrict head movements. A projector located outside the scanner

room was used to project task instructions and musical scores onto a semitransparent screen, positioned approximately 3 m from the participants' eyes. The participants viewed the screen through a custom-made binocular/mirror system (Lorentzen Instrument AB) mounted directly on top of the head coil. Conditions All participants performed three conditions: *Improvise*, *Reproduce*, and *Rest*. These were performed in trials lasting 40 sec. During the first 4 sec of a trial, the name of the condition was projected onto the screen. For the *Rest* condition, the screen after this went blank for the remaining 36 sec of the trial. For the other conditions, a musical score consisting of a simple eight-bar melody was displayed (Figure 1A). For a preparatory period of 8 sec, the score was surrounded by a red, rectangular frame. This frame was then removed, signaling to the participant to start playing. These final 28 sec of the trial, when the task was performed on the keyboard, were later used in the data analysis. A total of 12 musical scores of similar complexity were used in the study, 6 in F major, 6 in F minor. The main reason to use improvisation based on melodic templates, rather than completely free improvisation, was to make the improvisations Bengtsson, Csíkzentmihályi, and Ullén 831 more constrained, and thus, easier to remember. The scores were especially written for the present study, and thus, were unfamiliar to the participants. They were notated using the Finale music notation software (MakeMusic, Inc.). In *Improvise*, the displayed melody was used as a basis for an improvisation. The instructions to the participants were to employ any kind of modifications of the presented melodic template they wished, and when the improvisation was finished, to rest without any active movements until the next condition began (for examples of the employed modifications, see Figures 1B and 3A–B). They were also instructed to memorize the performance for subsequent reproduction. In *Reproduce*, the task was to reproduce, as faithfully as possible, the improvisation previously made upon the same melody. In *Rest*, the participants relaxed, viewing the screen without any movements. Five of the participants performed an additional condition, *FreeImp*, where the instruction was to improvise on the melody, as in *Improvise*, but without trying to memorize the performance.

Experimental Procedure Before the experiment, the participants were familiarized with the tasks and were given one practice trial of each condition outside the scanner room. When the participant was lying in the MR-scanner in a supine position, the conditions were practiced a second time. The pianists found the tasks enjoyable and interesting. The musical examples used during the practicing sessions were not used again during the experiment. We started the experiment by collecting a high-resolution T1-weighted anatomical image volume of the whole brain. Thereafter, fMRI data were recorded while the participants performed three sessions, each containing three trials of the different tasks. Musical scores were selected randomly from the database of 24 scores. For the same participant, a particular melody was only used once in each of the four conditions. Four such trials, where the same score was used, were always performed consecutively. To minimize task order effects, four different task orders were used in different sessions. A necessary constraint on the task order was obviously that *Improvise* had to be performed before *Reproduce*.

MRI Scanning Parameters The imaging parameters for the three-dimensional T1-weighted image were as follows: field of view, 22 cm; echo time, 6 msec; repetition time, 24 msec; flip angle, 358; and voxel size, 0.86 0.86 2 mm. Functional imaging data were recorded as gradient-echo, echo-planar (EPI) T2*-weighted images with blood oxygenation level dependent (BOLD) contrast. Image volumes of the whole brain were built up from 30 continuous axial slices. The following parameter values were used: field of view, 22 cm; echo time, 60 msec; repetition time, 4 sec; flip angle, 908; pixel size, 3.4 3.4 mm; slice thickness, 5.0 mm; matrix size, 64 64. During one session, 122 image volumes were collected continuously. At the beginning of the session, four “dummy” image volumes were scanned, but not saved, to allow for T1 equilibration effects.

Analysis of Behavioral Data The onset time and identity of all keys played during scanning were recorded on the PC. The main

purpose of the behavioral analysis was to determine how accurately participants reproduced a previous Improvise trial in the Reproduce condition. For this purpose, we performed three types of analysis. First, the total number of keys played in each trial were calculated. Paired t tests were employed to analyze differences in this parameter for corresponding trials of Improvise and Reproduce (i.e., trials where the same Figure 1. Examples of a musical template and ornamentations used during improvisation. (A) One of the musical templates presented to the participants. (B) The five most common types of modification of templates used in Improvise and FreeImp. Two bars of the original melody are shown to the left of the double bar line, and the improvised modification to the right. 832 Journal of Cognitive Neuroscience Volume 19, Number 5 musical score was presented). This analysis was performed on all the trials pooled together, as well as separately for the individual participants. Secondly, the same analyses were performed on the total duration of the performance in each trial. For descriptive purposes, number of played keys and duration were calculated also for the FreeImp trials. Finally, we evaluated the structural similarity of the performances in corresponding trials of Improvise and Reproduce. The Levenshtein edit distance (LED) is a measure of the degree of similarity between two arbitrary sequences (Levenshtein, 1966). It is defined as the minimum number of single element deletions, insertions, or substitutions required to transform one of the sequences into the other. For example, the LED between the two sequences F–A–C and F–G is 2 (F–A–C ! F–G–C ! F–G). It can easily be seen that the LED is at least as large as the difference in length between the two sequences, and 0 only in the case of identical sequences. The LED between different melodic structures, that is, the sequences of played keys, was calculated using a standard algorithm (Knuth, 1981) implemented in Matlab 6 (The MathWorks, Inc.). The LED between corresponding Improvise–Reproduce trials was investigated as a measure of the accuracy of the improvisations. The LED between each improvisation and its original template melody was used as a measure of the complexity of the improvisation. All statistical analyses were performed in Statistica (StatSoft, Inc.). Processing and Statistical Analysis of the fMRI Data The fMRI data were analyzed using the SPM99 software package (Wellcome Department of Imaging Neuroscience, London, UK). The scanned brain volumes were realigned to correct for head movements. Subsequently, they were coregistered to each individual's T1-weighted image (Ashburner & Friston, 1997) and normalized to the standard space (Talairach & Tournoux, 1988). Proportional scaling was applied to eliminate the effects of global changes in the signal. The time series were smoothed spatially with an isotropic Gaussian filter of 10 mm full width at half-maximum, and temporally with a Gaussian kernel of width 4 sec. The fMRI data were modeled with the general linear model, where we defined four conditions of interest corresponding to the periods in each epoch when the participants performed the task (the last 28 sec of the 40-sec epochs). We modeled the first 12 sec of each epoch (i.e., the presentation of the task instruction and the preparatory period) as conditions of no interests. The significance of the effects was assessed using onetailed t statistics for every voxel from the brain image, to create statistical parametric maps, which were transformed into Z statistics. Analyses were performed for contrast subtractions of interest within participants, followed by a between-participants random-effects analysis based on summary-statistics of the subtraction images created for each participant. In this way, the interparticipant variance was accounted for, and inferences can be extended to the population from which the participants are drawn. To localize brain regions involved in real-time improvisation and recall of a previous improvisation from memory, respectively, the contrasts Improvise–Reproduce and Reproduce–Improvise were investigated. To exclude the possibility that differences in these conditions reflected a deactivation, the contrasts Improvise–Rest and Reproduce–Rest, respectively, were used as inclusive masks. For both masks, an uncorrected p value of .05 was used. To investigate whether the brain activity seen in Improvise–

Reproduce could reflect reproduction errors, a regression analysis was performed across participants, to test if the parameter estimates for the Improvise–Reproduce contrast correlated with the mean LED between improvisations and reproductions for all trials performed by each participant. In a second between-subject regression analysis, Improvise–Reproduce activity was regressed on the mean LED between the original melodic template and improvisation, in order to localize brain activity related to the generation of more complex improvisations. Brain activity in the Improvise–Reproduce contrast could reflect storage in memory, as participants were required to reproduce the Improvise trials during Reproduce. We therefore investigated which of the activations in Improvise–Reproduce were also seen in the contrast FreeImp–Rest, using a conjunction analysis between these two contrasts. We utilized a “minimum statistic compared to the conjunction null” analysis, as described in Nichols, Brett, Andersson, Wager, and Poline (2005), which can be interpreted as a logical AND operation between the two contrasts. Because only five participants performed the FreeImp condition, the conjunction was analyzed using a fixed-effects model to increase statistical sensitivity. Finally, to investigate differences in activity between FreeImp and Improvise in regions that were involved in improvisation, the contrasts FreeImp–Improvise and Improvise–FreeImp were examined. Small volume corrections for multiple comparisons were employed, with spherical regions of interest (radius 10 mm) centered around the peak coordinates of the activations in Improvise–Reproduce. We report activations that were significant at $p < .05$ according to a False Discovery Rate (FDR) analysis (Genovese, Lazar, & Nichols, 2002). In this analysis, the results are corrected for multiple comparisons and a threshold is set to control the rate of false positives. The threshold of $p < .05$ thus means that, on average, less than 5% of the suprathreshold voxels are not truly active. For the contrast Improvise–Reproduce, no activity was found at this threshold in the presupplementary motor area (pre-SMA). However, a recent study by Lau Bengtsson, Csíkszentmihályi, and Ullén (2004) found the pre-SMA to be the one region where a parametrical relation between brain activity and performance in a free selection task was found. We therefore used a small volume correction within a spherical region of interest (radius 10 mm) in the preSMA, using the coordinate of the peak of activity ($x, y, z = 8, 16, 64$) in Lau et al. as the center of the sphere. Anatomical localizations of the activated regions were determined from an average image of normalized and intensity standardized T1-weighted images from all 11 participants. We used the anatomical terminology of Duvernoy (2000). To localize cerebellar activations, we used the atlas of Schmahmann, Doyon, Toga, Petrides, and Evans (2000).

RESULTS

Descriptive Characteristics of the Improvisations in Improvise and FreeImp

The identity and onset time of all piano keys played during scanning were recorded. Each condition was performed nine times, each time with a different melodic template, by each of the 11 participants, giving a total of 99 trials each of Improvise and Reproduce. During three of these trials (each in a different participant), a temporary mechanical error in the keyboard prevented proper recording of the behavioral data. Ninety-six trials of Improvise and Reproduce are thus included in the analysis below. FreeImp was performed by five subjects. Here, two trials in two different subjects had to be discarded for technical reasons, giving a total of 43 trials included in the analysis. The displayed melodic templates had, on average, 17.0 ± 2.6 (mean \pm SD) notes. For Improvise trials, the total number of played keys was 29.1 ± 9.4 , and the mean duration of the improvisations was 17.8 ± 3.2 sec. The mean LED between the melodic template and improvisation was 20.7 ± 10.6 . The improvisations in FreeImp were slightly more elaborate than in Improvise. They contained a larger number of notes (mean number of played keys 36.4 ± 9.2) than the corresponding performances in Improvise [paired t test: $t(42) = 6.02$; $p = .000$]. The total duration of the FreeImp improvisations was also longer (18.4 ± 3.6 sec) than in Improvise, although this trend did not reach significance [paired t test: $t(42) =$

1.84; $p = .07$]. The LED between FreeImp improvisations and their templates was higher (27.8 ± 9.6) than for Improvise [paired t test: $t(42) = 4.12$; $p = .000$]. During both Improvise and FreeImp, participants always played a modified version of the entire original melodic template, as written, that is, in no cases were only a part of the template or transformed (e.g., retrograde, mirrored) versions of template utilized as a basis for the improvisation. A qualitative analysis of all improvisations revealed that all modifications could be classified into 11 categories (Table 1): (i) Insertion of a fast group of one or more grace notes before a template note; (ii) substitution of a template note for another note; (iii) figuration, that is, expansion of the original template into melodic figures; (iv) insertion of a trill on a template note; (v) filling in, that is, insertion of chromatic or diatonic scales between template notes; (vi) repetitions of template notes; (vii) elimination of template notes; (viii) insertion of figures giving a broken two-part polyphony; (ix) rhythmization of the template; (x) insertion of a tremolo, that is, a trill-like figure between two notes with a larger interval than a second; and finally, (xi) switching of tonality from major to minor. Examples of the five most common types of modification (i–v), which together constitute more than 88% of the modifications in both Improvise and FreeImp, are shown in Figure 1B. The larger number of notes in the FreeImp improvisations was due to a larger mean number of modifications per improvisation [t test: $t(137) = 3.40$; $p = .001$] in FreeImp (7.9 ± 2.5) than in Improvise (6.4 ± 2.2). No differences in the relative frequencies of the 11 different modifications (Table 1) were found between the two conditions [paired t test: $t(10) = 0.000$; $p = 1.0$], nor was the mean number of notes per modification different [t test: $t(134) = 0.30$; $p = .77$] in Improvise (5.3 ± 3.0) and FreeImp (5.5 ± 4.2). Accuracy of the Reproductions Pooling data from all participants, no significant difference [paired t test: $t(95) = 1.58$; $p = .12$] was found Table 1. Modifications of the Melodic Templates Used in Improvise and FreeImp

Improvisation	Modification	n	% of Total	
Improvise	Grace note	247	40.1	
	Substitution	112	18.2	
	Figuration	74	12.0	
	Trill	73	11.9	
	Filling in	38	6.2	
FreeImp	Grace note	157	46.4	
	Substitution	76	22.5	
	Figuration	31	9.2	
	Trill	35	10.4	
	Filling in	9	2.7	
Improvise	Repetition	23	3.7	
	Elimination	9	2.7	
	Two part	12	1.9	
	Rhythmization	10	1.6	
	Tremolo	3	0.5	
FreeImp	Repetition	13	3.8	
	Elimination	3	0.9	
	Two part	1	0.3	
	Rhythmization	1	0.3	
	Tremolo	1	0.3	
Total	616	100	338	100

For each condition, the total number of modifications of a particular type (n), as well its relative frequency (% of total), is shown. 834 Journal of Cognitive Neuroscience Volume 19, Number 5 between the total number of keys played in Improvise and Reproduce trials (29.6 ± 9.8). Similarly, no difference [paired t test: $t(95) = 1.51$; $p = .13$] was found in the total mean duration of Improvise and Reproduce (17.6 ± 3.4 sec) trials. Nor could any significant differences in these variables be found within single participants. The mean number of played keys per trial in Improvise and Reproduce is shown for each participant in Figure 2A. When analyzing all participants individually with repeated paired t tests, no significant differences were found (all Bonferroni-corrected p values $> .20$). Individual data for trial durations are shown in Figure 2B. No significant differences were found in the durations using paired t tests within each participant (corrected p values $> .52$). In terms of overall motor output—number of key strokes and duration of the performances—participants were thus highly consistent in Improvise and Reproduce. To further investigate how well each improvisation was reproduced structurally, we calculated the LED between the key sequences played in corresponding trials of Improvise and Reproduce (see Methods). The mean LED for all trial pairs was 7.5 ± 4.9 . Many of these single key edits were due to minor, and musically irrelevant, differences for instance, in the number of notes included in a trill or other ornament. An example of an Improvise–Reproduce trial pair where the reproduction was of average accuracy (LED 8) is illustrated in Figure 3. The diagrams (Figure 3A, C) show the onset time of each key stroke. The same trials are illustrated in musical notation in panels B and D. The two trials are practically identical in overall conception, and highly similar also in the individual details. In this case, four single edits were due to that fact that one single

ornament (encircled) was forgotten in the Reproduce trial. The remaining single key edits are due to minor differences in the execution of the details of other ornaments. In summary, the participants were able to reproduce their performances in Improvise with remarkable accuracy in the Reproduce condition. To further investigate whether differences in reproduction accuracy influenced the observed brain activity, a participant level regression analysis was performed between mean LED and activity in the Improvise–Reproduce contrast (see below). fMRI Data Brain areas with significantly higher BOLD response during Improvise than during Reproduce are summarized in Table 2 and illustrated in Figure 4. The histograms in Figure 4 show, for those subjects who performed all four conditions, the mean percent signal change in BOLD signal for each condition in peak voxels of the active regions, with the Rest condition as zero. In the frontal lobe, activations were found in the right DLPFC and pre-SMA, and bilaterally in the rostral portion of the dorsal premotor cortex (PMD). Temporal lobe activations were found in the left posterior superior temporal gyrus (STG), close to the temporo-parietal junction, and in the fusiform gyrus. Bilateral occipital activity was found in the middle occipital gyrus. For each peak of activity found in this contrast, we have indicated (Table 2, rightmost column) whether the same region was also activated in a conjunction between Improvise–Reproduce and FreeImp–Rest. This was the case for all activations, except for the peak in the left STG and one of the peaks in the left PMD. However, peaks were found in the close vicinity of these regions (Table 2, footnotes). The durations of the improvisations were variable, and shorter than the 28-sec epoch length (mean duration 17.8 sec; see above). To verify that the observed activations were not confounded with brain activity occurring after the improvisations, we therefore also performed a separate analysis where only the first 16 sec of the improvisations were included. All activations in Table 2 were found also in this analysis. To test whether the activations in Improvise–Reproduce correlated with the accuracy of the reproductions, we regressed single-participant activations in this contrast on the mean LED between improvisations and reproductions in all trials performed by each participant. No significant positive or negative correlations were found. Neither were significant correlations found in the Reproduce–

Figure 2. Behavioral data recorded during the scanning. (A) The mean number of played keys per trial in Improvise and Reproduce for each individual participant. (B) The mean duration of Improvise and Reproduce trials for each participant. In both A and B, error bars indicate standard deviations. Bengtsson, Csíkszentmihályi, and Ullén 835 Improvise contrast at the current threshold (FDR <0.05), or when using a more liberal threshold of FDR <0.2. To localize brain activity related to the complexity of the improvisations, brain activity in Improvise–Reproduce was regressed onto the mean LED between improvisations and the original melody template for each participant. A significant positive relation was found in the pre-SMA (Figure 5). The diagram shows the correlation ($r = .71$; $p = .01$; Pearson Product–Moment Correlation) between BOLD activity in the peak coordinate of the cluster ($x, y, z = 12, 15, 54$) and improvisation complexity. As can be seen, one of the participants produced much more complex improvisations than the rest of the group. When removing this outlier, a positive trend remained ($r = .28$), but did not reach significance ($p = .43$). No activations were significant at $p < .05$ (FDR) in the contrasts FreeImp–Improvise and Improvise–FreeImp. In FreeImp–Improvise, nonsignificant trends were found in the DLPFC ($p = .27$; $t = 2.24$; $x, y, z = 30, 45, 21$) and the middle occipital gyrus ($p = .12$; $t = 2.41$; $x, y, z = 42, 81, 2$). In Improvise–FreeImp, nonsignificant trends were seen in the PMD ($p = .15$; $t = 2.48$; $x, y, z = 24, 9, 60$) and the middle occipital gyrus ($p = .07$; $t = 2.65$; $x, y, z = 33, 78, 27$). In no other regions were voxels found above a threshold of $p = .05$, uncorrected.

DISCUSSION We compared brain activity during on-line improvisation (Improvise) and the reproduction of a previously created improvisation from memory (Reproduce). Three important questions have to be considered when interpreting the Improvise–Reproduce contrast. First, the pianists did

not reproduce their improvisations with perfect accuracy. Does the brain activity in *Improvise–Reproduce* reflect these minor differences in motor output? Several observations speak against this. The number of played keys did not differ between the two tasks. In fact, a nonsignificant trend was found for a larger total motor output in *Reproduce* than in *Improvise*. One could therefore expect brain activity related to differences in motor output to appear in the *Reproduce–Improvise* contrast, but no significant activations were seen in that comparison. Furthermore, the duration (i.e., time on task) of improvisations and corresponding reproductions did not differ. Finally, corresponding trials were highly similar in terms of Figure 3. An example of a typical *Improvise–Reproduce* trial pair. The diagrams (A, C) show the onset time of each key stroke of the performance. The same trials are illustrated in musical notation in panels B and D. One ornament, which was not properly reproduced, is encircled in A and B. 836 *Journal of Cognitive Neuroscience* Volume 19, Number 5 sequential structure, and no correlations were found between an index of structural similarity (LED) and brain activity at the single-participant level. Had the activations reflected motor output differences, one would have expected a higher level of activity in participants with a higher mean LED value, as this implies larger discrepancies between the improvisations and the reproductions. For the same reasons, we consider *Improvise* and *Reproduce* to be essentially equivalent in terms of sensory input (i.e., auditory and somatosensory feedback). Secondly, the improvisations were of variable duration. Could activations in the *Improvise–Reproduce* contrast be confounded with non-task-related brain activity occurring after the performance? Two facts speak against this. First, the same set of activations were seen in the *Improvise–Reproduce* contrast when analyzing only the first 16 sec of the improvisations. Secondly, participants were instructed to rest passively after finishing the performance. Thirdly, because the improvisations had to be reproduced, the *Improvise* condition required both improvisation and storage of the performance in working and long-term memory. To what extent does the neural activity in *Improvise–Reproduce* reflect the latter processes? To evaluate this question, we investigated which of the activated brain areas were also seen in the contrast *FreeImp–Rest*. For the *FreeImp* condition, the participants had been instructed to improvise without memorizing their performance. The fact that the same types of modifications of the template were used with the same relative frequencies in *FreeImp* and *Improvise* suggests that no major differences in improvisatory strategies were used in these two conditions. All major regions active in *Improvise–Reproduce*—the DLPFC, the rostral PMD, the left temporo-parietal region, and the middle occipital gyri—were also active in the conjunction analysis. In summary, we therefore argue that the activity in these brain regions reflects neural processes involved in the generation of new musical material during improvisation. Dorsolateral Prefrontal Cortex A key finding in the present study is that the DLPFC is involved in the generation of musical structures during improvisation. This is of interest because it demonstrates that the DLPFC is involved in the creative aspects of a complex and ecologically relevant behavior, where the free selection of responses is adapted to an overall goal of producing an aesthetically satisfactory end-result. The finding is in line with the many earlier studies that have used simpler model behaviors to investigate the involvement of the DLPFC in free response selection. The DLPFC is consistently more active during motor tasks when movement parameters such as effector (Frith, Friston, Liddle, & Frackowiak, 1991), movement direction or target (Rowe, Stephan, Friston, Frackowiak, & Passingham, 2005; Playford et al., 1992; Deiber et al., 1991), and movement timing (Jahanshahi, Jenkins, Brown, Marsden, Brooks, et al., 1995; Jahanshahi, Jenkins, Brown, Marsden, Passingham, et al., 1995) are freely chosen, as opposed to repetitive or externally determined by a stimulus. Similarly, DLPFC activity is related to free selection in cognitive tasks. This has been shown, for instance, for word generation (Frith et al., 1991; Petersen, Fox, Posner, Nintus, & Raichle, 1988), number generation (Jahanshahi et

al., 2000), word-stem completion (Desmond et al., 1998), and sentence completion (Nathaniel-James & Frith, 2002). It can also be noted that there was a trend for higher DLPFC activity during FreeImp than during Improvise, which could be related to the slightly higher level of complexity (larger number of modifications) of the improvisations in FreeImp.

Table 2. Brain Regions with Significantly Increased BOLD Contrast Signal in Improvise–Reproduce

Brain Region	Side	x	y	z	t Value	Conja
Frontal lobe Middle frontal g. (DLPFC)	R	33	39	27	5.24	+
Superior frontal sulcus (PMD)	L	24	12	48	4.41	b
Superior frontal g. (pre-SMA)	R	9	12	54	2.88	c
Middle frontal g. (PMD)	L	33	3	42	6.14	+
Temporal lobe Posterior STG	L	60	39	15	7.42	d
Fusiform g.	R	45	51	12	4.70	+
Occipital lobe Middle occipital g.	L	36	78	18	4.20	+
	R	39	78	6	4.57	+
	R	39	81	0	4.77	+

a A (+) sign in this column indicates that activity (FDR < 0.05) in this region was also found in a conjunction between (Improvise–Reproduce) and (FreeImp–Rest). b The nearest active voxel in the conjunction was found in the L PMD at 33, 6, 45 (x, y, z). c Significant at FDR < 0.05 after a small volume correction based on an a priori hypothesis, but not in a whole-brain analysis. d The nearest active voxel in the conjunction was found in the inferior parietal cortex immediately above the temporo-parietal junction, at 51, 39, 30 (x, y, z).

Bengtsson, Csíkszentmihályi, and Ullén 837 What are the specific functional roles of the DLPFC in this type of tasks? Part of the activity may relate to attention to the selection of action, rather than free choice per se (Lau et al., 2004; Jueptner et al., 1997). Lau et al. (2004) found that the DLPFC was activated during selection between several possible responses, whether these were externally specified or free. However, other studies have reported a positive relation between the number of available alternatives in a free choice situation and the level of DLPFC activity (Nathaniel-James & Frith, 2002; Desmond et al., 1998), suggesting that the DLPFC is also involved in the selection process. It should be noted that “free” in free-selection tasks typically means pseudorandom. The apparent simplicity of such a task is obviously deceptive (Jahanshahi et al., 1998). To emulate randomness, participants must rely on some strategy to produce an irregular output. One task for the DLPFC is thus presumably to maintain earlier responses in working memory. In this way, different response alternatives can be compared to previous output to avoid regularities. The DLPFC is strongly implicated in working memory for action-relevant information (for a review, see Fuster, 2001), and is important for the continuous comparison of consecutive stimuli (Petrides, 1995). Transcranial magnetic stimulation experiments show that disruption of DLPFC activity during pseudorandom generation of numbers (Jahanshahi et al., 1998) or letters (Jahanshahi & Dirnberger, 1999) tends to increase response regularity (Figure 5). The pre-SMA and improvisation complexity. In the pre-SMA, a positive relation was found between brain activity in the Improvise–Reproduce contrast, and the degree of complexity of the improvisations, operationalized as the LED between improvisation and template. Adjusted fMRI data from the peak voxel of the cluster (the red cross in the activity map; x, y, z = 12, 15, 54) are plotted against mean improvisation complexity for each participant in the graph. Each dot in the plot represents an individual participant. Figure 4. Brain regions active in the Improvise–Reproduce contrast. Activity maps of brain regions with significantly increased BOLD contrast signal are shown for the right dorsolateral prefrontal cortex (DLPFC; slice y = 39), the left superior temporal gyrus (STG; slice x = 60), and the bilateral dorsal premotor cortices (PMD; slices y = 6 and z = 45). The color scale shows t values. R and L denote the left and right sides, respectively. The histograms show mean percent signal change in BOLD signal for each condition in peak voxels of the active regions, with the Rest condition as zero. Error bars show standard error of the mean (SEM). Names of conditions are abbreviated as follows: B = Rest (baseline); I = Improvise; R = Reproduce; F = FreeImp.

838 Journal of Cognitive Neuroscience Volume 19, Number 5 to make the responses more stereotyped. One role of the DLPFC in free selection may thus be to inhibit unwanted, habitual responses. All

these subfunctions of the DLPFC—attention to action, monitoring in working memory, response selection, and suppression of stereotype responses—may be of importance during improvisation. In addition, it appears likely that improvisation, perhaps to a larger degree than attempts at random behavior, relies on the higher, integrative mechanisms of the DLPFC. During *Improvise*, a whole set of freely selected modifications of the original melody must be temporally organized according to a musically meaningful overall plan. A central role for the DLPFC in planning and performance of novel or complex behavioral sequences, including language and thought, is demonstrated by a vast body of neurological and experimental data (for reviews, see Fuster, 2001; Cummings, 1993; Baddeley, 1986; Luria, 1966). Our data are in line with that one central function of the DLPFC during improvisation is supervisory: to maintain and execute an overall plan for the improvisation through top-down influences on the activity, for instance, in subordinate premotor areas. One aspect of this may be “sculpting of the response space” (Frith, 2000), that is, the selection of a set of responses suitable for a particular improvisation. These influences can be mediated by the extensive connections from the DLPFC to the motor system, including the rostral premotor areas (Fuster, 2001; Picard & Strick, 2001). Notably, the DLPFC activation was in the right hemisphere. This is consistent with a number of earlier studies which also found predominantly right-sided activity during divergent tasks (Howard-Jones et al., 2005; Carlsson et al., 2000; Seger et al., 2000; Abdullaev & Posner, 1997). Rostral Premotor Cortices Activity in *Improvise–Reproduce* was also found in rostral premotor areas, mesially in the pre-SMA as well as laterally in the PMD. Our findings fit the general view that the rostral portion of the premotor cortex is involved in cognitive aspects of action (Picard & Strick, 2001). Both the pre-SMA (Johansen-Berg et al., 2004; Lu, Preston, & Strick, 1994; Bates & Goldman-Rakic, 1993) and the rostral PMD (Lu et al., 1994; Barbas & Pandya, 1987) are, unlike caudal premotor areas, interconnected with the DLPFC. The pre-SMA has been implicated in free choice, in particular, when the timing of a response is selected (Jahanshahi, Jenkins, Brown, Marsden, Passingham, et al., 1995). Interestingly, Lau et al. (2004) recently found that not only was the pre-SMA active in free selection but the level of pre-SMA activity also correlated with response time between participants. The finding of a positive relation between pre-SMA activity and the complexity of the improvisations is in line with a role of the pre-SMA in the selection process. This correlation did not remain significant when removing one outlier participant that produced highly complex improvisations. However, because a positive trend was still seen, it seems likely that this reflects a restriction of range in terms of improvisational complexity among the other participants. Our data thus indicate that the pre-SMA is involved in response selection also in more complex divergent tasks such as musical improvisation. The involvement of the pre-SMA in temporal selection is of interest in relation to the consistent finding that this region is active during rhythmic sequence performance (Bengtsson, Ehrsson, Forssberg, & Ullén, 2004, 2005; Lewis, Wing, Pope, Praamstra, & Miall, 2004; Schubotz & von Cramon, 2001; Lutz, Specht, Shah, & Jäncke, 2000; Larsson, Gulya's, & Roland, 1996) as well as during perceptual timing tasks (Macar et al., 2002). One could therefore suggest that the pre-SMA activity during improvisation may be particularly related to decisions about timing and rhythmic patterning. In addition, it seems plausible that demands on temporal processing are higher during improvisation, when generated ornaments have to be fitted into a given metric structure, than during reproduction. The PMD receives a large input from the superior parietal lobule, and plays important roles for visuomotor control, sequencing, and spatially targeted movements (Andersen, Snyder, Bradley, & Xing, 1997; Wise, Boussaoud, Johnson, & Caminiti, 1997). As for the medial wall motor areas, more rostral activations are associated with higher-order, non-movement-related processing (Picard & Strick, 2001). Two findings on the rostral PMD can be mentioned, in particular, in relation to our results. First, the rostral

PMD is implied in response selection in visual choice reaction time tasks (Grafton, Fagg, & Arbib, 1998). Secondly, neurons in this region have been shown to be involved in transforming a series of positional cues kept in working memory, into a sequential motor program of targeted movements (Ohbayashi, Ohki, & Miyashita, 2003). The rostral PMD could be involved in similar operations— response selection based on visual cues, that is, musical notation, and transformation of information held in working memory by the DLPFC and the pre-SMA into movement sequences—during improvisation. The trend for higher PMD activity during *Improvise* than during *FreeImp* could reflect a higher load on working memory in *Improvise*, where the participants had to memorize their performance. Earlier work on movement sequence production has indicated that medial premotor areas are more important for timing, whereas lateral premotor cortex activity is more related to sequencing of the movements in the correct order (Bengtsson et al., 2004; Schubotz & von Cramon, 2001). An interesting possibility is that a similar division of labor holds also during improvisation so that the rostral PMD and the pre-SMA are more involved in the shaping of melodic and rhythmic structures, respectively.

Temporal and Occipital Areas We found activity specifically related to *Improvise* in a portion of the posterior STG, close to the temporo-parietal junction. This region, area Spt (Hickok, Buchsbaum, Humphries, & Muftuler, 2003), has consistently been found active in studies that require auditory–motor integration, such as rhythmic sequence performance (Bengtsson et al., 2004, 2005; Lewis et al., 2004; Jańcke, Loose, Lutz, Specht, & Shah, 2000; Lutz et al., 2000) and vocal rehearsal of words or music (Hickok et al., 2003). It can affect the motor system through connections with inferior frontal regions, via the arcuate fasciculus (Hickok & Poeppel, 2000). We suggest that the area Spt activation in the present study may reflect a larger load on auditory–motor feedback loops during *Improvise*, for example, to adapt the improvisation to ongoing performance. In addition, the posterior superior temporal cortex is involved in auditory working memory of melodic structures (Gaab, Gaser, Zaehle, Jancke, & Schlaug, 2003; Patterson, Uppenkamp, Johnsrude, & Griffiths, 2002; Griffiths, Buchel, Frackowiak, & Patterson, 1998), and may thus be of importance for auditory monitoring of the ongoing performance. Finally, the different modifications of the original template employed in the improvisations are obviously part of a common “vocabulary” of ornaments used in Western art music (see Palmer, 2001). One possibility is that the area Spt is involved in retrieval of such musical structures from long-term memory, in analogy with its role in lexical retrieval in linguistic tasks (Hickok & Poeppel, 2000). A number of small clusters of activity were found in higher-order visual areas in the fusiform and middle occipital gyri. These activations may be due to a more intense visual processing of the musical score when this was used as a basis for improvisations, rather than as a template to recall a previous performance. Notably, two of these regions (right fusiform and left middle occipital gyri) were found to be involved in music reading in another study on the same group of participants (Bengtsson & Ullén, 2006).

Conclusion We have provided evidence that a set of frontal and temporal association areas are specifically involved in the free creation of musical structures during improvisation. We suggest that the DLPFC interacts with the rostral PMD and the pre-SMA in processes of free selection, selective attention, as well as the sequential and temporal organization of the behavior, and with area Spt in the superior temporal cortex for auditory working memory, retrieval of musical standard ornaments from long-term memory, and auditory–motor integration. For the pre-SMA, increased activity related to the generation of more complex improvisations could be demonstrated. We believe this study demonstrates that musical improvisation may be a useful behavior for studies of the neurocognitive processes underlying an ecologically relevant creative behavior. An important next step will be to analyze the neural underpinnings of the cognitive components of improvisation, such as production of melodic and rhythmic structures, and the interaction

between systems for planning, motor attention, response generation, and selection. The brain regions shown to be involved in musical improvisation in the present study are part of a larger set of neural regions active during piano performance (Bengtsson & Ullén, 2006; Parsons, Sergent, Hodges, & Fox, 2005). It would be of interest to examine to what extent these are specifically involved in creative behaviors in other domains. Acknowledgments We thank Lea Forsman, Hans Forssberg, Guy Madison, and Jeanne Nakamura for comments on the manuscript. This work was funded by the Swedish Research Council; the Freemasons in Stockholm Foundation for Children's Welfare, Sweden the Medici II symposia on positive psychology; the Templeton Foundation; and Linnea och Josef Carlssons Stiftelse, Sweden. The present address of S. L. B. is Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, UK. Reprint requests should be sent to Dr. Fredrik Ullén, Stockholm Brain Institute, Neuropediatric Research Unit Q2:07, Department of Women and Child Health, Karolinska Institutet, SE-171 76 Stockholm, Sweden, or via e-mail: Fredrik.Ullen@ki.se.

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CONCEPTUAL AND MOTOR LEARNING IN MUSIC PERFORMANCE Caroline Palmer and Rosalee K. Meyer Ohio State University Abstract—Are the mental plans for action abstract or specified in terms of the movements with which they are produced? We report motor independence for expert music performance but not for novice performance in a transfer-of-learning task. Skilled adult pianists practiced musical pieces and transferred to

new pieces with the same or different motor (hand and finger) requirements and conceptual (melodic) relations. Greatest transfer in sequence duration was observed when the same conceptual relations were retained from training to transfer, regardless of motor movements. In a second experiment, novice child pianists performed the same task. More experienced child pianists showed transfer on both the motor and the conceptual dimensions; the least experienced child pianists demonstrated transfer only to sequences with identical motor and conceptual dimensions. These findings suggest that mental plans for action become independent of the required movements only at advanced skill levels. A long-standing question in motor learning is whether mental plans for action are specified in terms of the movements with which they are produced (cf. Bartlett, 1948). Although this question is addressed most often in the domain of skilled behavior, the answer may differ for early stages of motor learning (cf. Adams, 1987). Motor learning refers to changes—mental or physical—associated with practice or experience that provide the capability for producing skilled actions. We report here cognitive changes that occur for novice and experienced musicians as they learn to perform unfamiliar music. Music performance is a highly complex skill on many dimensions, including its conceptual structure (such as harmony and rhythm) and its motor requirements (such as hand and finger movements). We report motor independence in mental plans for music performances by expert musicians but not by novice musicians. Transfer-of-learning tasks, in which movement control is learned in one situation and transferred to another, often provide insight into the contents of mental plans for actions (Schmidt & Young, 1987). Transfer of learning refers to a change in response on a novel task as a function of experience on a prior task. Experiments with keypressing tasks have demonstrated transfer of learning between sequences that require different arm or finger movements, suggesting that abstract representations underlie sequence production (Cohen, Ivry, & Keele, 1990; Keele, Cohen, & Ivry, 1990). MacKay and Bowman (1969) demonstrated transfer between two languages in sentence production; bilingual speakers practiced reading a sentence aloud in one language (English or German) under speeded conditions, and then produced either a translation (same meaning) or a new sentence (different meaning) in another language. Only the translations were produced as quickly as the original practiced sentences, indicating that speakers' representations were abstracted from the particular articulatory movements used to produce the two languages. Overall, these findings suggest that mental plans for action are independent of the necessary motor movements, at least at fairly skilled levels of performance. However, several factors limit generalizations to domains such as music performance. First, novel (unfamiliar) tasks are often the object of experimental study, and generalizations to well-learned naturalistic tasks such as performing music may not hold. Second, music performance has different motor and structural requirements from other production domains. Hand and finger movements in piano performance frequently reach temporal limits under natural speeded conditions, and these movements are often correlated with abstract conceptual structures, such as how hand positions on a piano keyboard achieve particular harmonies (chords). Furthermore, pianists' hand and finger movements generate expressive nuances in timing and intensity that increasingly reflect the structure of a musical sequence the more familiar or well-learned the sequence (cf. Gabrielsson, 1999; Palmer, 1997). Thus, mental plans may reflect motor movements even more with increased skill because movements in music performance often correlate with abstract structural relationships. Piano performance offers an excellent domain in which to contrast motor-specific and motor-independent representations in sequence production, because different melodies (pitch sequences) can be produced with the same sequence of hand and finger movements, and, conversely, the same melody can be produced with different hand and finger movements (e.g., by switching between hands). We used a transfer-of-learning paradigm to document how learning to perform one musical melody

affects pianists' ability to perform another melody. Learning effects were measured under speeded performance conditions during transfer to melodies that contained the same or different motor requirements (hand and finger assignments) and the same or different conceptual requirements (pitch sequence). Transfer of learning between melodies that share or differ in motor movements and pitch structure should be informative about the role of motor-specific information in representations for sequence production. We also investigated how sequence learning differs for novice and advanced performers. Although few studies of motor learning have addressed how mental plans for action change with expertise, a common belief is that independence from motor requirements is not acquired until advanced skill levels. In fact, teaching methods for beginner pianists often focus on hand and finger positions, whereas advanced methods focus more on conceptual or interpretive aspects of musical structure. We tested changes in the role of motor variables in sequence learning by contrasting transfer-of-learning effects in skilled adult pianists and novice child pianists, who performed the same task of learning novel melodies.

EXPERIMENT 1: SKILLED ADULT PIANISTS

The first experiment investigated the nature of sequence learning in skilled music performance. Skilled adult performers practiced a

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short musical sequence under speeded conditions and then performed a second sequence with the same or different motor (hand and finger) assignments and the same or different conceptual relations (pitch sequence). Evidence for whether sequence learning was based on motor or conceptual aspects was measured by the amount of transfer (change in total sequence duration) from the final training trial to the transfer trials. We predicted that greatest transfer would occur when both motor and conceptual factors were the same as in training trials, and no transfer would occur when both motor and conceptual factors were different from what they were in the training trials. Most important, we predicted positive transfer would occur when conceptual aspects were retained from training, regardless of whether the motor assignments were retained.

Method

Participants

Sixteen adult pianists from the Columbus, Ohio, music community participated. Participants had a mean age of 26 years and a mean of 18 years' piano performing experience (range of 10–38 years). Informed consent was obtained.

Materials and apparatus

Simple melodies that could be performed by beginners (Experiment 2) as well as experts (Experiment 1) were created. We constructed four sets of eight isochronous (constant-duration) sequences, each containing 12 quarter-note pitches notated in 4/4 time signature. Each stimulus set was composed in a different musical key (half were major and half were minor) so it would be distinguishable melodically. Four sequences in each set were notated in the treble clef. Two of these sequences were notated for the right hand and fingers, and two were notated for the left hand and fingers. In addition, two were based on one pitch sequence (melody), and two were based on a different pitch sequence. The remaining four sequences in each set were identical in all motor and pitch information, but were notated in the bass clef (in a different octave), to be visually distinguishable. Thus, each set of eight sequences contained all combinations of clef (treble, bass), hand and fingers (right, left), and pitch sequences (melody). Participants performed on a computer-monitored Yamaha MX100 upright acoustic piano (2-ms resolution). Computer software determined key-press onsets and offsets and identified pitch errors by comparing the performance with the information in the notated musical score.

Design and procedure

The experiment used a 2×2 within-subjects design with independent variables of motor assignments (same or different hand and fingers, called *M_{same}* and *M_{diff}*, respectively) and conceptual relationships (same or different pitch

sequence, called Csame and Cdiff, respectively). The dependent variables were total sequence duration (onset of last tone minus onset of first tone) and percentage of pitch errors per sequence. The four conditions were ordered within an experimental session according to a Latin square design, with a different stimulus set assigned to each condition for each subject. Each stimulus appeared equally often in each condition across subjects. The following variables were balanced across subjects and conditions: whether the musical sequence was performed by the left or right hand, whether the sequence was notated in the treble or bass clef, and which stimulus set was assigned to each condition. Furthermore, hand and finger assignments for melodies were counterbalanced across both conditions and performers. Participants completed the following procedure for each condition: They first performed a musical sequence slowly with a metronome (m.m. 4 69 bpm) until no errors were made (to ensure that any errors under speeded conditions were not due to perceptual or reading errors); all participants performed the sequence without any errors within three pretraining trials. Then participants performed the same sequence 10 times, as quickly as possible. They then performed one of four related transfer sequences from the same stimulus set. Examples of training and transfer stimuli for the four conditions are shown in Figure 1. Depending on the condition, this transfer sequence differed from the training sequence in conceptual (melody) relations only (Cdiff-Msame), in motor (hand and finger) assignments only (CsameMdiff), in both conceptual relations and motor assignments (CdiffMdiff), or in neither conceptual relations nor motor assignments (Csame-Msame; this condition yielded the original melody). The transfer sequences were distinguishable from the training sequences because they were notated in a different octave and clef. Participants performed the transfer sequence four times as quickly as possible. This procedure was repeated for each condition with sequences from a new stimulus set. Fig. 1. Example of musical sequences used in the training and transfer conditions. The numbers indicate the fingering to be used, with 1 representing the thumb. Labels for the transfer conditions indicate whether the conceptual relations and motor assignments were the same as in the training sequence: Csame 4 same conceptual relations; Cdiff 4 different conceptual relations; Msame 4 same motor assignments; Mdiff 4 different motor assignments.

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Results Sequence duration Analyses of variance on the difference between the sequence duration of the last training trial (Trial 10) and the mean duration of the transfer trials (11–14) indicated significant effects of the conceptual condition, $F(1, 15) = 16.4$, $p < .01$, but not the motor condition. As shown in Figure 2, transfer was greatest when the conceptual melodic relationships were retained across sequences, regardless of whether the hand and finger movements remained the same. Planned comparisons among all pairs of conditions supported these findings; the only significant differences were between the Csame-Msame and Cdiff-Msame conditions and between the Csame-Mdiff and CdiffMdiff conditions ($p < .05$). “Perfect” transfer (no significant change in sequence duration between training and transfer) was obtained for the Csame-Msame condition only. There were no significant effects on amount of transfer due to pianists’ musical experience or training, handedness, or hand assignments at transfer. Errors The percentages of pitch errors showed no significant differences between training and transfer trials; performance was close to perfect in all conditions (mean error 4 3.0%). Thus, differences in sequence duration across conditions were not simply a function of a speed-accuracy trade-off.

EXPERIMENT 2: NOVICE CHILD PIANISTS Experiment 2 investigated the nature of sequence learning for novice child pianists, using the same transfer-of-learning paradigm as in Experiment 1. Although skilled pianists’ representations for musical sequences are abstracted from the necessary hand and finger movements, novices may not yet have separated the abstract pitch relations from the

motor movements that give rise to them. In Experiment 2, novice child pianists performed simplified musical sequences similar to those used in Experiment 1, under the same speeded conditions. As in Experiment 1, we predicted positive transfer when conceptual factors were the same from training to transfer. However, we also predicted positive transfer when motor (hand and finger) assignments were retained from training to transfer.

Method
Participants Sixteen child pianists (mean age 4 11.2 years) from the Columbus, Ohio, community participated. The pianists had a mean of 4.7 years of piano performing experience. The 8 pianists with the least amount of performing experience had a mean age of 10.5 years and a mean of 3.6 years' piano experience (range: 3–4). The 8 pianists with the most performing experience had a mean age of 11.9 years and a mean of 5.8 years' piano experience (range: 5–7). Parental consent was obtained in advance for all children.

Materials and apparatus The stimulus materials from Experiment 1 were used; some were simplified (they were transposed to musical keys that contained fewer 1. Although performance on the first transfer trial was slower than performance on the first training trial in some conditions, this difference is probably an effect of practice gained during the pretraining trial (trials) at the slow tempo (to eliminate perceptual or reading errors), rather than a true negative transfer.

Fig. 2. Mean sequence durations in training and transfer trials for skilled adult pianists in Experiment 1. Labels for the transfer conditions indicate whether the conceptual relations and motor assignments were the same as in the training sequence: Csame 4 same conceptual relations; Cdiff 4 different conceptual relations; Msame 4 same motor assignments; Mdiff 4 different motor assignments.

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black keys or accidentals). The same apparatus was used as in Experiment 1.

Procedure The procedure was similar to that of Experiment 1, except that the child participants played the first musical sequence at a slow rate without a metronome, until they could perform it without any errors (by the third trial). In addition, the children were told explicitly about the sequence to be performed (its key signature and starting hand position). These changes were introduced to make the task easier for the children.

Total sequence duration and percentage of pitch errors were measured as before.

Results
Sequence duration As shown in Figure 3, transfer was significant on both the motor and the conceptual dimensions. An analysis of variance on the difference between the sequence duration for the last training trial (10) and the mean duration of the transfer trials (11–14) indicated both a significant effect of motor condition, $F(1, 15) = 4.65, p < .05$, and a significant effect of conceptual condition, $F(1, 15) = 7.68, p < .05$. Planned comparisons supported these findings: There were significant differences between the Csame-Msame and Csame-Mdiff conditions and between the Csame-Msame and Cdiff-Msame conditions ($p < .05$). Thus, performance improved with both motor and conceptual similarity between musical sequences. “Perfect” transfer (no significant change in sequence duration from training to transfer) was obtained for the Csame-Msame condition only.

Errors Percentages of pitch errors indicated performance was close to perfect (mean 4 2.6%), with no differences across conditions. Thus, differences in sequence duration across conditions were not simply a function of a speed-accuracy trade-off.

Effects of musical experience Although there were no effects of children's handedness alone or hand assignment at transfer, amount of piano experience (years of performing piano) did influence transfer in children's performances. Total sequence durations for the 8 least experienced pianists (3–4 years' piano experience) and 8 most experienced pianists (5–7 years) are shown in Figure 4. Differences between sequence duration on the last training trial and mean duration on the transfer trials indicated both a significant effect of motor condition and a significant effect of conceptual condition ($p < .05$) for the most experienced child pianists. In contrast, neither dimension had a significant effect for the least experienced children; transfer was obtained only for the same melody,

produced with the same hand and finger movements. (The 95% confidence intervals indicated significant differences only between the Csame-Msame condition and all remaining conditions, $p < .05$.) The least experienced child pianists showed transfer of learning only to a particular instance of a sequence (Fig. 4a), whereas more experienced child pianists showed transfer to new sequences that were similar on either motor or conceptual dimensions (Fig. 4b).

GENERAL DISCUSSION

Musicians' transfer of learning across novel melodies indicates that as skill increases, mental representations for performance become Fig. 3. Mean sequence durations in training and transfer trials for novice child pianists in Experiment 2. Labels for the transfer conditions indicate whether the conceptual relations and motor assignments were the same as in the training sequence: Csame 4 same conceptual relations; Cdiff 4 different conceptual relations; Msame 4 same motor assignments; Mdiff 4 different motor assignments.

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dissociated from the movements required to produce a musical sequence; advanced performers' mental plans are based on abstract, conceptual pitch relations. These findings are consistent with evidence that conceptual (meaning) dimensions dominate articulatory movements in transfer tasks with speech (MacKay, 1987; MacKay & Bowman, 1969), and that conceptual (melodic) dimensions are independent of hand and finger movements in error patterns in piano performance (Palmer & van de Sande, 1993). In contrast to the results for skilled adults, the results for novice children showed transfer of learning that reflected the movements as much as the abstract pitch relationships. Thus, results of transfer tasks may not generalize from skilled to novice performers; compared with novice performers, skilled performers demonstrate more dissociation between abstract sequence dimensions and movements, and a lower weighting of the movement dimension. Differences in sequence representations were found even within Fig. 4. Mean sequence durations of (a) the least experienced and (b) most experienced child pianists in Experiment 2. Labels for the transfer conditions indicate whether the conceptual relations and motor assignments were the same as in the training sequence: Csame 4 same conceptual relations; Cdiff 4 different conceptual relations; Msame 4 same motor assignments; Mdiff 4 different motor assignments.

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novice children's performances. More experienced child pianists (5–7 years of piano experience) showed both motor and conceptual transfer, but less experienced pianists (3–4 years) showed instance-based learning only (i.e., transfer occurred for the same musical sequence only). These findings suggest that the motor and conceptual dimensions become differentiated within a sequence representation as learning to perform progresses; only then are similarities across instances recognized in terms of those dimensions, resulting in transfer between different sequences. These findings are analogous to predictions of perceptual learning theories proposing that features of stimuli become discriminable as responses to those stimuli are learned (see Adams, 1987). Although some change in sequence representation may be maturational (the more experienced children were 1 year older on average than the less experienced children), age is not likely to be a main determinant, because differences were larger qualitatively between less and more experienced children than between children and adults. Findings of greatest change at early stages of learning are also consistent with the power law of practice (Newell & Rosenbloom, 1981), and with other music performance studies that indicate cognitive changes are largest at early stages of skill acquisition, independent of age of acquisition (Palmer & Drake, 1997). Two issues raised by these findings include whether the motor transfer reflected hand movements, finger movements, or both and whether the task demands were too simple motorically for skilled pianists. The hand and finger movements were altered simultaneously

in this study, to allow for stimulus melodies with simple fingerings that child novices could perform. Although further study is required to separate the role of hand and finger movements, three factors suggest that the motor transfer reflected primarily finger (not hand) movements: The amount of transfer was not affected by the hand used in the training conditions, by differences between hands within each transfer condition, or by the handedness of the pianists, for the experts or the novices. The second issue, that the task may have been simpler motorically for experts than for novices and therefore allowed more room for motor learning by novices, may account for the lack of motor effects in experts' performances. However, the novices' simplified musical sequences led to the same low error rates (2–3%) as the sequences performed by the skilled performers, suggesting that the task was of equivalent difficulty for the two groups. Extensions of this task to more complex music are needed. Most important, these findings extend definitions of motor skills that combine cognitive and motor functions (Adams, 1987; Bartlett, 1948), indicating that mental plans for behaviors such as music performance become increasingly abstract and decreasingly motoric as skill increases. In contrast to previous transfer studies of motor learning that relied primarily on simple materials or unfamiliar tasks, studies of music performance utilize a naturalistic task that reflects complex stimulus structure. This fact, combined with the equivalence of task difficulty observed for the children and adults, offers compelling grounds for generalization of these findings to other motor domains. Finally, the greatest representational change in sequence learning was observed at relatively inexperienced skill levels. As Adams (1987) pointed out, investigators should have only a passing interest in behavior at its (highly skilled) asymptote; a scientific understanding of motor skills must be concerned with all levels of skill acquisition. Acknowledgments—This research was supported by Grant R01-45764 from the National Institute of Mental Health to the first author. We thank Neal Johnson, Isabelle Peretz, Peter Pfordresher, and an anonymous reviewer for comments and Danielle Brink for assistance with the project.

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Neuroscience and Biobehavioral Reviews 51 (2015) 108–117 Contents lists available at ScienceDirect Neuroscience and Biobehavioral Reviews journal homepage: www.elsevier.com/locate/neubiorev Review The neuroscience of musical improvisation Roger E. Beaty* University of North Carolina at Greensboro, United States a r t i c l e i n f o

Article history: Received 10 June 2014 Received in revised form 5 January 2015 Accepted 8 January 2015 Available online 16 January 2015 Keywords: Creativity Expertise Music Improvisation Premotor fMRI a b s t r a c t Researchers have recently begun to examine the neural basis of musical improvisation, one of the most complex forms of creative behavior. The emerging field of improvisation neuroscience has implications not only for the study of artistic expertise, but also for understanding the neural underpinnings of domain-general processes such as motor control and language production. This review synthesizes functional magnetic resonance imaging (fMRI) studies of musical improvisation, including vocal and instrumental improvisation, with samples of jazz pianists, classical musicians, freestyle rap artists, and non-musicians. A network of prefrontal brain regions commonly linked to improvisatory behavior is highlighted, including the pre-supplementary motor area, medial prefrontal cortex, inferior frontal gyrus, dorsolateral prefrontal cortex, and dorsal premotor cortex. Activation of premotor and lateral prefrontal regions suggests that a seemingly unconstrained behavior may actually benefit from motor planning and cognitive control. Yet activation of cortical midline regions points to a role of spontaneous cognition characteristic of the default network. Together, such results may reflect cooperation between large-scale brain networks associated with cognitive control and spontaneous thought. The improvisation literature is integrated with Pressing's theoretical model, and discussed within the broader context of research on the brain basis of creative cognition. © 2015 Elsevier Ltd. All rights reserved. Contents 1.

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115 * Correspondence to: Department of Psychology, P.O.Box 26170, University of North Carolina at Greensboro, Greensboro, NC 27402-6170, United States. Tel.: +1 7174976365. E-mail address: rebeaty@uncg.edu <http://dx.doi.org/10.1016/j.neubiorev.2015.01.004> 0149-7634/© 2015 Elsevier Ltd. All rights reserved. R.E. Beaty / Neuroscience and Biobehavioral Reviews 51 (2015) 108–117 109

1. Introduction

Improvisation is one of the most complex forms of creative behavior. The improvising musician faces the unique challenge of managing several simultaneous processes in real-time — generating and evaluating melodic and rhythmic sequences, coordinating performance with other musicians in an ensemble, and executing elaborate fine-motor movements—all with the overall goal of creating esthetically appealing music. Other forms of artistic performance, while similarly demanding, do not require such spontaneous creativity. The question of how musicians improvise is relevant not only to the psychology of music, it also has implications for the psychology of creativity, as understanding the nature of creativity at a high level of skilled performance may shed light on domain-general processes underlying creative cognition. Improvisation research may also inform basic cognitive neuroscience because it provides a unique look at how acquired expertise shapes brain structure and function. An increasing number of studies are employing neuroimaging methods to explore the brain basis of spontaneous musical composition, using samples of jazz pianists, classical musicians, freestyle rap artists, and non-musicians. Much of this research has focused on understanding the extent to which brain regions associated with executive control mechanisms underlie improvised behavior. Does improvisation rely on the musician’s ability to control the creative process, or rather on his or her ability to “let go” of control and allow spontaneous processes to unfold? This review examines the issue of cognitive control in creative thought with the overarching goal of understanding the cognitive and neural underpinnings of musical improvisation.

1.1. Pressing’s model of improvisation

Perhaps the most influential model of musical improvisation was developed by Pressing (1988, 1998). Following in the literature on expert performance (Ericsson et al., 1993), Pressing’s theory is grounded in the notion that improvisation is an acquired skill that requires a substantial amount of training to achieve expertise. A large body of research in a range of domains suggests that expertise is achieved through deliberate practice, an individually tailored regimen of intensive training typically undertaken with the guidance of an expert instructor (Ericsson et al., 1993). According to the deliberate practice view, eminence in a domain is rarely achieved without thousands of hours of deliberate practice: Ericsson and colleagues have repeatedly demonstrated that experts typically engage in 10,000 h of deliberate practice over the course of ten years before achieving eminence in their field (i.e., the “10-year rule”; Simon and Chase, 1973). Recently, however, researchers have emphasized the role of general cognitive abilities (e.g., working memory capacity; Meinz and Hambrick, 2010) and genetic predispositions (Ericsson, 2013; Tucker and Collins, 2012) in explaining expert performance, thus providing support for the notion that practice is “necessary but not sufficient” for high-level performance (Hambrick et al., 2014; Hambrick and Meinz, 2011). Domain-specific expertise seems especially relevant to musical improvisation. In addition to the physical and psychological constraints common to other domains of skilled performance, jazz musicians must perform under extraordinary temporal constraints. Improvising requires the simultaneous execution of several processes in

real-time, including sensory and perceptual encoding, motor control, performance monitoring, and memory retrieval, among others (Pressing, 1988). Deliberate practice automates some of these processes, freeing attentional resources for other higherorder processes (e.g., generating and evaluating musical ideas). In the absence of such improvisational fluency, the improviser will have difficulty effectively interacting with other members of an ensemble and exerting control over the development of his or her performance. According to Pressing's model, improvisational expertise involves the interplay between referent processes and a domainspecific knowledge base. Referents consist of cognitive, perceptual, or emotional processes; the knowledge base consists of hierarchical knowledge structures stored in long-term memory (Pressing, 1988). Pressing described referents as a series of well-rehearsed retrieval cues that are deployed during performance, minimizing processing demands and guiding idea generation. Referents interact with procedural and declarative information stored in a domain-specific knowledge base. Through deliberate practice, musicians build a database of generalized motor programs, which can be fluently accessed and executed during performance. Another component of Pressing's model is perceptual feedback and error correction. These processes allow the improviser to minimize the distance between intended and actual performance (Pressing, 1988, 1998). Pressing distinguishes between short-term (ongoing motor movements) and long-term (decision making and response selection) feedback—both of which are essential for improvisational fluency. In contrast to “open-loop” theories of skilled performance, which consist of a simple input, processing, and output procedure, Pressing advances a “closed loop” model, which extends open-loop models by including feedback integration within the system. Ongoing performance is thus monitored by comparing actual output with intended output, and future performance is adjusted accordingly. Pressing (1988) conceptualized improvisation as a series of generative and evaluative processes. Although these processes involve some level of cognitive control and conscious monitoring, Pressing emphasized the role of automatized motor processes and routines (e.g., well-rehearsed action sequences). Because of the high demands on information processing and decision-making, Pressing argued that improvisational fluency relies on automatized processes that require minimal conscious attention. The extent to which creative thought relies upon such top-down and bottomup processes remains a point of debate in the literature on musical improvisation as well as in the literature on domain-general creative cognition (cf. Abraham, 2014; Beaty et al., 2014c; Jung et al., 2013; McMillan et al., 2013; Mok, 2014; Sowden et al., 2014).

1.2. Domain-general creative cognition

The study of musical improvisation provides an opportunity to investigate creativity at a high level of skilled performance. Although improvisation research has traditionally been restricted to the field of musicology, it is also of growing interest to researchers in the field of creativity science. Several literature reviews and meta-analyses on the neuroscience of creativity include studies on musical improvisation (e.g., Dietrich and Kanso, 2010; Gonen-Yaacovi et al., 2013). Moreover, results from behavioral and neurophysiological research suggest that improvisation taps domain-general processes such as divergent thinking (Beaty et al., 2013) and cognitive flexibility (deManzano and Ullén, 2012b). The cognitive and neural basis of creative thought has been a topic of increasing empirical interest. Much of this work has employed divergent thinking tasks, the most common of which is the alternate uses task. Such tasks require the generation of novel uses for everyday objects (e.g., a brick), and they are typically scored in terms of fluency (the number of ideas) and originality (the creative quality of ideas). A growing body of evidence suggests that individual differences in divergent thinking reflect a domaingeneral creative ability: performance on divergent thinking tasks has been shown to predict both past and future creative achievements (Jauk et al., 2014; Plucker, 1999; Torrance, 1988). Moreover, a recent study found that divergent thinking ability in jazz

Biobehavioral Reviews 51 (2015) 108–117 Table 1 Summary of methods used to study improvisation with fMRI. Study Year # of subjects Type of musician Contrast Response type

Bengtsson et al. 2007 11 Classically-trained pianists (graduate) Improvise > Memory retrieval MRI-compatible keyboard (12 keys) Berkowitz and Ansari 2008 13 Classically-trained pianists (undergraduate) Improvise melody > Improvise rhythm Conventional MRI response box (5 buttons) Berkowitz and Ansari 2010 26 Classically-trained pianists & non-musicians (undergraduate) Between-subjects design Conventional MRI response box (5 buttons) de Manzano and Ullén 2012a 17 Classically-trained pianists (undergraduate) Improvise melody > Improvise rhythm MRI-compatible keyboard (12 keys) de Manzano and Ullén 2012b 18 Classically-trained pianists (undergraduate) Improvise > Random motor generation MRI-compatible keyboard (12 keys) Donnay et al. 2014 11 Jazz musicians (professional) Improvise > Memory retrieval MRI-compatible keyboard (35 keys) Limb and Braun 2008 6 Jazz musicians (professional) Improvise > Memory retrieval MRI-compatible keyboard (35 keys) Liu et al. 2012 12 Freestyle rap musicians (professional) Improvise > Memory retrieval Optical microphone Pinho et al. 2014 39 Pianists with various levels of improvisational expertise Improvise > Rest MRI-compatible keyboard (12 keys) students predicted expert ratings of improvisational performance, controlling for cumulative lifetime practice hours (Beaty et al., 2013).

Researchers have long conceptualized creative cognition as an associative process that passively unfolds in long-term memory (Mednick, 1962). In general, such work suggests that creative ideas largely result from the spreading activation of concepts in semantic networks, and that individual differences in creative ability result from variation in the structural organization of semantic memory. More recently, researchers have explored the cognitive processes involved in divergent thinking, the ability to generate several novel solutions to open-ended problems. Behavioral (Barr et al., 2014; Beaty and Silvia, 2012, 2013; Benedek et al., 2014c; Lee and Theriault, 2013; Nusbaum and Silvia, 2011; Nusbaum et al., 2014; Silvia et al., 2013) and neurophysiological (Beaty et al., 2014a,b; Benedek et al., 2014; Fink and Benedek, 2014; Fink et al., 2009; Gonen-Yaacovi et al., 2013) research suggests that higher-order cognitive processes underlie creative cognition, such as controlled memory retrieval, pre-potent response inhibition, fluid intelligence, and working memory capacity. Such processes are hypothesized to support creative thought by providing the executive control needed to manage complex search processes and inhibit salient conceptual information that can interfere with idea generation (Beaty and Silvia, 2012). Recent behavioral and neuroimaging research suggests that musical improvisation may also recruit domain-general processes (Beaty et al., 2013; de Manzano and Ullén, 2012b). Although improvisational expertise, like any other acquired skill, is undoubtedly a function of domain-specific training, there is evidence to suggest that divergent thinking and domain-general mental flexibility play an important role. A growing literature provides support for the notion that creative cognition recruits brain regions linked with executive processes (e.g., strategic memory retrieval and prepotent response inhibition). Nevertheless, the role of executive processes in creative thought remains a point of contention in both the general creativity literature and the literature on musical improvisation.

1.3. Organization of the review

The following review synthesizes neuroimaging research on musical improvisation. Table 1 summarizes the studies included in the review; Figs. 1 and 2 depict activation foci resulting from positive task contrasts in select fMRI studies of improvisation. Pressing's (1988) theoretical model of improvisation is used as a guiding framework for interpreting the brain imaging literature. The literature is also framed within the ongoing debate on whether creativity arises from controlled cognitive processes. Special attention is given to Fig. 1. Visualization of activation foci reported in select studies of improvisation. Note: Activation foci and Brodmann area borders were overlaid on an inflated brain using the Connectome Workbench. Highlighted regions indicate areas with activation reported in at

least two of the seven studies included in the figure. For clarity, only positive activation foci are displayed. Studies that report only deactivations (Berkowitz and Ansari, 2010) and only functional connectivity results (Pinho et al., 2014) were not included. R.E. Beaty / Neuroscience and Biobehavioral Reviews 51 (2015) 108–117 111 Fig. 2. Visualization of cerebellar activation foci reported in select studies of improvisation. Note: Activation foci are overlaid on an inflated cerebellum using the Connectome Workbench. A posterior view of the cerebellum is depicted.

given to neuroimaging research on domain-general creativity, in light of recent evidence pointing to an overlap between general creativity and musical improvisation. The review has three broad goals: (1) to synthesize the improvisation neuroscience literature, (2) to provide a conceptual framework for interpreting brain imaging results on improvisation, and (3) to integrate these findings with the literature on domain-general creative thought. A variety of experimental approaches and participant samples have been employed to study improvisation (see Table 1). Several notable differences in task design are apparent in the literature: while some studies contrasted improvisation with memory retrieval (Bengtsson et al., 2007; Limb and Braun, 2008), others contrasted specific modes of improvisation, such as melodic and rhythmic (Berkowitz and Ansari, 2008, 2010; de Manzano and Ullén, 2012a). Moreover, some researchers have been interested in analyzing the effects of musical expertise (e.g., Berkowitz and Ansari, 2008; Pinho et al., 2014) and collaboration (Donnay et al., 2014) on brain activity during improvisation. Such methodological differences are important to consider when comparing results across studies. The review is organized by the main experimental paradigms used to study improvisation. I begin by summarizing the methods and results of studies within each paradigm (e.g., improvisation vs. memory retrieval), noting similarities and differences within and between task paradigms. I then draw some parallels between the improvisation literature and neuroimaging research on domain-general cognitive and creative abilities. In the Discussion, I highlight some emerging trends and conflicting results in improvisation research, focusing on methodological variability as a possible explanation for discrepant findings. Finally, I conclude with some potential directions for future research.

2. Experimental methods and results

2.1. Improvisation and memory retrieval

A common approach in the improvisation literature is to contrast improvisation with memory retrieval. Such designs allow researchers to identify brain regions involved in the spontaneous composition of novel melodic sequences, while controlling for the influence of simply recalling previously performed sequences from memory. Limb and Braun (2008) conducted one of the earliest studies that used this approach. Professional jazz musicians were asked to memorize a novel melody before the study. The experimental paradigm involved performing musical sequences on an MRI-compatible keyboard while a pre-recorded jazz rhythm section played through headphones in the scanner. Participants were cued to perform the memorized melody, freely improvise over the pre-recorded rhythm, play a one-octave scale, or improvise. Compared to memory retrieval, improvisation was related to activation of a distributed network of brain regions, including the left inferior frontal gyrus (IFG), anterior cingulate cortex (ACC), and the medial prefrontal cortex (MPFC), among several others. Interestingly, the authors reported widespread deactivation of regions within the frontal lobes, including the lateral orbitofrontal cortex (LOFC) and the dorsolateral prefrontal cortex (DLPFC). DLPFC deactivation was interpreted as reflecting a suspension of inhibitory or conscious monitoring processes, while MPFC activity was thought to reflect self-generated, stimulus independent cognitive processes. A similar experimental approach was employed by Bengtsson et al. (2007). However, this study differed from Limb and Braun (2008) in terms of the memory retrieval condition employed: instead of requiring participants to recall a single, overlearned melodic sequence, Bengtsson et al. asked participants to retrieve self-generated melodies that were previously improvised in the scanner. In addition, improvisation was constrained to

modifying simple, eight-bar melodic sequences presented, whereas other studies permitted largely unconstrained improvisation (e.g., Donnay et al., 2014; Limb and Braun, 2008; Liu et al., 2012). Bengtsson and colleagues reported improvisation-related activity in several prefrontal regions, including the DLPFC, right pre-SMA, and bilateral dorsal premotor cortex (PMD). The authors suggest that such activity reflects increased demands on selective retrieval and inhibitory mechanisms, as improvisation involves selecting responses among a set of competing alternatives; prefrontal regions may also be involved in maintaining higher-order generative strategies (cf. Pressing, 1998). Thus, in contrast to Limb and Braun (2008), Bengtsson et al. suggest that improvisation places greater demands on cognitive and motor control systems. Researchers have also been interested in exploring the neural correlates of vocal improvisation (e.g., Brown et al., 2006; Liu et al., 2012). Liu and colleagues recruited professional freestyle rap artists to vocally improvise during functional imaging. The authors used a memory retrieval task as a baseline to contrast with improvisation. Similar to the experimental designs of Limb and Braun (2008), participants recited the lyrics from a prerecorded audio sample composed by the authors, or they spontaneously improvised lyrics, using the same instrumental recording. Results showed improvisation-related activation of the pre-SMA, the dorsal premotor cortex (PMD), and the left IFG, among several other regions. Notably, the authors also reported decreased activation of the DLPFC and increased activation of the MPFC. This pattern mirrors the results of Limb and Braun's (2008) study of instrumental improvisation that suggested less involvement of executive control mechanisms, although several prefrontal regions associated with executive control showed increased activity during improvisation (i.e., pre-SMA, PMD, and IFG). Such seemingly discrepant findings have led to different interpretations on the role of cognitive control in improvisation. Limb and Braun (2008) interpreted DLPFC deactivation as reflecting a suspension of inhibitory or conscious monitoring processes. Moreover, activation of the MPFC was thought to reflect self-generated, stimulus independent cognitive processes—hallmark features of the default mode network (Andrews-Hanna et al., 2014). This network shows a correlated pattern of functional connectivity in the absence of external task demands, thus researchers hypothesize that its activation reflects internally-directed attention (Buckner and Carroll, 2007). Default mode activity has also been associated with mind-wandering (Andrews-Hanna, 2012; O'Callaghan et al., 2015), theory of mind reasoning (Buckner and Carroll, 2007), and mental simulation (e.g., episodic future thinking; Schacter et al., 2012). According to Limb and Braun (2008), activation of default mode regions during improvisation indicates internally-driven, self-referential mechanisms, which may allow the improviser to suspend conscious monitoring and enter a “flow-like” state. This pattern of results was largely similar to Liu and colleagues' study of lyrical improvisation. Both studies reported increased activity of the MPFC and decreased activity of the DLPFC. Such findings supported the authors' contention that spontaneous composition involves the suppression of executive control systems and 112 R.E. Beaty / Neuroscience and Biobehavioral Reviews 51 (2015) 108–117

activation of default mode regions. But the results of both studies also point to a degree of cognitive control during improvisation, as both Liu et al. (2012) and Limb and Braun (2008) reported activation of the ACC, SMA, PMD, and IFG—regions associated with cognitive and motor control.

2.2. Melodic and rhythmic improvisation

Pressing (1988) conceptualized improvisation as a dynamic interplay between several processes, including the generation, evaluation, and execution of novel motor sequences. Investigating such a multi-component processes poses challenges for researchers attempting to isolate its neural correlates. The experiments described above contrasted relatively unconstrained improvisation with some form of basic memory retrieval (e.g., Limb and Braun, 2008; Liu et al., 2012). Although these approaches tend to preserve the complexity and ecological validity of improvisation compared to others, they also typically yield a large number of significant activation peaks,

raising questions about the role of specific subprocesses (Berkowitz, 2010). A more nuanced approach has been to examine different modes of improvisation, such as melodic and rhythmic improvisation. Berkowitz and Ansari (2008) employed experimental conditions that varied in terms of melodic and rhythmic constraints. The authors used tasks that allowed for more or less spontaneous behavior within each mode of improvisation. In a fixed rhythm and free melody condition, for example, rhythm was constrained by a metronome and the notes were freely chosen by the participants; this permitted an analysis of brain activity related to melodic improvisation, controlling for the influence of rhythmic variability. Results showed that improvising novel melodic patterns was related to activation of bilateral dorsal PMD, the ACC, and the right supramarginal gyrus (SMG); melodic improvisation was also related to the deactivation of several brain regions, including the right angular gyrus, the right superior frontal gyrus, and bilateral posterior cingulate. In contrast, rhythmic improvisation was related to increased activity in the ACC, the left IFG, bilateral PMD, and the left superior and inferior parietal lobules (IPL). A conjunction analysis, which analyzed the common activity of melodic and rhythmic improvisation, found significant activation in the left inferior frontal gyrus (IFG), PMD, and rostral ACC. Berkowitz and Ansari (2008) thus revealed common and distinct neural correlates of melodic and rhythmic improvisation, providing greater insight into general and specific aspects of spontaneous composition. Several prefrontal and parietal brain regions have often been associated with improvised performance. Two of the most frequently implicated regions are the pre-SMA and the PMD, regions involved in the coordinated selection of novel motor sequences (Beudel and de Jong, 2009). These regions were among the most commonly activated in studies contrasting improvisation with memory retrieval (e.g., Bengtsson et al., 2007; Liu et al., 2012). Although these regions appear to be responsible for similar processes, past research suggests subtle differences in their functional roles in motor behavior, which has important implications for understanding their contribution to musical improvisation. On the one hand, the pre-SMA is commonly implicated in the generation, perception, and learning of temporal-motor sequences (Bengtsson et al., 2004, 2009; Karabanov et al., 2009; Schubotz and von Cramon, 2001). On the other hand, the PMD is commonly implicated in tasks involving the generation, perception, and learning of spatial-motor sequences (Bischoff-Grethe et al., 2004; Bengtsson et al., 2004). In light of the differential functions of the pre-SMA and the PMD, de Manzano and Ullén (2012a) sought to determine their unique contributions to musical improvisation by manipulating spatial and temporal aspects of spontaneous composition. Similar to Berkowitz and Ansari (2008), this experiment involved constraining either melodic or rhythmic improvisation. Results showed that melodic improvisation was associated with increased activity in both the left PMD and the left pre-SMA; rhythmic improvisation was also associated with increased activity in the left pre-SMA. The role of the pre-SMA in improvisation was further supported by de Manzano and Ullén (2012b), who explored whether musical improvisation taps similar neural substrates as pseudorandom response generation (PRG)—a domain-general measure of cognitive flexibility that requires top-down control to generate novel motor sequences (Beudel and de Jong, 2009). de Manzano and Ullén (2012b) asked participants to spontaneously compose melodies or press the keys of an MRI-compatible keyboard in a random fashion. A conjunction analysis revealed increased activation in bilateral IFG, bilateral pre-SMA, left DLPFC, right ACC, bilateral insula, and bilateral cerebellar regions. Interestingly, an analysis exploring the brain activity unique to improvising notes compared to pseudo-random generation did not reveal any significant differences, suggesting widespread overlap between the two conditions. The reverse contrast, however, revealed several areas related to random generation, including the right temporoparietal junction (TPJ), medial and lateral premotor areas, the DLPFC, and the cerebellum. The results of de Manzano and Ullén (2012a) and Berkowitz and Ansari (2008)

suggest that the premotor cortex plays a central role in melodic and rhythmic improvisation. Across both studies, the dorsal PMD showed robust activity during conditions requiring spontaneous generation of rhythmic sequences. de Manzano and Ullén (2012b) conclude that melodic improvisation and pseudo-random motor movements recruit some of the same neural mechanisms. Similar to other studies of melodic and rhythmic improvisation, the pre-SMA was found to play a critical role. This notion was further reinforced by activation of other regions involved in executive processes, such as the left DLPFC, right ACC, and bilateral IFG. Activation of prefrontal regions were also reported in studies contrasting improvisation and memory retrieval (e.g., Bengtsson et al., 2007; Donnay et al., 2014). Berkowitz and Ansari (2008) provide support for several of Pressing's (1988, 1998) theoretical predictions. Pressing conceptualized improvisation as the generation, selection, and execution of novel melodic and motor sequences, processes that appear to correspond to the functional roles of brain regions reported in Berkowitz and Ansari (2008). Specifically, the left IFG is associated with performance on tasks that require controlled retrieval from long-term memory (e.g., verbal fluency; Badre et al., 2005; Hirshorn and Thompson-Schill, 2006). Moreover, Berkowitz and Ansari (2008) reported activation of the ACC during both melodic and rhythmic improvisation. The ACC is associated with conflict monitoring (Botvinick et al., 2004), voluntary selection (Forstmann et al., 2006), and decision making (Walton et al., 2004)—all of which are components of Pressing's (1988) model of improvisation.

2.3. The role of musical expertise

To what extent does improvisational expertise influence the neural correlates of spontaneous performance? Pressing (1988) argued that expertise was critical to improvisational fluency. Because improvisation places substantial demands on information processing, Pressing viewed expertise as a means to automate low-level sensorimotor and cognitive processes so that attention could be allocated to higher-order performance goals. Berkowitz and Ansari (2010) provided seminal evidence that musical expertise affects brain mechanisms involved during improvisation. The authors used the same experimental paradigm as Berkowitz and Ansari (2008) to analyze the effects of musical expertise in improvisation. However, the key difference was the sample, which now included a second control group of undergraduate R.E. Beaty / *Neuroscience and Biobehavioral Reviews* 51 (2015) 108–117 113 non-musicians. Analysis of the main effect of melodic improvisation revealed that the only significant difference between musicians and non-musicians was a deactivation of the right temporoparietal junction (TPJ) in musicians. The ability of musicians to deactivate the right TPJ during improvisation may thus reflect neurophysiological changes associated with acquired expertise. Other researchers have sought to determine the role of improvisational expertise by studying pianists with a variety of improvisational experience (Pinho et al., 2014). Pinho and colleagues contrasted brain activation during improvisation with activation at rest, and correlated this activity with self-reported lifetime improvisation hours. Interestingly, improvisational expertise was negatively correlated with activation in a right-lateralized network of brain regions, including the DLPFC, IFG, anterior insula, and angular gyrus. The authors also specified six seed regions of interests (ROIs) based on activations reported in past work (de Manzano and Ullén, 2012a,b): bilateral DLPFC, bilateral dorsal premotor area, and bilateral pre-SMA. A functional connectivity analysis revealed extensive expertise-related positive connectivity between the prefrontal seed ROIs and other regions of the brain. Most notably, experts showed greater functional connectivity between the DFLPC and premotor cortex during improvisation (i.e., bilateral PMD and pre-SMA). Premotor seed regions also showed widespread connectivity across the cortex and within regions of the cerebellum. Pinho and colleagues interpret their findings as evidence in support for Pressing's (1988) model of improvisation. They argue that the relative deactivation of executive control networks in experts may correspond to an overall automation of domainspecific cognitive processes, and

increased functional connectivity between frontal regions may translate to more efficient access to pre-learned motor patterns and generative strategies stored in long-term memory. Overall, these findings are consistent with Pressing's (1988) position regarding the function of acquired expertise in improvisation—as expertise increases, processing demands should be minimized, allowing attention to be allocated to higher-order goals and performance monitoring. Berkowitz and Ansari (2010) found that musical expertise was related to a deactivation of the right TPJ. The right TPJ lies in close proximity to the right angular gyrus, a region also found to be deactivated during improvisation in Berkowitz and Ansari (2008). The right TPJ is part of the ventral attention network (Corbetta and Shulman, 2002), which is comprised of the right TPJ and ventral frontal cortex. Suppression of this network is thought to reflect top-down control during tasks requiring focused internal attention (Corbetta et al., 2008; Corbetta and Shulman, 2002). Modulation of the ventral attention network may provide “task shielding” by filtering or inhibiting information unrelated to the task at hand (Dreisbach and Haider, 2009); deactivation of nodes within the ventral attention network may therefore correspond to internally directed attention during creative idea production (cf. Benedek et al., 2014). Deactivation of the right TPJ has also been reported in studies of divergent thinking (e.g., Benedek et al., 2014b; Fink et al., 2009), creative writing (Howard-Jones et al., 2005), and product design (Kowatari et al., 2009). Thus, in the context of Berkowitz and Ansari (2010), deactivation of the right TPJ may reflect a greater ability of musicians to focus attention on internal processes during improvisation (e.g., generation and evaluation of novel musical sequences; Pressing, 1988).

2.4. Collaborative improvisation

Improvisation often occurs in group settings with multiple artists contributing to a common esthetic work. Collaborative improvisation is notably different from solo improvisation in terms of performance monitoring and perceptual feedback. An individual's performance must be integrated with multiple streams of sensory information (Pressing, 1988). The improviser must therefore allocate considerable attentional resources to both internal (e.g., generative) and external (e.g., communicative) sources. Recently, Donnay and colleagues explored the neural correlates of collaborative improvisation in a sample of professional jazz pianists (Donnay et al., 2014). The experimental procedure involved “trading fours” with an experimenter (also a jazz musician) in a nearby control room; participants and the experimenter took turns performing four-bar musical segments—a common mode of improvisation in jazz ensembles. Participants used an MRI-compatible piano keyboard and were given headphones to listen to their own and the experimenters' musical performance. A pre-recorded rhythm section also streamed through the headphones. Participants alternated between the experimental conditions of interest: playing a scale, performing a memorized melody sequence, or improvising; rhythm was constrained to one note per beat. Compared to performing the memorized melody, improvising was related to increased activation of the pre-SMA, bilateral IFG, bilateral DLPFC, and the posterior superior temporal gyrus (STG); improvising was also related to deactivation of bilateral angular gyrus. The authors also conducted a functional connectivity analysis to determine whether bilateral IFG showed greater functional connectivity with other regions during improvisation. This analysis revealed significantly greater positive connectivity between the left and right IFG. Bilateral IFG activity was also negatively correlated with activity in the STG, and the left IFG was anticorrelated with bilateral angular gyrus during the improvisation condition. The results of Donnay et al. (2014) provide an interesting contrast to the earlier work of Limb and Braun (2008). In Limb and Braun (2008), musicians showed deactivation of the DLPFC, suggesting less attention control during improvisation. Moreover, regions of the default mode network were found to be more relevant to improvisation in Limb and Braun (2008). Donnay et al. (2014), in contrast, reported increased activation of the DLPFC during collaborative improvisation. The authors note, however, that the nature of collaborative improvisation

appears to be different from solo improvisation, which was of interest in Limb and Braun (2008). They suggest that collaborative improvisation involves a distinct type of musical communication that requires greater demands on performance monitoring. 3. Discussion 3.1. Improvisation and domain-general processes Neuroimaging studies have shed light on the role of domain-specific training on brain activation during improvisation (e.g., Berkowitz and Ansari, 2010; Pinho et al., 2014). But to what extent does improvisation involve domain-general processes? de Manzano and Ullén (2012b) found that generating pseudo-random motor sequences activated the same brain regions as improvising new melodic sequences. This suggests that generating musical ideas may share similar underlying processes as those involved in general cognitive flexibility. The literature on general creativity provides further evidence for a relationship between improvisation and domain-general creative cognition. Neuroimaging studies of divergent thinking, for example, consistently report activation of the left IFG during tasks involving idea generation (for a review, see Gonen-Yaacovi et al., 2013). Several studies implicate this region in processes involving the generation and evaluation of candidate ideas retrieved from long-term memory (Badre et al., 2005). Improvisation and divergent thinking may thus recruit selective retrieval mechanisms common to the left IFG, providing further support for the theoretical predictions of Pressing (1988, 1998). 114 R.E. Beaty / Neuroscience and Biobehavioral Reviews 51 (2015) 108–117 The left IFG has been implicated in nearly all of the studies described above (e.g., Berkowitz and Ansari, 2008; Donnay et al., 2014; de Manzano and Ullén, 2012b). In de Manzano and Ullén (2012b), for example, a conjunction analysis found that both improvisation and pseudo-random key pressing activated the left IFG, as well as the left pre-SMA, the left DLPFC, bilateral insular cortex, and bilateral cerebellum. A similar pattern was also reported by Berkowitz and Ansari (2008), who found overlapping activation in the left IFG during conditions requiring rhythmic and melodic improvisation. A large body of research points to an important role of the left IFG in controlled memory retrieval (Corbetta et al., 2008; Corbetta and Shulman, 2002). Much of this work has used verbal fluency tasks to assess the neural correlates of retrieval from long-term memory. Verbal fluency tasks are often used to assess deficits in executive functioning (Troyer et al., 1998). Such tasks are thought to require attention control and strategic access to memory (Unsworth and Engle, 2007). The left IFG seems to be especially involved when demands on retrieval increase, such as when competing representations in semantic memory are high and when switching between semantic categories is required (Hirshorn and Thompson-Schill, 2006). Researchers hypothesize that activation of the left IFG during improvisation reflects similar retrieval mechanisms (e.g., Berkowitz, 2010). Generating melodic sequences, for example, requires the dynamic interaction between higher-order generative processes and a domain-specific knowledge (Pressing, 1998). In this context, the left IFG may support the generation, evaluation, and selection of to-be-performed musical sequences. The left IFG is often implicated in fMRI studies of divergent thinking. Divergent thinking is a domain-general creative thought process that involves generating ideas in response to open-ended prompts (e.g., inventing alternate uses for common objects). A recent review of 34 fMRI studies of divergent thinking found that the left IFG was among the most strongly activated during tasks involving creative idea generation (Gonen-Yaacovi et al., 2013). In addition, a recent resting-state fMRI study showed greater functional connectivity between the left IFG and default mode regions in individuals of high divergent thinking ability (Beaty et al., 2014a,b). The left IFG therefore appears to be important for a range of cognitive processes requiring controlled search from long-term memory, including musical improvisation and divergent thinking. Further evidence for a role of the inferior prefrontal cortex comes from a recent study on creative drawing (Ellamil et al., 2012). This work examined the neural mechanisms underlying generative and evaluative processes related to drawing ability in a sample of undergraduate art students.

Overall, compared to evaluation, generation was associated with increased activation of the left IFG, bilateral premotor cortex, inferior and superior parietal lobes, and bilateral medial temporal lobes; compared to generation, evaluation was associated with greater activity in several regions within executive control and default mode networks. A functional connectivity analysis further revealed greater functional coupling between executive and default networks during evaluation, pointing to a greater cooperation between controlled and spontaneous thought processes (cf. Beaty et al., 2014a,b; McMillan et al., 2013; Mok, 2014). A recent behavioral study suggests that musical improvisation may tap individual differences in domain-general creative cognition (Beaty et al., 2013). In this study, semi-professional jazz musicians were asked to improvise with a trio; they also completed a questionnaire regarding their instrumental practice regimen, as well as an alternate-uses divergent thinking task to assess general creative thinking ability. The improvisations were recorded and scored for creative quality by a team of expert raters. As expected, the number of practice hours was the strongest predictor of improvisation scores. But divergent thinking also predicted improvisation scores, even after controlling for practice hours. The results of this study and other recent work (e.g., Benedek et al., 2014a; Lewis and Lovatt, 2013) point to a potential overlap between the ability to generate creative ideas in general and the ability of jazz musicians to generate novel musical sequences. Pressing (1988) conceptualized improvisation as the interaction between higher-order referent processes and long-term memory. The neuroimaging literature on improvisation consistently implicates brain regions associated with cognitive control (e.g., the left IFG and the DLPFC); the literature also points to an overlap between domain-specific musical improvisation and domain-general cognitive processes (e.g., de Manzano and Ullén, 2012b). Taken together, a growing body of research supports Pressing's (1988, 1998) model of improvisation and further suggests that improvisation may rely on general creative processes.

3.2. The cognitive control of creative behavior

One point of contention in the literature is whether improvisation is under the deliberate control of the improviser. On the one hand, several studies implicate brain regions associated with working memory capacity (DLPFC), controlled memory retrieval (left IFG), and volitional motor control (PMD; Bengtsson et al., 2007; de Manzano and Ullén, 2012a; Donnay et al., 2014). On the other hand, there is evidence to suggest that such processes are less involved during improvisation (Limb and Braun, 2008), and that improvisational expertise corresponds to decreased activity within executive control regions (Pinho et al., 2014). Limb and Braun (2008), for example, reported widespread deactivation of lateral prefrontal cortex (i.e., the DLPFC) and increased activation of the MPFC, a region associated with spontaneous thought processes (e.g., mind wandering; Andrews-Hanna, 2012). What might account for such discrepant findings? One key methodological difference between Limb and Braun (2008) and others is the sample composition: Limb and Braun (2008) included professional jazz musicians, while most other studies included either classically-trained musicians or non-musicians. Studies with classically-trained musicians that report increased activity within executive control regions could simply be a function of increased task demands, since these musicians are presumably less familiar with improvisation. The results of Pinho et al. (2014) suggest that expert improvisers indeed show less activation of lateral prefrontal cortex while improvising compared to novices. However, experts also showed increased functional connectivity between premotor and executive control regions, which suggests that although experts show less activation within lateral prefrontal cortex, they also show greater connectivity between such regions during improvisation. Pinho and colleagues posit that this pattern may reflect a greater automaticity of cognitive processes in experts (cf. Pressing, 1998). Another possibility is that decreased activation of prefrontal regions reflects greater neural efficiency in experts (cf. Grabner et al., 2006; Neubauer and Fink, 2009). Because improvisation requires the simultaneous execution of several cognitive

processes (Pressing, 1988), the expert improviser, unlike the novice, may be better able to manage these demanding processes, thus reflected in lower levels of metabolic activity in lateral prefrontal cortex. Greater functional connectivity between premotor and executive control regions further supports a neural efficiency hypothesis of improvisational expertise—through practice, musicians may gradually strengthen neural connections, facilitating a more efficient transfer of information between nodes within a larger neural network. Several other methodological differences may also help to explain disparate patterns of results across the literature. Berkowitz (2010) notes that Limb and Braun (2008) used an experimental design that was less constrained than other studies with classical R.E. Beaty / *Neuroscience and Biobehavioral Reviews* 51 (2015) 108–117 115 musicians (e.g., Berkowitz and Ansari, 2008, 2010). According to Berkowitz (2010), Limb and Braun “allowed their subject performers to draw on an actual composition for material, with all of its associations—harmonic, melodic, rhythmic, structural, emotions, etc.—in contrast to the much more limited possibilities in our study. Thus, in addition to the active regions shared by our study and theirs, Limb and Braun saw changes in activity in over forty regions” (pp. 142–143). Berkowitz (2010) further argues that while the methodological approach of Limb and Braun (2008) may be more similar to real-world improvisation, it may not provide the type of experimental control required to isolate unique neural mechanisms involved in specific improvisational processes (e.g., improvising melodies versus improvising rhythms). de Manzano and Ullén (2012a) also point to differences in experimental contrasts chosen across studies. Indeed, determining an appropriate baseline condition for contrasting an experimental condition of interest is a fundamental issue in fMRI research (Gusnard and Raichle, 2001). de Manzano and Ullén (2012a) note that several studies that used similar task paradigms, experimental contrasts, and samples reported similar patterns of functional activity, including the DLPFC, pre-SMA, and PMD (Bengtsson et al., 2007; Berkowitz and Ansari, 2008; de Manzano and Ullén, 2012a; Donnay et al., 2014). Moreover, unlike Limb and Braun (2008), these studies did not report activation within default mode regions (i.e., MPFC), nor did they report widespread deactivation of the DLPFC. Interestingly, Donnay and colleagues did not replicate the results of Limb and Braun (2008). In contrast, they found increased activation of the DLPFC and no significant activation increases in the MPFC. The authors pointed to differences in experimental design between their study and Limb and Braun (2008)—most notably, the addition of a second musician who collaborated with subjects—resulting in greater demands on externally-directed processes associated with executive control (e.g., performance monitoring). On the other hand, musicians in Limb and Braun (2008) did not have such demands on external attention and could thus focus attention on internally-directed processes (e.g., idea generation), possibly reflecting greater involvement of default network regions. Future research could further explore the extent to which the default and executive networks contribute to improvisation by directly contrasting collaborative and individual improvisation. Although default and executive activity may correspond to greater demands on internally- vs. externally-directed attention, the concurrent activation of both networks’ hubs reported in past work suggests that these two networks may not show an antagonistic or “anticorrelated” pattern of activity during improvisation. Instead, such networks may exhibit differential involvement as a function of task demands (cf. Chrysikou et al., 2014). A growing literature points to several cognitive processes associated with large-scale network cooperation, including mind-wandering (Christoff et al., 2009), future planning (Gerlach et al., 2014; Spreng et al., 2010), and even cognitive control (Cocchi et al., 2013; Spreng et al., 2014). Default and executive network interaction during improvisation would also be consistent with recent functional connectivity analyses showing cooperation between these networks during other creative thinking tasks, such as divergent thinking (e.g., Beaty et al., 2014a) and artistic drawing (Ellamil et al., 2012). Such tasks are hypothesized to invoke a

state of focused internal attention (Andrews-Hanna et al., 2014; Benedek et al., 2014d), an ability that seems especially relevant to musical improvisation.

4. Future directions

In addition to the cognitive processes covered in this review, several non-cognitive, social factors are thought to influence improvisation (e.g., group interaction and audience feedback; Sawyer, 1992, 2003). McPherson and Limb (2013) raise the question of whether real-world creative performance can even be studied empirically without fundamentally changing the essence of the art. Although constraining musical performance comes at the cost of ecological validity, neuroimaging methods offer powerful tools for isolating specific sub-processes of improvisational cognition while controlling for other related processes. Future researchers should continue to strike a balance between ecological validity and experimental control (cf. Hasson and Honey, 2012). Throughout this review, Pressing's (1998) model was used as a framework for interpreting the results of neuroimaging studies on improvisation. Importantly, although the model seems to fit with the literature, the extent to which activation patterns reflect theoretical mechanisms remains unclear. Indeed, one's ability to retrospectively associate brain activity with theory relies on some degree of reverse inference (Poldrack, 2006). Future work should test specific hypotheses related to Pressing's (1998) model and rely less on reverse inferences. To further validate results, researchers could collect behavioral data (e.g., response times) in addition to brain imaging data, which could be used to correlate with activation within a specific region of interest (Poldrack, 2006). Such approaches have already been employed in past work. For example, Bengtsson et al. (2007) assessed the numerical deviation of improvised melodies from predetermined templates and found that as improvised melodies deviated more from the templates, activation within the pre-SMA increased. Future research should use similar approaches to determine the cognitive processes underlying musical improvisation. Improvisation research should continue to employ both behavioral and neurophysiological techniques to study spontaneous creativity. Several innovative methods have already been developed to study improvisation behaviorally (e.g., Goldman, 2013; Norgaard, 2011, 2014; Norgaard et al., 2013). Improvisation researchers would also benefit from embracing new and emerging methods in cognitive neuroscience. Like other forms of complex cognition, improvisation involves dynamic communication between regions across the entire cortex. Functional connectivity methods provide useful tools for analyzing the relative influence of nodes within large-scale functional networks (Bullmore and Sporns, 2009; van den Heuvel and Hulshoff Pol, 2010). Such methods have begun to emerge in the improvisation literature (e.g., Donnay et al., 2014; Pinho et al., 2014; Wan et al., 2014). Adopting a network-based approach will allow researchers to move beyond analyzing discrete regions in isolation, and transition toward a more fine-grained understanding of the mechanisms underlying musical improvisation.

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Ann. N.Y. Acad. Sci. ISSN 0077-8923 ANNALS OF THE NEW YORK ACADEMY OF SCIENCES Special Issue: The Neurosciences and Music VI REVIEW Rapid and flexible creativity in musical improvisation: review and a model Psyche Loui Department of Psychology and Program in Neuroscience & Behavior, Wesleyan University, Middletown, Connecticut Address for correspondence: Psyche Loui, Department of Psychology, Wesleyan University, 207 High St, Middletown, CT 06459. ploui@wesleyan.edu Creativity has been defined as the ability to produce output that is novel, useful, beneficial, and desired by an audience. But what is musical creativity, and relatedly, to what extent does creativity depend on domain-general or domain-specific neural and cognitive processes? To what extent can musical creativity be taught? To answer these questions from a reductionist scientific approach, we must attempt to isolate the creative process as it pertains to music. Recent work in the neuroscience of creativity has turned to musical improvisation as a window into real-time musical creative process in the brain. Here, I provide an overview of recent research in the neuroscience of musical improvisation, especially focusing on multimodal neuroimaging studies. This research informs a model of creativity as a combination of generative and reactive processes that coordinate their functions to give rise to perpetually novel and aesthetically rewarding improvised musical output. Keywords: creativity; improvisation; entropy; default network; perception action; executive control Introduction The current work seeks to define a rigorous but nuanced model of musical improvisation, by conceptualizing it as a complex system that includes computational, algorithmic, and implementational levels of analysis.² The mounting research literature suggests that musical improvisation, such as that which is commonly taught in modern jazz training, offers a useful window through which to understand real-time creativity.³ Thus, a model of musical improvisation as a complex system will be informative for cognitive scientists, musical educators, and anyone seeking to better understand creativity. Conceptualizing the real-time creative musical process

Following classic work in cognitive science, a complex system can be described at three levels.² At the highest, computational level, the model addresses the goal of the overall system: in this case, successful musical improvisation. At the middle, algorithmic level, the model describes the cognitive processes and transformations that must occur to accomplish the goal. And at the lowest, implementational level, the model provides a physical realization of neural substrates necessary for implementing the required cognitive processes. Musical improvisation lends itself well to scientific study at multiple levels because it involves complex but rapid interactions of many components. In contrast to other forms of musical creativity, such as composition, ideas in musical improvisation (e.g., melodic, harmonic, and rhythmic patterns) are generated and evaluated on a relatively fast timescale within a performance. Between performances, musical ideas are also generated and evaluated over the course of long-term training in the classroom as well as in private instruction.^{4,5} Training and experience give rise to the psychological constraints that enable the real-time improvisatory experience. These psychological constraints include the referent (cognitive/perceptual/emotional guidelines or structures), the knowledge base (musical materials and repertoire), and domain-specific memory for previously encountered auditory-motor patterns.⁶ Also, guiding improvisations are motor (or doi: 10.1111/nyas.13628 Ann. N.Y. Acad. Sci. xxxx (2018) 1–8) © 2018 New York Academy of Sciences. 1 Creativity in musical improvisation (Loui biomechanical) constraints that are shaped by experience. The goal of successful improvisations, then, entails filtering the referent through the performer's own knowledge base to generate fluent, cohesive auditory-motor sequences that are intrinsically rewarding. How does the cognitive system accomplish this goal? At an algorithmic level, models of creativity entail idea generation and evaluation, in a cognitive cycle akin to the blind variation and selective retention process⁷ that is assessed by psychometric studies such as Divergent Thinking tests.^{8,9} Idea generation is the process of mentally combining or recombining existing elements to give rise to multiple possible solutions, whereas idea evaluation entails selecting from the array of generated ideas, using internally or externally generated feedback. Because feedback can come from multiple sources at different times during or after the performance, this feedforward/feedback cycle between idea generation and evaluation occurs at multiple timescales.^{10–12} At an implementational level, this interplay of idea generation and evaluation likely entails the coordinated activity of the default mode and executive control networks in the brain as detailed in the next section.¹³ As ideas in improvised music are implemented as auditory-motor sequences, the perception and production of these sound targets further engages the auditory perception–action network,^{14,15} which is strengthened in its connectivity by musical training.¹⁶ Figure 1 shows a model of musical improvisation at the computational, algorithmic, and implementation levels. A review of neuroimaging studies on musical improvisation

Some insights into the neural implementation of musical improvisation come from functional neuroimaging. Several functional magnetic resonance imaging (fMRI) studies have asked jazz musicians to improvise in the scanner, and compared brain activity or connectivity against control tasks of producing nonimprovised sequences (such as musical scales or memorized passages). In the first fMRI study on jazz improvisation, Limb and Braun compared brain activity in jazz pianists between improvised and overlearned productions of performances of a previously memorized novel melody.¹⁷ This first study showed increased activity during improvisation in several regions within the frontal lobe, including the medial prefrontal cortex, cingulate cortex, inferior frontal gyrus, and supplementary motor areas, as well as in the auditory processing areas in the temporal lobe, including superior and middle temporal gyri. In contrast, the dorsolateral prefrontal cortex was mostly deactivated during improvisation. These differences were not explained by differences in the number or variability of notes played during the improvisation condition, as

these were controlled in this study. This pattern of results has given rise to the influential hypothesis that creativity entails an upregulation of mesial prefrontal regions (e.g., medial prefrontal cortex and cingulate cortex) accompanied by a downregulation of lateral prefrontal regions (e.g., dorsolateral prefrontal cortex (DLPFC)). However, the specific decrease in DLPFC activity could also arise from the relatively low working memory demands of the improvisation task relative to the control task, which required the recall and production of a newly learned melody. Nevertheless, the balance of mesial to lateral activity can be an important measure, in part because these mesial and lateral prefrontal structures belong to different resting state brain networks, including the default mode network and the executive control network. Following up on the idea of mesial to lateral activity, Liu et al. investigated functional activity and connectivity using fMRI during freestyle rap, comparing spontaneous lyrical improvisation against conventional, rehearsed performance conditions in freestyle artists.¹⁸ Again, improvisation was associated with increased activity in the medial prefrontal cortex, especially in the left hemisphere, and decreased activity in the dorsolateral prefrontal cortex, especially in the right hemisphere. Furthermore, functional connectivity analyses showed that seed regions in the medial prefrontal cortex were positively associated with the inferior frontal gyrus and cingulate cortex, and negatively associated with the dorsolateral prefrontal cortex and intraparietal sulcus. These results provide further support for the role of dissociated activity between medial and dorsolateral prefrontal cortices in guiding improvisatory behavior. The authors speculate that the medial prefrontal cortex might guide behavior through “alternate cingulate pathways” that effect motor control by “linking intention, affect, language, and action.”¹⁸ According to this view, the cingulate cortex and the medial prefrontal cortex

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Loui Creativity in musical improvisation Referrent Patterns Reward Perception Action Generation Evaluation Auditory–motor Default Executive control base Knowledge Figure 1. A model of musical improvisation at computational, algorithmic, and implementation levels. The computational level specifies the goal of real-time musical creativity via improvisation as a system. This is closely tied to the algorithmic level, which describes how the goals specified at the top level are accomplished. At the lowest level are the neural systems that implement the steps of perception and action, idea generation and evaluation, and learning and motor plan selection as shown in the algorithmic level. cortex, although they are anatomically distinct from each other, are nevertheless able to act together.¹⁹ The cingulate cortex may serve as a hub that acts upon the auditory perception–action cycle to choose appropriate auditory-motor patterns to maximize reward.²⁰ The auditory perception–action cycle has been extensively studied due to its importance not only in music, but also in speech and language as well as in hearing more generally. The first cortical waystation of the auditory perception–action pathway lies in the superior temporal lobe, where input from subcortical areas along the auditory pathway is coded in the core, belt, and parabelt areas of the auditory cortex. From the level of the auditory cortex, much evidence supports a dualstream model of auditory processing. The dorsal stream supports sensorimotor control/integration, whereas the ventral stream supports object-based sound categorization.^{21,22} The significance of dorsal versus ventral pathways in music has also been shown, notably in behavioral and neuroimaging work on tone-deafness, or congenital amusia.^{23–25} Specifically, the dorsal network involves areas connected by the arcuate fasciculus, which is a major white matter pathway connecting endpoints of cortical gray matter in the superior temporal lobe (superior and middle temporal gyri) and the frontal lobe (inferior frontal gyrus).¹⁴ The ventral network includes middle temporal gyrus and inferior frontal regions connected via the uncinate and inferior longitudinal fasciculi.^{14,26} Together, these dorsal and ventral pathways enable sensorimotor translation as well as category-based representation of sound targets in a feedforward and feedback process. Applied to the study

of real-time creativity such as in musical improvisation, this perception–action feedforward–feedback cycle must additionally subserve the generation of novel ideas, a process that must also take into account one’s knowledge Ann. N.Y. Acad. Sci. xxxx (2018) 1–8 © 2018 New York Academy of Sciences. 3 Creativity in musical improvisation Loui base (e.g., previously known melodic fragments or “licks,” or chord progressions). In another fMRI study,²⁷ classically trained pianists were asked to improvise on a given melody and produce pseudo-random key-presses, compared with a control task of sight-reading. Both improvisation and pseudo-random conditions showed activity in bilateral inferior frontal gyri and insula, anterior cingulate cortex, left presupplementary motor area (pre-SMA), and bilateral cerebellum. Pseudo-random sequence generation additionally recruited superior frontal gyrus and precentral gyri. The pseudorandom sequence generation task also showed activity in the lingual and fusiform gyri in the occipital lobe. This converges with the Liu et al. and Limb and Braun findings reviewed above in highlighting the role of mesial and lateral prefrontal cortices, but the differences may have to do with differential task demands, as this is the only study that employed a pseudo-random sequence generation task. Pinho et al. investigated musical improvisations in jazz and classical pianists and found that while total hours of improvisation experience were negatively associated with activity in the frontoparietal association areas, improvisation training was positively associated with functional connectivity of the bilateral dorsolateral prefrontal cortices, dorsal premotor cortices, and presupplementary motor areas.²⁸ Although most studies reviewed thus far showed relatively little activity in inferior frontal cortices, Donnay et al. showed that language areas (inferior frontal gyrus) are active during trading fours, which is a form of interpersonal musical interaction common in improvised jazz.²⁹ Taken together, fMRI studies of musical improvisation activated frontal, temporal, and parietal areas, with special emphasis paid to a group of prefrontal regions, including the medial prefrontal and cingulate cortex, dorsolateral prefrontal cortex, and premotor and presupplementary and supplementary motor areas. As shown in a recent review,¹³ these regions belong to several known functional networks including the default and executive networks. Inherent challenges and possible solutions Results have generally shown differences in the frontal lobe; specifically, the medial prefrontal cortex is frequently active during improvisation, whereas the dorsolateral prefrontal cortex is frequently more active during control. However, it is unclear whether the mesial activity reflects overactivation during novel musical idea generation, or whether it reflects underactivation or deactivation during the control condition. Similarly, it is also unclear whether the lateral activity reflects overactivation during control tasks, which often require more memory, or whether it reflects deactivation of the dorsolateral prefrontal cortex during novel musical idea generation. Besides the above point, there were other discrepant findings between studies, even within the frontal lobe. These discrepancies arise from intrinsic variability in the mental process of improvisation: during a single given moment in the improvisation task, subjects could have been utilizing any number of available mental resources (e.g., visuospatial and/or auditory/phonological components of working memory, autobiographical memory recall, motor planning, attentional selection, and affective communication, just to name a few) to engage in the idea generation and evaluation process. This poses an inherent challenge in task fMRI studies of jazz improvisation. One approach to address this challenge is to control the stimulus completely by presenting the same predetermined stimuli to all subjects, and to measure the extent to which jazz improvising musicians differ in their perceptual and cognitive processing of matched stimuli. Although this removes the improvisational process from the study, given the appropriate experimental controls, people with different levels of improvisatory training can be reasonably expected to respond differently to the same stimuli as a result of their training. Another approach around the inherent challenge is to remove the task from the scanner completely and to compare

resting state functional MRI which captures connectivity of the brain without a task at hand. Subjects are simply asked to daydream in the MRI. “Daydreaming” is associated with resting brain activity in the default mode network, which has been tied to idea generation.⁴⁰ Thus, comparing the default mode and other networks between subjects with different levels of improvisational experience may also offer a window into neural substrates of stimulus-independent thought processes including creativity. 4 Ann. N.Y. Acad. Sci. xxxx (2018) 1–8

© 2018 New York Academy of Sciences. Loui Creativity in musical improvisation A third way around the inherent challenge is to compare structural differences in the brain and to relate these differences to measures of musical production outside of the scanner environment, which might elucidate the structural neural mechanisms of idea generation in a more ecologically valid setting. For each of these approaches, a systematic relationship between brain structure or function and improvisatory behavior can only be established after eliminating as many other sources of confounds as possible via careful selection of active control groups. In the remainder of this article, I review a series of recent studies that uses each of these three approaches to tackle the problem of musical improvisation while circumventing the inherent challenge of variability in the improvisational process. In all studies, we use multiple control groups, comparing jazz improvising musicians, classical nonimprovising musicians, and nonmusicians. Classical and jazz groups are matched on pitch discrimination thresholds, duration of general musical training, and in familiarity with their instrument, but only the jazz group has experience in rapid musical idea generation (for details, see Refs. 25 and 37). Thus, with the help of multiple control groups, we can tease apart whether any differences between groups arise from general perceptual-motor training (by comparing both groups of musicians against nonmusicians), or whether they arise from improvisation training per se (by comparing jazz musicians against the other groups).

Evaluating and predicting creativity How do we assess jazz musicians’ performance? Here, we used an improvisation-continuation task, in which subjects are given a simple, repeated musical motif, and are asked to reproduce and then to improvise on it. The stimulus motifs ([https:// wesfiles.wesleyan.edu/home/ploui/web/JazzCreativity/ImprovCont/Motives/](https://wesfiles.wesleyan.edu/home/ploui/web/JazzCreativity/ImprovCont/Motives/)) and examples of subjects’ recorded productions are available online ([https:// wesfiles.wesleyan.edu/home/ploui/web/ImprovCont/](https://wesfiles.wesleyan.edu/home/ploui/web/ImprovCont/)). Subjective listening to the recordings ensured that all subjects were able to reproduce the stimuli, and also to improvise on them to the best of their ability. Creativity has been defined as the ability to produce output that is novel, useful, beneficial, and desired by an audience.¹ When considering how creative output can be evaluated, it is worth noting that creative works never stand in isolation.

Csikszentmihalyi describes creativity as a three-part system that includes the domain (e.g., mathematics and painting), the field (consisting of all experts or professionals in the domain), and the individual creator.³⁰ The judgment of experts in the field is an important validation of creative output, and the evaluation of musical ideas is crucial to improvisation at the algorithmic level. Thus, we first used a consensual assessment technique to assess creativity of our subjects’ output.^{31,32} We invited professional musicians and jazz instructors (see Acknowledgments) to listen to each clip and rate them on creativity. Raters showed generally high agreement, and averaged ratings were higher for jazz musicians than for the other two groups.³³ In addition to subjective methods, we further sought to identify objective, data-driven measures from the subjects’ recorded output that would be useful in predicting experts’ creativity ratings, which could then be applied toward informationtheoretic analyses of new recordings. Previous studies of creativity, reviewed above, have used entropy as an information-theoretic measure to analyze their subjects’ behavioral output.^{27,28} Since its first definition,³⁴ entropy has been used to quantify information content in neuroscience³⁵ and to model statistical learning in the musical modality.⁴⁰ Here, we hypothesized that more creative performers would play more notes (i.e., be more fluent) and play more varied notes.

We therefore computed two measures, fluency and entropy, for each recording. Fluency was simply defined as the number of notes played per trial. Entropy was defined as the negative sum of the log probability of each note weighted by its probability: $H(X) = -\sum p_i \log(p_i)$, where p_i refers to the probability of each note. Intuitively, if one only plays a single note within the whole recording ($p_i = 1$), then $H(X)$ is 0, whereas if one plays many varied notes, this would result in a positive entropy value. Although this is a simple measure that does not yet take into account any music-theoretical or motoric constraints, this struck us as a valid firstpass measure of creativity, because more creative players could be expected to play more notes and include more different pitches within the course of a single trial. Performances from jazz improvising musicians showed higher fluency and higher entropy. Fluency, entropy, and creativity ratings are Ann. N.Y. Acad. Sci. xxxx (2018) 1–8 © 2018 New York Academy of Sciences. 5 Creativity in musical improvisation Loui all highly correlated ($r > 0.8$). Fluency and entropy together explain 80% of variance in experts' creativity ratings. Fluency and entropy are highly correlated ($r = 0.877$), but fluency explains additional variability in creativity ratings (partial $r = 0.49$) even after accounting for the variability explained by entropy.^{33,36} It is worth noting that although entropy is useful as a first measure of the variety of notes played, it cannot be expected to capture all of creativity. Maximum entropy could be achieved by completely random playing on an instrument, whereas maximum fluency would entail playing as many notes as possible, both of which few listeners would find highly creative. Nevertheless, in our sample, most subjects were fixated on a few keys, possibly due to the nature of the task, and those who played more notes (high fluency) and more varied notes (high entropy) were also rated as more creative by the experts. Thus, while our current results show positive relationships between fluency, entropy, and creativity, future work is needed to refine the information-theoretic measures that are best applied toward predicting creativity. Voxel-based morphometry (VBM) was used to relate fluency and entropy to gray matter volume. VBM results showed significant negative associations between entropy and gray matter volume in three regions: the left middle temporal gyrus, the supplementary motor area, and the medial cingulate cortex, whereas fluency was associated with gray matter volume in the left middle temporal gyrus only.³⁶ These regions correspond to the auditorymotor and default mode networks, respectively. Interestingly, all associations observed were negative, with individuals who produced more entropy possessing less gray matter volume in these regions. One hypothetical explanation is that individuals with high gray matter volume in these regions may have had more inhibitory processes leading to less entropic performances. In addition to gray matter differences, white matter differences were also observed between jazz improvisers and their nonimprovising counterparts. A whole-brain diffusion tensor imaging comparison between jazz musicians and controls showed that jazz musicians had higher fractional anisotropy (FA) in mesial regions in the corpus callosum and cingulum.³³ Furthermore, FA in the middle cingulate cortex was correlated with entropy (but not with fluency). A probabilistic tractography analysis using the mesial significant cluster in the corpus callosum and cingulum as a seed region of interest, and the lateral endpoints of the arcuate fasciculus as waypoint regions of interest, showed higher tract volume and FA in tracts identified between the mesial region of interest (ROI) and the left superior temporal gyrus, and between the mesial ROI and right inferior frontal gyrus. This provides anatomical support for the integration between areas in the lateral perception-action network and mesial areas in the default and executive control networks, which may be related to interhemispheric connectivity in the corpus callosum as well as cognitive control processes in the cingulate cortex. Role of expectation in idea evaluation Idea evaluation is a crucial aspect of the algorithm in the present model of musical improvisation. The ability to compare and select musical ideas could be assessed by presenting the same musical ideas to multiple groups who differed in their improvisatory

experience, and comparing their rapid evaluative responses to the same stimuli. We measured using event-related brain responses to musical chord progressions in jazz improvising musicians, classical musicians, and nonmusicians using the well-replicated harmonic expectation paradigm,³⁶ in which subjects listened to expected, slightly unexpected, and highly unexpected chord progressions, and rated their preference for each chord progression. Behaviorally, jazz musicians preferred the slightly unexpected chord progressions, whereas both other groups preferred the highly expected.³⁷ Event-related potentials showed larger amplitude of the early right anterior negativity (ERAN) in response to unexpected chords in jazz musicians, suggesting increased perceptual sensitivity to unexpected musical events. This ERAN difference was followed by a sharper and higher amplitude P3b waveform, which indicates more cognitive engagement in jazz musicians.³⁷ The P3b was followed by a late parietal positivity that was larger in classical musicians compared with jazz musicians, suggesting an acceptance of the unexpected chord on the part of the jazz musicians, but a continued perturbation or delayed return to baseline among the classical musicians. Results highlight the rapid temporal evolution of different types of neural processing of unexpected sounds between classical musicians, jazz musicians, 6 *Ann. N.Y. Acad. Sci.* xxxx (2018) 1–8

© 2018 New York Academy of Sciences. Loui Creativity in musical improvisation and those with no formal musical training. Notably, the ERAN and P3b correlated with scores on the Divergent Thinking Task,⁹ which is a psychometric test for creativity that does not utilize any musical material. This suggests that the differences in neural processing of unexpected sounds may reflect some domain-general aspects of creativity.³⁷

Summary and conclusions

Creativity is a fundamental capacity of the mind that drives human culture and invention. Despite its importance, creativity has not received the scientific attention it deserves, due to inherent challenges in defining and isolating its component processes.³⁸ Precisely, because it is hard to define, it behooves us to find a more computationally tractable definition of creativity. Here, I outline a model of musical improvisation, a subset of creativity with real-time constraints. I propose that creativity can be redefined as the fluent production of high information content, and that a window into real-time creative behavior is musical improvisation, which can be understood as a complex system with multiple levels. Structural and functional neuroimaging studies highlight the role of mesial and lateral integration in subserving creativity, and the ERP results show that expectation plays a central role. Lateral regions include the endpoints of the arcuate fasciculus, namely, the superior and middle temporal and inferior frontal gyri, which are endpoints of the perception–action pathway. Mesial regions include the cingulate, supplementary motor area, and corpus callosum, which are crucial for interhemispheric communication that facilitate the integration of different functions, as well as medial prefrontal cortex and the cingulate cortex, which have been associated with mind-wandering and cognitive control functions, respectively. Future work will try to identify how these pathways are sensitive to training-induced plasticity. Understanding the ability to improvise, and how it can improve as a function of training, may translate to more targeted strategies in music pedagogy,⁴ thus having implications for fostering a more creative classroom.

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Competing interests

The author declares no competing interests.

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