Generation of novel motor sequences: The neural correlates of musical improvisation

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While some motor behavior is instinctive and stereotyped or learned and re-executed, much action is a spontaneous response to a novel set of environmental conditions. The neural correlates of both pre-learned and cued motor sequences have been previously studied, but novel motor behavior has thus far not been examined through brain imaging. In this paper, we report a study of musical improvisation in trained pianists with functional magnetic resonance imaging (fMRI), using improvisation as a case study of novel action generation. We demonstrate that both rhythmic (temporal) and melodic (ordinal) motor sequence creation modulate activity in a network of brain regions comprised of the dorsal premotor cortex, the rostral cingulate zone of the anterior cingulate cortex, and the inferior frontal gyrus. These findings are consistent with a role for the dorsal premotor cortex in movement coordination, the rostral cingulate zone in voluntary selection, and the inferior frontal gyrus in sequence generation. Thus, the invention of novel motor sequences in musical improvisation recruits a network of brain regions coordinated to generate possible sequences, select among them, and execute the decided-upon sequence.
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Introduction

From the everyday movements of locomotion and speech to the adept actions of acrobats and athletes, the neuromuscular system is capable of producing a diverse array of motor sequences. Some motor sequences are executed automatically (e.g., reflexes), while other movements are learned and re-used. Other action sequences,

however, must be spontaneously created by combining pre-existing, elemental movements to fit a unique set of environmental circumstances at a given moment in time. Previous neuroimaging work examining motor sequencing has studied the performance of pre-learned sequences (Roland et al., 1982; Catalan et al., 1998; Bengtsson et al., 2004), auditorily-cued sequences (Lewis et al., 2004), and visually-cued sequences (Harrington et al., 2000; Haaland et al., 2004; Bengtsson and Ullen, 2006), as well as sequence learning (Grafton et al., 1995, Müller, 2002; for reviews see Ivry and Helmuth, 2003; Janata and Grafton, 2003). However, to the best of our knowledge, the neurobiological basis of the generation of novel motor sequences has thus far not been studied.

Musical improvisation represents an ideal realm through which to study the neural bases of the invention of action sequences. In musical improvisation, musicians combine a finite collection of notes and rhythms to create a potentially infinite number of musical phrases that correspond to a particular musical idiom (for reviews see Pressing, 1988, 1998). In terms of cognitive processes, improvisation can be defined as the spontaneous generation, selection, and execution of novel auditory–motor sequences. Previous brain imaging studies in music cognition have largely focused on the brain mechanisms underlying music perception and processing (for reviews see Koelsch and Siebel, 2005; Peretz and Zatorre, 2005). The few published studies of musical production have been limited to performance of previously memorized (Parsons et al., 2005) or visually presented music (Sergent et al., 1992; Schön et al., 2002; Stewart, 2005; Bengtsson and Ullen, 2006); true production, that is, the real-time creation of novel music, has not to our knowledge been previously investigated with functional magnetic resonance imaging (fMRI).

We studied the neural activity during improvisation among highly trained pianist subjects in order to examine the neural basis of novel action sequencing. Specifically, we employed a 2×2 factorial design, varying melodic freedom (ordinal freedom, i.e., choice of pitch) and rhythmic freedom (temporal freedom, i.e., choice of duration) both separately and together (Fig. 1; see also
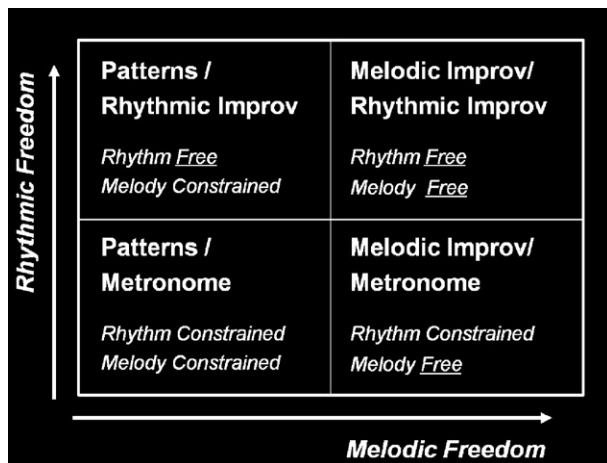
Fig. 1. Task design. Four conditions with varying degrees of rhythmic and melodic freedom.

Methods). Subjects either continuously invented and performed novel 5-note melodies on a 5-key piano-like keyboard (Melodic Improvisation) or played extremely simple pre-learned 5-note patterns in a random order (Patterns). In both Melodic Improvisation and Patterns conditions, subjects performed the task while either generating novel rhythms (Rhythmic Improvisation) or playing isochronously, with one note per beat synchronized with a metronome click every 500 ms (Metronome). These four conditions (see Methods for additional details) allowed for examination of melodic and rhythmic freedom separately, as well as the combined effect of freedom in both parameters. We were particularly interested in observing which areas were commonly activated by both rhythmic and melodic freedom, since such overlapping areas would ostensibly be involved in generation, selection, and execution of novel motor sequences most generally.

Methods

Subjects

We recruited 13 classically trained undergraduate pianists from the Dartmouth College Music Department (8 female, mean age=21.9, mean musical training=13 years piano experience). One subject's data were excluded due to excessive head movement, leaving a total of twelve participants in the final analyses.

Task

Prior to functional scanning, each subject was familiarized with the 5-key piano keyboard and the four tasks were explained. Subjects were told that they would see two types of task instructions, either "Make up melodies" or "Play patterns." For "Make up melodies," subjects were told to make up as many unique 5-note melodies as they could in each block. For "Play patterns," seven simple pattern sequences were demonstrated to each subject: five sequential presses of any key (CCCCC, DDDDD, etc.), a 5-note ascending scale (CDEFG), and a 5-note descending scale (GFEDC). Subjects were told that they could play the patterns in any random order of their choosing during "Play patterns" conditions. All subjects were able to immediately recall and demonstrate these patterns before scanning, suggesting that the simplicity of these

patterns created no significant memory load. Subjects were told that in both conditions, they may or may not hear a metronome click. If the click was present, subjects were told to play one note of their patterns or made-up melodies with each click. If there was no click present, subjects were told that they should make up their own rhythms for the patterns or made-up melodies. Subjects were instructed to carefully follow only whether a click sound came through the headphones, and to ignore any regular clicking or beeping sounds made by the scanner.

During scanning, subjects performed the four different tasks with the right hand on a five-key piano-like keyboard (notes: C, D, E, F, G), and heard what they were playing through headphones in real time. In order to study the effects of different types of freedom on novel motor sequence generation, we varied constraints on note choice and rhythm across the four tasks (see Fig. 1): (1) *Patterns/Metronome* (note choice and rhythm both constrained): Subjects played any of the seven simple, pre-instructed 5-note patterns described above in any order of their choosing. Subjects played one note per beat coordinated with a 2-beats-per-second metronome click. (2) *Melodic Improvisation/Metronome* (note choice free, rhythm constrained): Subjects spontaneously invented and performed 5-note melodies with the metronome click. (3) *Patterns/Rhythmic Improvisation* (note choice constrained, rhythm free): Subjects played the 5-note patterns in (1) without metronome, continually making up novel rhythms for the patterns. (4) *Melodic Improvisation/Rhythmic Improvisation* (both note choice and rhythm free): Subjects improvised 5-note melodies as in (2), but with no metronome, allowing for rhythmic improvisation as well as melodic improvisation.

Design

A block design was used, and each subject performed 5 runs in which each of the 4 tasks was presented once. In each run, subjects performed each task once for 40 s with 30 s of rest between tasks. Task instructions ("Play patterns" and "Make up melodies") were presented onto a screen positioned for viewing in the scanner, and responses (notes) and metronome were heard through headphones. Response data was collected using e-Prime software (Psychological Software Tools, Pittsburgh, PA), recording each key press and the inter-press duration.

Stimulus delivery

Subjects performed the task on a 5-note response box resembling a five-key piano keyboard. Each key triggered the playing of a wave file of the given note by e-Prime software. We used the following five sequential notes: C (262 Hz; "middle C"), D (294 Hz), E (330 Hz), F (349 Hz), and G (392 Hz). The sounds were synthesized with an "acoustic piano sound" on Finale for Macintosh (MakeMusic, Inc., Eden Prairie, MN). These sounds were then delivered to the subject in real time at the moment of key press through MR-safe headphones. In metronome conditions, the metronome click was also presented through the headphones at 120 beats per minute, or one beat every 500 ms.

Imaging parameters

Functional and structural images were acquired in a 3T Phillips Intera Allegra whole-body MRI scanner using an 8-Channel Phillips Sense head-coil. A gradient echo-planar imaging T2*-sequence sensitive to blood-oxygenation level-dependent (BOLD) contrast was used to acquire functional images. Functional images

consisted of 30 noncontiguous slices acquired in an interleaved order (4 mm thickness, .5 mm gap, 80×80 matrix, repetition time, 2500 ms, echo time: 35 ms, flip angle: 90°, field of view 240×240 mm). For each of the 5 functional runs, 123 volumes were acquired. Three-dimensional whole-brain high-resolution T1-weighted images (160) were acquired in the sagittal plane ($1 \times .94 \times .94$) with a standard Phillips MPRage 3-D sequence.

Behavioral data analysis

Assessment of rhythmic freedom (comparison of Rhythmic Improvisation versus Metronome conditions): inter-press interval variability

To assess rhythmic freedom in the Rhythmic Improvisation conditions compared to the Metronome conditions, we quantified inter-press interval variability by recording the proportion of responses falling between 350 and 650 ms in each of the four conditions. Since the metronome click was presented every 500 ms, we predicted that most responses should be within 150 ms of 500 ms (350–650 ms) when the metronome was presented, and that the inter-press interval variability (the percent of presses falling outside this range) would be greater in the Rhythmic Improvisation compared with the Metronome conditions, since subjects were instructed to play rhythmically freely when no metronome was present.

Assessment of melodic freedom (comparison of Melodic Improvisation versus Patterns conditions): variety of note combinations and percentage of unique note sequences

We compared Melodic Improvisation and Patterns conditions using two different measures. The first, variety of note combinations, allowed us to assess both whether subjects played the pre-instructed patterns in the Patterns conditions, and whether subjects exhibited greater variety of note combinations in the Melodic Improvisation conditions. The second, percentage of unique note sequences, allowed us to determine what percentage of improvised note sequences in Melodic Improvisation conditions were played once and only once in a given condition across all blocks, or across the entire experiment.

Variety of note combinations

We measured the proportion of responses that fell on either the same note as the previous press or on an adjacent note. We predicted that a very high percentage of notes in Patterns conditions should fall on the same note as before (given patterns CCCCC, DDDDD, EEEEE, etc.) or on an adjacent note (given patterns CDEFG and GFEDC); only transitions between patterns could deviate from this. Conversely, we predicted that during Melodic Improvisation conditions, subjects would exhibit a significantly lower percentage of such same or adjacent key presses in sequence, indicating greater variety of note combinations.

Percentage of unique note sequences

We examined the number of unique 5-note sequences generated in both Melodic Improvisation and Patterns conditions by each subject across the entire experiment. Since subjects were asked to try to invent as many novel sequences as possible in the Melodic Improvisation conditions, we predicted a relatively high percentage of unique note sequences in these conditions. In contrast, in Patterns conditions, we expected that the percentage of unique sequences would be quite low, since subjects were instructed to play only the seven pre-learned patterns.

In addition to examining the percentage of unique note sequences played by each subject across all runs of each of the four conditions, we also examined the percentage of note sequences that were unique across both Melodic Improvisation conditions (Melodic Improvisation/Patterns + Melodic Improvisation/Rhythmic Improvisation). That is, we examined the percentage of improvised note sequences that were played once and only once throughout the entire experiment to study the extent of novelty of subjects' improvised sequences. We also computed this measure across both Patterns conditions (Patterns/Rhythmic Improvisation + Patterns/Metronome), and predicted a low percentage of unique note sequences here, given that subjects were instructed to play the same pre-learned patterns in both Patterns sub-conditions.

Imaging data analysis

Structural and functional brain images were analyzed using BrainVoyager QX 1.8.6 (Brain Innovation, Maastricht, Holland). Functional images were corrected for slice-time acquisition differences, head motion, temporal high-pass filtering to remove low-frequency nonlinear drifts of three or fewer cycles per time-course, and linear trend removal. Those runs with more than 3 mm motion over the run or more than 1 mm motion between two adjacent volumes within a run were excluded from the analysis. Eleven out of sixty runs total across twelve subjects (18.3%) were removed, and one subjects' data were excluded entirely. Additionally, four total runs (each from a different subject) were excluded due to equipment problems. We thus evaluated a total of forty-five runs across twelve subjects (66.7% of experimental runs acquired). In the spatial domain, data were smoothed with a Gaussian smoothing kernel of 6 mm FWHM. Following initial automatic alignment, the alignment of functional images to the high-resolution T1 structural images was manually fine-tuned. The realigned functional data set was then transformed into Talairach space (Talairach and Tournoux, 1988). The expected BOLD signal was modeled using a two gamma hemodynamic response function (Friston et al., 1998).

The data were analyzed using a random-effects, whole-brain, voxelwise, repeated measures analysis of variance (ANOVA) with MELODIC FREEDOM (Melodic Improvisation versus Patterns) and RHYTHMIC FREEDOM (Rhythmic Improvisation versus Metronome) as within-subjects factors. Voxels were considered to be significantly activated when they passed a statistical threshold of $p < .001$, uncorrected, with a cluster threshold of a minimum of 50 contiguous interpolated voxels. Since F tests are not indicative of the directionality of results, we examined beta weights for individual regions to ascertain whether effects were due to a positive or negative difference between conditions. It should be noted that all the activations reported to be significant at $p < .001$, uncorrected were also significantly activated at a cluster-level corrected threshold of $p < .05$ when the initial uncorrected threshold was set to $p < .005$, uncorrected. Thus, we chose the more conservative uncorrected p-value to report significant effects in our whole-brain, random-effects analysis.

Results

Behavioral results

In a post-scan questionnaire, when asked to "Give examples of made-up melodies that you played during the experiment," subjects

Table 1
Behavioral results

Measure	PM (mean±SD)	P/RI (mean±SD)	MI/M (mean±SD)	MI/RI (mean±SD)
% Inter-press interval 350–650 ms	68.5±14.6	49.8±18.5	62.9±17.9	39.8±11.6
% Same/adjacent key	91.9±2.9	86.9±13.5	65.1±8.5	71.1±12.8
% Unique Sequences	17.7±5.7	17.3±7.3	86.8±14.3	84.3±14.5
# presses/condition	72.2±9.4	81.0±16.7	72.1±10.1	77.9±17.4

Means and standard deviations (+/−) for all subjects in the four experimental conditions for the following variables: 1. % Inter-press interval 350–650 ms measures the percentage of inter-press intervals that fell between 350 and 650 ms for each condition, demonstrating the amount of rhythmic variability (therefore the higher the percentage the lower the inter-press interval variability). 2. % Same/adjacent key gives the percent of key presses that fell either on the same key as previously pressed or an adjacent key, demonstrating the variety of note combinations (therefore the greater the percentage of same/adjacent key presses the lower the variety of note combinations). 3. % Unique sequences gives the percentage of 5-note melodies that were played once and only once in each condition. 4. # presses/condition gives the average number of presses per condition. PM = Patterns with Metronome, P/RI = Patterns with Rhythmic Improvisation (no metronome), MI/M = Melodic Improvisation with Metronome, and MI/RI = Melodic and Rhythmic Improvisation (no metronome).

listed several 5-note sequences, separated by blank space. This confirmed that subjects indeed heeded the task instructions to improvise 5-note melodies. The descriptive statistics for the behavioral analysis are presented in Table 1.

Assessment of rhythmic freedom (comparison of Rhythmic Improvisation versus Metronome conditions): inter-press interval variability

As expected, a main effect of RHYTHMIC FREEDOM (Rhythmic Improvisation versus Metronome) [$F(1,11)=32.15$, $p<.0001$, $\eta^2=.74$] occurred in the inter-press interval variability, indicating that the variability in the time between keyboard presses was greater in the Rhythmic Improvisation conditions. There was also a main effect of MELODIC FREEDOM (Melodic Improvisation versus Patterns) [$F(1,11)=12.5$, $p<.005$, $\eta^2=.35$] on the inter-press interval variability. No significant interaction between of RHYTHMIC and MELODIC FREEDOM on inter-press interval variability was found.

Assessment of melodic freedom (comparison of Melodic Improvisation versus Patterns conditions): variety of note combinations

As expected, we found a main effect of MELODIC FREEDOM on the variety of note combinations [$F(1,11)=70.9$, $p<.0001$, $\eta^2=.86$]. Specifically, on average, 89.4% of the subjects' presses across both Patterns conditions fell on the same or an adjacent key to the previous press, whereas only 68.1% did across both Melodic Improvisation conditions. Furthermore, the main effect of RHYTHMIC FREEDOM on the variety of note combinations was not significant [$F(1,11)=.04$, $p=.84$, $\eta^2=.004$]. In addition, the interaction effect of MELODIC FREEDOM and RHYTHMIC FREEDOM was found to be significant [$F(1,11)=6.2$, $p=.03$, $\eta^2=.36$]. Post-hoc *t*-test indicated that variety of presses was marginally greater in the Melodic Improvisation/Metronome condition than in the Melodic Improvisation/Rhythmic Improvisation condition [$t(11)=2.2$, $p=.051$], while there was no significant

Table 2
Table of regions modulated by main effects

Main effect of melodic freedom (Melodic Improvisation>Patterns)							Main effect of rhythmic freedom (Rhythmic Improvisation>Metronome)						
Region	Hemisphere	X	Y	Z	F	K	Region	Hemisphere	X	Y	Z	F	K
Rostral cingulate zone (RCZ)	L [a]	−1	21	34	21.39	68	Rostral cingulate zone (RCZ)	L [a]	−3	19	35	21.73	109
Anterior cingulate cortex (ACC)	L [a]	−1	5	47	21.70	111	Anterior cingulate cortex (ACC)	L [a]	−9	−1	38	21.15	129
							Inferior frontal gyrus (IFG)	L	−34	29	18	22.64	158
Ventral premotor cortex (vPMC)	L	−47	7	23	22.97	157							
Dorsal premotor cortex (dPMC)	L	−20	2	49	26.27	754	Dorsal premotor cortex (dPMC)	L	−17	2	43	23.79	385
Dorsal premotor cortex (dPMC)	R	23	−4	45	23.90	273							
							Sensorimotor cortex	L	−25	−14	44	22.84	99
							Superior parietal lobule	L	−20	−60	47	22.53	381
							Inferior parietal lobule	L	−36	−40	39	22.71	157
Supramarginal gyrus [b]	R	61	−42	14	22.77	56							
Cerebellum	L	−19	−61	−11	23.50	332							
Deactivations [c]													
Medial frontal gyrus	R	36	45	8	23.37	89							
Superior frontal gyrus (SFG)	R	15	63	12	25.44	302							
Posterior cingulate	L	−6	−38	34	21.80	112							
Posterior cingulate	R	11	−36	39	21.42	130							
Supramarginal gyrus	L	−58	−45	28	24.04	273							
Angular gyrus	R	45	−46	27	22.35	520							

Main effect of melodic freedom on left, rhythmic freedom on right. X, Y, and Z are Talairach coordinates of regions. F is the F value of the ANOVA. K represents the size of the region in contiguous voxels in mm³.
[a] Although the centers of mass of the ACC regions were in the left hemisphere, these regions extended across the midline.
[b] The right supramarginal gyrus showed a main effect in the opposite direction: less active with increasing melodic freedom.
[c] Deactivated in all tasks relative to rest, and also increasingly deactivated / with increasing melodic freedom.

difference between Metronome and Rhythmic Improvisation sub-conditions for the Patterns conditions [$t(11)=-1.2$, $p=.26$].

Assessment of melodic freedom (comparison of Melodic Improvisation versus Patterns conditions): percentage of unique note sequences

As expected, there was a main effect of MELODIC FREEDOM on the percentage of unique note sequences played [$F(1,11)=233.00$, $p=.0001$, $\eta^2=.95$] and no significant main effect of RHYTHMIC FREEDOM on percentage of unique note sequences, [$F(1,11)=2.59$, $p=.13$, $\eta^2=.19$]; there was no interaction of MELODIC and RHYTHMIC FREEDOM on this measure [$F(1,11)=.50$, $p=.50$, $\eta^2=.043$]. Additionally, across both Metronome and Rhythmic Improvisation conditions, the percentage of unique note sequences was significantly different between Melodic Improvisation and Patterns conditions [$t(11)=14.9$, $p=.0001$]. Specifically, the average percentage of unique note sequences played across both Improvisation conditions (i.e., played once and only once throughout all runs of both Melodic Improvisation/Rhythmic Improvisation and Melodic Improvisation/Metronome conditions over the entire experiment) was

79.2%, and across both Patterns conditions (Patterns/Metronome and Patterns/Rhythmic Freedom conditions over the entire experiment) was 10.3%.

The number of presses was not significantly affected by whether or not subjects improvised or played patterns [$F(1,11)=.71$, $p=.42$, $\eta^2=.06$]. However a small effect of RHYTHMIC FREEDOM on the number of presses was found [$F(1,11)=7.4$, $p=.02$, $\eta^2=.40$]. Post-hoc *t*-test revealed that while there was a slightly greater number of presses in the Patterns/Rhythmic Improvisation compared to the Patterns/Metronome condition [mean difference=8.8 presses/run, $t(11)=3.0$, $p=.011$], the difference in number of presses did not reach significance when comparing Melodic Improvisation/Rhythmic Improvisation with Melodic Improvisation/Metronome [difference=5.8 presses/run, $t(11)=1.9$, $p=.08$]. Thus, this is a relatively small effect, mainly driven by a small difference between the Patterns/Metronome and Patterns/Rhythmic Improvisation conditions. No significant interaction effect of MELODIC FREEDOM and RHYTHMIC FREEDOM on the total number of presses was found [$F(1,11)=1.6$, $p=.23$, $\eta^2=.12$].
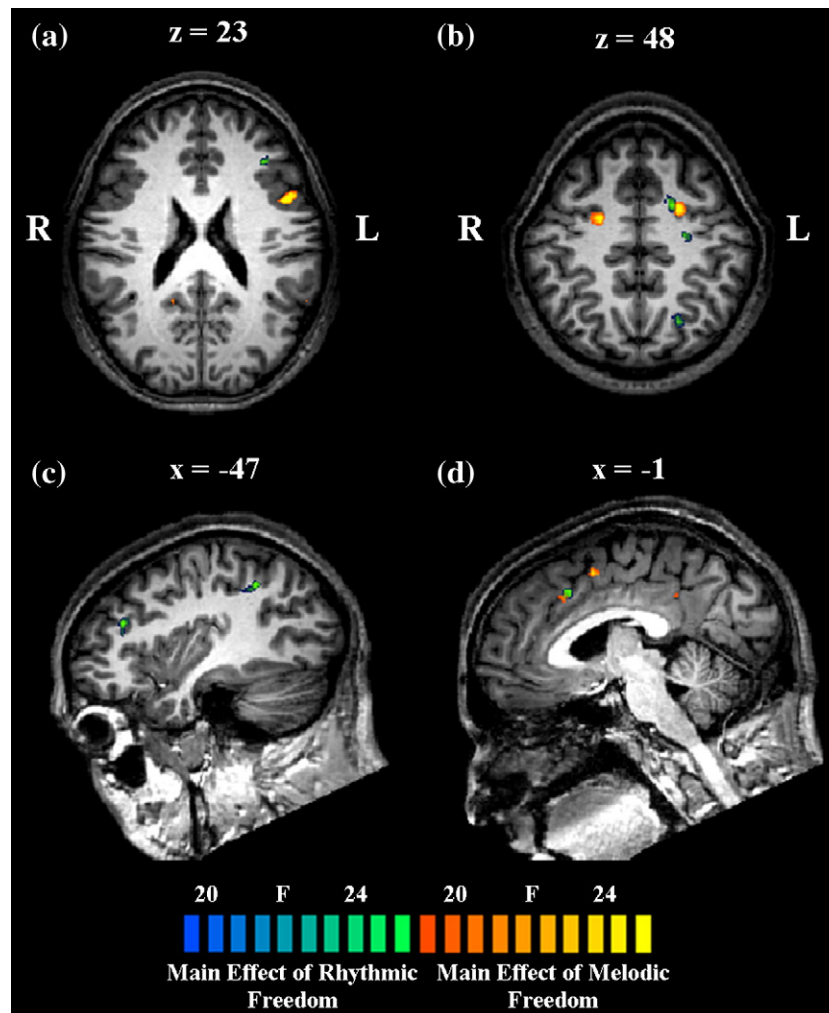

Fig. 2. Main effects of rhythmic and melodic freedom at $p<.001$, uncorrected. Main effect of rhythmic freedom in blue/green, main effect of melodic freedom in yellow/orange. Panel (a) shows activation in the IFG/vPMC, panel (b) shows activation in bilateral dorsal premotor cortices, panel (c) shows activation in IFG and superior parietal lobe, and panel (d) shows activation in the ACC.

Imaging results

Main effects

Main effect of melodic freedom (Melodic Improvisation versus Patterns).   The main effect of melodic freedom modulated the fMRI BOLD signal in a network of regions listed in Table 2, and shown in yellow/orange in Fig. 2: the rostral cingulate zone (RCZ) and a more posterior region of the anterior cingulate cortex (ACC), left ventral premotor cortex (vPMC)/inferior frontal gyrus (IFG), left dorsal premotor cortex (dPMC), the right dorsal premotor cortex, and the left cerebellum. Additionally, there was a network of regions deactivated relative to rest in all conditions, with a main effect of melodic freedom (i.e., increased deactivation with increasing melodic freedom): right medial frontal gyrus, right superior frontal gyrus, right angular gyrus, left supramarginal gyrus, and bilateral posterior cingulate cortex. The right supramarginal gyrus showed a main effect of decreasing activity with increasing melodic freedom.

Main effect of rhythmic freedom (Rhythmic Improvisation versus Metronome).   The main effect of rhythmic freedom modulated the fMRI BOLD signal in a network of regions listed in Table 2, and shown in blue/green in Fig. 2: rostral cingulate zone (RCZ), anterior cingulate cortex (ACC), left inferior frontal gyrus (IFG), left sensorimotor cortex, left superior parietal gyrus, and left inferior parietal lobule.

Interaction of melodic freedom and rhythmic freedom

No significant interaction effect of melodic and rhythmic freedom was found. This suggests that no regions were additionally responsive to the combined effects of rhythmic freedom and melodic freedom, and also that the networks activated by the two main effects were not quantitatively different from each other.

Conjunction of the main effects

To demonstrate the regions commonly activated by melodic freedom and rhythmic freedom, we performed a conjunction analysis of the two main effects (Fig. 3). This demonstrated activation in the
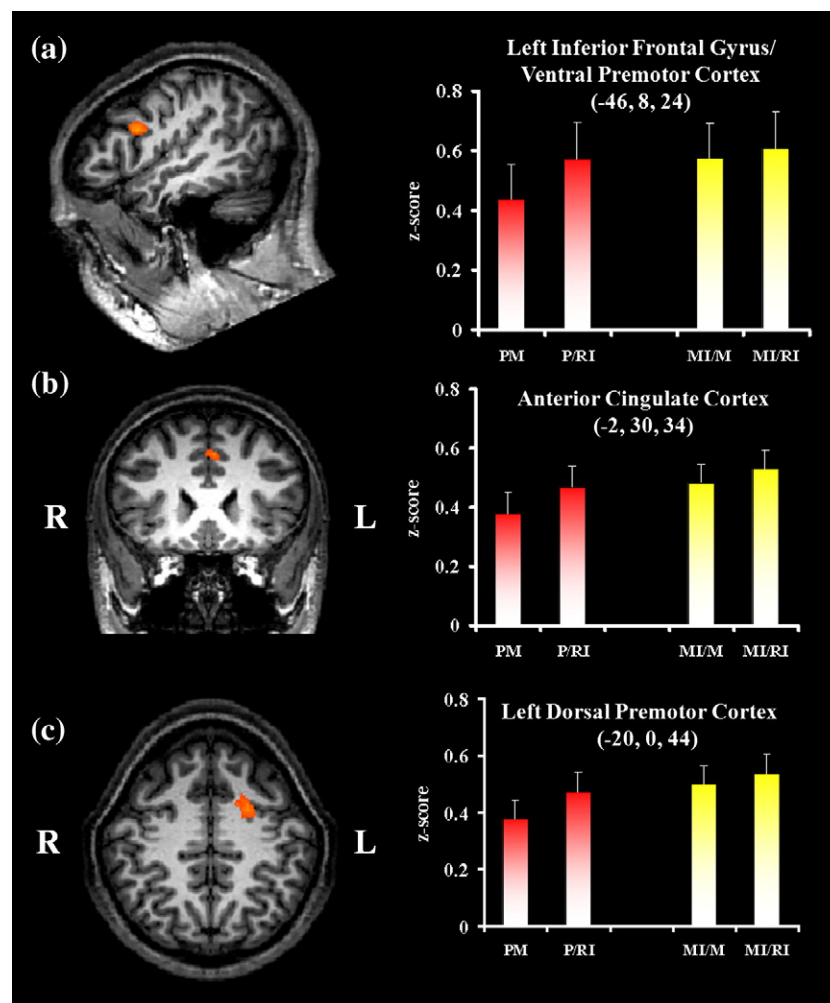

Fig. 3. Conjunction of main effects. Contrast images for the conjunction of the main effects of melodic and rhythmic freedom and bar charts showing the *z*-scores from the areas, with the error bars representing the standard error of the mean. Panel (a) shows the left IFG/vPMC and its beta plots for the four conditions ($p < .001$). Panel (b) shows the RCZ of the ACC and its beta plots for the four conditions ($p < .005$). Panel (c) shows the left dPMC and its beta plots for the four conditions ($p < .001$). PM = Patterns with Metronome, P/RI = Patterns with Rhythmic Improvisation (no metronome), MI/M = Melodic Improvisation with Metronome, and MI/RI = Melodic and Rhythmic Improvisation (no metronome).

IFG/vPMC and dPMC at $p < .001$, uncorrected. Since the RCZ of the ACC showed activation in both main effects, we looked for activation of this region in the conjunction analysis at the slightly more liberal threshold of $p < .005$, and found it indeed to show activation at this threshold.

Discussion

Real-world motor behavior requires spontaneous adaptation to a constantly changing environment. By studying improvisation in pianists with fMRI, we have elucidated the brain regions involved in the generation of novel motor sequences under varying degrees of freedom and constraint. To our knowledge, this represents the first brain imaging study of this novel, generative component of human action.

The behavioral results demonstrate that the subjects were more rhythmically free in the Rhythmic Improvisation conditions (main effect of rhythmic freedom on inter-press interval variability) and more melodically free in the Melodic Improvisation conditions (main effect of melodic freedom on variety of note freedom). We can only speculate as to the main effect of melodic freedom on inter-press duration variability and the interaction of rhythmic freedom and melodic freedom on the variety of note combinations. These effects may indicate that either type of freedom encourages the other type of freedom, i.e., that the more subjects focus on improvising in one domain, the more likely they are to exhibit variety in the other domain. However, as can be seen from the effect sizes above, these effects were relatively low in power and significance. It should also be noted that while melodic freedom was limited to five note choices, rhythmic freedom was potentially unlimited in its possibilities.

Melodic improvisation is further exemplified by subjects' maximization of novelty in Improvisation conditions: the average percentage of invented sequences played only once by a subject throughout all runs of the Improvisation conditions over the entire experiment was 79.2%. This high degree of novelty confirms that subjects sought to generate as many unique melodies as possible, and makes it unlikely that subjects were simply executing random or previously stored sequences. Our brain imaging data reveal that rhythmic (temporal) and melodic (ordinal) improvisation significantly modulate activity in several overlapping brain regions: rostral cingulate zone (RCZ) of the anterior cingulate cortex (ACC), inferior frontal gyrus/ventral premotor cortex (IFG/vPMC), and dorsal premotor cortex (dPMC) (Fig. 3). The common activation of these regions in both main effects suggests that this network is involved in the invention and selection of novel motor sequences irrespective of whether the improvisation is melodic or rhythmic.

Improvisation involves the generation of possible musical phrases, selection among these at any given moment, and execution of the decided-upon motor output. Our results suggest that these processes appear to be subserved by dPMC, IFG/vPMC, and ACC. The dPMC is commonly involved in motor tasks, consistent with a role in the selection and performance of movements (for review see Chouinard and Paus, 2006). Previous studies of piano performance have not reported activation of the IFG and ACC in performance of a memorized piece of music (Parsons et al., 2005). Thus, in light of previous work, our activation of IFG and ACC is likely related to generative nature of our task. Although some studies of music reading have revealed activation of the IFG (Sergent et al., 1992; Bengtsson and Ullen, 2006), this is most likely due to visuo-motor association between visual aspects of the score and motor response

preparation (Muller et al., 2002; Stewart et al., 2003), since a study of music reading with a control visuo-motor condition that did not include musical notes did not yield any activation in IFG/vPMC (Schön et al., 2002).

The left IFG and vPMC are part of Broca's area. Though classically considered a language area, more general functions have been ascribed to this region including sequence processing (Gelfand and Bookheimer, 2003; Schubotz and von Cramon, 2004; Fiebach and Schubotz, 2006; Molnar-Szakacs et al., 2006), selection and retrieval (Badre et al., 2005; Rushworth et al., 2005; Hirshorn and Thompson-Schill, 2006), and maintenance of rules (Bunge et al., 2005) and task set (Brass et al., 2005). The IFG and vPMC have been implicated in language production and processing, as well as action and both visual and auditory perception of action, suggesting the presence of a mirror system in these regions as is thought to exist in their monkey homolog, F5 (Johnson-Frey et al., 2003; Iacoboni et al., 2005; Lahav et al., 2007; for reviews see Rizzolatti and Craighero, 2004; Binkofski and Buccino, 2006). IFG and vPMC regions have also been shown to be involved in music processing (for reviews see Koelsch and Siebel, 2005; Koelsch, 2006). In combination with these results, our demonstration of the involvement of these regions in the production of novel musical sequences may be consistent with a mirror system for music in this region, i.e., a system for both perception and production of music (Molnar-Szakacs and Overy, 2006). Taken together, these results suggest that if a mirror system exists in IFG/vPMC, it is involved most generally in the domain-general processing and production of action sequences, whether such actions are musical, linguistic, or gestural.

The ACC is thought to be involved in voluntary selection (Forstmann et al., 2006), internally selected actions as compared to externally stimulated actions (Mueller et al., 2007), conflict monitoring (Botvinick et al., 2004), decision making (Bush et al., 2002; Walton et al., 2004), unrehearsed movements (Procyk et al., 2000), and, more broadly, willed action (Frith et al., 1991; Paus, 2001). Our result is consistent with many of these proposed functions of the ACC, since improvising musicians go through a continual process of decision making, selecting among a multitude of unrehearsed, conflicting possible musical phrases to play at any given moment, and then intentionally executing their final choice. Consistent with the results presented by Forstmann et al. (2006), we demonstrated an effect of increased freedom for voluntary selection in the rostral cingulate zone (RCZ) of the ACC. The results of Forstmann et al. revealed no difference in activation in the RCZ when the subjects had three versus two degrees of freedom; similarly we did not find a combined effect (interaction) of both rhythmic and melodic freedom beyond the effect of either type of freedom alone. Our results and those of Forstmann et al. thus underscore the importance of the RCZ when voluntary selection is involved, though neither result demonstrates an effect of increased activation with increased degree of selective freedom.

Although the sequences generated in the Melodic Improvisation conditions of our experiment were more complex than what was played in Patterns conditions, the IFG and RCZ activation in rhythmic and melodic improvisation cannot exclusively be explained by this increase in sequence complexity for several reasons. First, it has been shown previously that trained pianists demonstrate no qualitative or quantitative differences in activation pattern for complex versus simple finger sequences (Meister et al., 2005). Second, previous studies of sequence complexity have shown neural activity to be correlated with sequence complexity predominantly in medial motor areas (e.g., SMA), dPMC, and parietal regions. Third,

IFG/vPMC activation has, in the past, not been found to correlate with sequence complexity (for review see Harrington et al., 2000), except when sequences are pre-learned (Haslinger et al., 2002; Lewis et al., 2004) or visually cued (Harrington et al., 2000; Müller et al., 2002). While sequence complexity has not been shown to modulate activity in the anterior cingulate cortex in several studies (Catalan et al., 1998; Harrington et al., 2000; Haaland et al., 2004; Lewis et al., 2004), a meta-analysis of sequence complexity studies has shown some correlation of complexity and anterior cingulate cortex activation (Janata and Grafton 2003). This meta-analysis, however, includes studies of sequence learning, whereas the four studies cited above examine sequence production only.

Though the lack of an interaction between melodic and rhythmic freedom suggests that the networks activated by rhythmic and melodic freedom were not quantitatively different from one another, certain regions were present in one main effect but not the other (at the selected threshold). The main effect of melodic, but not rhythmic, freedom yielded activation in the right premotor cortex (ipsilateral to the task) and left cerebellum (contralateral to task), both probably involved in sequence selection and production (Harrington et al., 2000; Chouinard and Paus, 2006). Additionally, the main effect of melodic freedom revealed deactivations in several regions when compared to playing patterns: right superior and medial frontal gyri, right angular gyrus and posterior cingulate, and the left supramarginal gyrus. These deactivations with increasing melodic freedom are consistent with task-induced deactivation seen in goal-directed action and under conditions requiring increased attention (Frith et al., 1991; Gusnard and Raichle, 2001; McKiernan et al., 2003), both of which apply to improvisation as compared to playing patterns. The parietal activity in the main effect of rhythmic freedom is consistent with the role of these parietal regions in spatiomotor integration, action representation, movement selection, and, most generally, skilled action (Catalan et al., 1998; Haslinger et al., 2002; Johnson-Frey, 2003; Jeannerod, 2003).

While earlier work in music cognition sought to examine which brain regions were involved in various aspects of musical processing and performance, more recent research has shifted toward using music to examine more general aspects of cognition such as plasticity (Gaser and Schlaug, 2003), auditory learning and memory (Gaab et al., 2006), visuo-motor transformations (Schön et al., 2002; Stewart, 2005; Bengtsson and Ullen, 2006), audiomotor integration (Lahav et al., 2007), and emotion (Koelsch et al., 2006). In a similar vein, we used improvisation by pianists as a way to study the neural correlates of novel motor sequence generation under varying degrees of freedom and constraint, a fundamental aspect of real world motor behavior. The present findings therefore demonstrate the utility of using music as a case study to investigate the neural correlates of domain-general cognitive phenomena.

In sum, the data reveal that musical improvisation activates ACC, IFG/vPMC, and dPMC irrespective of the domain of improvisatory freedom (rhythmic versus melodic), suggesting a role for these regions in the generation of novel motor sequences. Future work will need to examine to what extent this network is truly domain-general by examining the real-time production of novel non-musical motor sequences under varying conditions.

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