NeuroImage 49 (2010) 712–719

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

# Expertise-related deactivation of the right temporoparietal junction during musical improvisation

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ARTICLE INFO

*Article history:*
Received 26 July 2009
Revised 11 August 2009
Accepted 18 August 2009
Available online 26 August 2009

*Keywords:*
Motor sequences
Music
Expertise
Improvisation
fMRI
Temporoparietal junction

## ABSTRACT

Musical training has been associated with structural changes in the brain as well as functional differences in brain activity when musicians are compared to nonmusicians on both perceptual and motor tasks. Previous neuroimaging comparisons of musicians and nonmusicians in the motor domain have used tasks involving prelearned motor sequences or synchronization with an auditorily presented sequence during the experiment. Here we use functional magnetic resonance imaging (fMRI) to examine expertise-related differences in brain activity between musicians and nonmusicians during improvisation – the generation of novel musical–motor sequences – using a paradigm that we previously used in musicians alone. Despite behaviorally matched performance, the two groups showed significant differences in functional brain activity during improvisation. Specifically, musicians deactivated the right temporoparietal junction (rTPJ) during melodic improvisation, while nonmusicians showed no change in activity in this region. The rTPJ is thought to be part of a ventral attentional network for bottom-up stimulus-driven processing, and it has been postulated that deactivation of this region occurs in order to inhibit attentional shifts toward task-irrelevant stimuli during top-down, goal-driven behavior. We propose that the musicians' deactivation of the rTPJ during melodic improvisation may represent a training-induced shift toward inhibition of stimulus-driven attention, allowing for a more goal-directed performance state that aids in creative thought.

## Introduction

The musician's brain has come to serve as a model system for the study of expertise-related changes in the brain (for reviews, see Schlaug, 2001; Münte et al., 2002, Pantev et al., 2003). Musicians spend years training their fine motor skills, perception and cognition of auditory patterns, and multimodal processing (e.g., visual–motor and visual–auditory transformations in score reading, auditory–motor processing in performance). The effects of such musical training have been associated with increases in gray matter volume in motor and auditory cortices (Gaser and Schlaug, 2003; Bangert and Schlaug, 2006) as well as in frontal, parietal, and occipital regions (Hyde et al., 2009); increases in white matter tract size (Schlaug et al., 1995) and organization (Bengtsson et al., 2005); and enlargements of both somatosensory (Elbert et al., 1995) and auditory cortical representations (Pantev et al., 1998).

In addition, musical training can lead to changes in patterns of brain activation when musicians are compared to nonmusicians in tasks of auditory perception (Hodges et al., 2005), auditory memory (Gaab et al., 2006), and motor sequencing (Hund-Georgiadis and von Cramon 1999; Krings et al., 2000; Jäncke et al., 2000; Lotze et al., 2003; Chen et al., 2008). These results suggest that musical training can lead to shifts in cognitive strategy on music-related tasks, reflected in changes in the neural networks recruited to perform these tasks.

Most functional brain imaging studies comparing musicians and nonmusicians on perceptual and motor tasks have not used particularly ‘musical’ paradigms, but rather have isolated pitch memory (Gaab et al., 2006) or rhythmic performance (Chen et al., 2008), for example, outside of their musical context. This is, of course, understandable: nonmusicians, by definition, are not trained in specific musical skills, and thus it would be impractical to test them on such skills (e.g., performance of a piece, auditory analysis of a complex example). Although nonmusicians are not typically trained to play pieces of music from memory, they are quite able to improvise melodies and rhythms (Sági and Vityáni, 1988). Thus, in the present study, we compared musicians and nonmusicians during improvisation, the generation of novel auditory–motor sequences. In so doing, we were able to examine the expertise-related differences in

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doi:10.1016/j.neuroimage.2009.08.042

functional brain activity when subjects performed a musical task involving creative decision making. While previous work has demonstrated the use of improvisation to study the neural correlates of spontaneous novel motor sequence generation in musicians (Brown et al., 2006; Bengtsson et al., 2007; Limb and Braun, 2008; Berkowitz and Ansari, 2008), the degree to which activity in such brain networks represents a specialization due to musical training has thus far not been systematically explored.

In our previous study, we used functional magnetic resonance imaging (fMRI) to examine the neural correlates of musical improvisation by classically trained pianists (Berkowitz and Ansari 2008). We used the same paradigm in the present study with nonmusicians, and compared results between musicians and nonmusicians. Of course it would be nearly impossible to fully replicate the experience of improvisation in the scanner environment: improvisation often takes place in groups, and solo improvisation usually takes place in a meaningful context, both physically (a concert hall, a jazz club, etc.) and musically. Even if it were possible to study the full spectrum of live improvisation in the scanner, the resulting neural activation would represent diverse cognitive processes (decision making, creativity, emotion, memory, attention, etc.), and it would be difficult to tease apart which networks of regions were responsible for which underlying processes. We thus designed a set of tasks that allowed us to focus on the creative decision making involved in generating novel motor sequences in both the rhythmic and melodic domains. Thus, while our tasks may not represent musical improvisation to the fullest extent possible, they are certainly improvisatory, and provide a window into the neural correlates involved in creative decision making in the auditory-motor domain.

Subjects performed four tasks on a 5-key piano keyboard (Fig. 1; see also Methods), and heard what they played in real time through scanner safe headphones. When asked to improvise melodies, subjects continuously invented 5-note melodies. This was compared to subjects' performance of simple, prelearned 5-note patterns to assess brain activity in melodic improvisation. Each of these two conditions had two subconditions: subjects either synchronized their improvised melodies or patterns with a metronome or improvised their own rhythms to those invented sequences or patterns. Comparison of rhythmic improvisation conditions with metronome conditions allowed for the examination of rhythmic freedom. The four conditions were thus Patterns/Metronome, Melodic Improvisation/Metronome, Patterns/Rhythmic Improvisation, Melodic Improvisation/Rhythmic Improvisation.

Using this paradigm with trained musicians (Berkowitz and Ansari 2008), we found that brain areas demonstrating changes in activity included the inferior frontal gyrus (IFG), rostral cingulate zone (RCZ) of the anterior cingulate cortex (ACC), and dorsal premotor cortex (dPMC) for both melodic and rhythmic freedom; ipsilateral sensorimotor cortex, superior parietal lobule, and inferior parietal lobule for rhythmic freedom alone; and deactivations for melodic freedom alone including the right middle and superior frontal gyrus, bilateral posterior cingulate, left supramarginal gyrus, and right angular gyrus. We interpreted the activations in IFG, RCZ, and dPMC in the previous study as being involved in the generation, selection, and execution of novel auditory–motor sequences; the parietal activation to be involved in spatiomotor integration for movement selection and skilled action; and the deactivations to be task-induced, associated with the goal-directed and attention-requiring nature of improvisation. Using the same tasks, in the present study, we sought to examine which, if any, of the brain regions active in musicians in our previous study or other regions differed in activation between musicians versus nonmusicians.

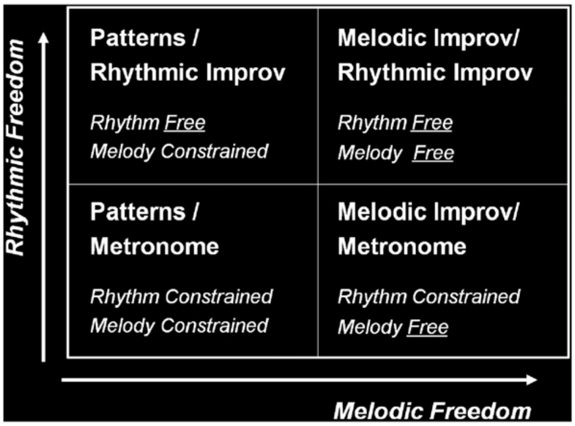

**Fig. 1.** Task design. Four conditions with varying degrees of rhythmic and melodic freedom.

We hypothesized that given that both groups would be involved in a task of motor creativity requiring goal-directed attention, they would likely differ in degree of activation in one or more of the regions listed above rather than having involvement of a different network entirely, presuming matched motor performance. Specifically, we suspected that the regions involved in generation and selection (i.e., the IFG, RCZ, and dPMC) would be activated to a greater degree in musicians rather than nonmusicians, since musicians would ostensibly be generating more possible musical sequences among which to select and execute.

## Methods

Our methods with respect to the behavioral paradigm, analysis of behavioral results, imaging parameters, and imaging analysis were identical to that in our previous study (Berkowitz and Ansari, 2008), with the addition of the between-groups comparisons on all measures. We have reiterated our methods here for the reader's convenience.

### *Subjects*

We recruited 13 classically trained undergraduate pianists from the Dartmouth College Music Department (8 female, mean age = 21.9 years, mean musical training = 13 years of piano experience) and 15 subjects from the Dartmouth community at large who do not currently and have not recently played a musical instrument, and whose past experience playing and/or learning a musical instrument was for 3 years or less (7 female, mean age = 22.9 years, mean musical training = 0.67 years [8 subjects had no musical training at all, and of those with training during childhood, one had 1 year, two had 2 years, and one had 3 years of music lessons]). The musician subjects were the same as the subjects whose data were analyzed in Berkowitz and Ansari (2008). One musician subject and three nonmusician subjects were excluded from analysis because of excessive head motion, leaving 12 subjects in each group 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 (Fig. 1): (1) *Patterns/Metronome* (note choice and rhythm both constrained): subjects played any of the seven simple, preinstructed 5-note patterns described above in any order of their choosing. Subjects played one note per beat coordinated with a 2-beat-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 five runs in which each of the four 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 were collected using e-Prime software (Psychological Software Tools, Pittsburgh, PA), recording each key press and the interpress duration.

### Stimulus delivery

Subjects performed the task on a 5-note response box resembling a 5-key piano keyboard. Each key triggered the playing of a wave file of the given note by ePrime 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 3-T Phillips Intera Allegra whole-body MRI scanner using an 8-Channel Phillips Sense head-coil. A gradient echo-planar imaging $T_2$*-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, 0.5 mm gap, $80\times80$ matrix, repetition time, 2500 ms, echo time: 35 ms, flip angle: 90°, field of view $240\times240$ mm). For each of the 5 functional runs, 123 volumes were acquired. Three-dimensional whole-brain high-resolution $T_1$-weighted images (160) were acquired in the sagittal plane ($1\times0.94\times0.94$) with a standard Phillips MPRage 3D sequence.

### Behavioral data analysis

We designed several measures to confirm that groups performed the tasks appropriately, namely, playing patterns when they were asked to do so, improvising melodies when they were asked to do so, playing with the metronome when they were asked to do so, and exhibiting more rhythmic freedom when asked to improvise rhythms. We deemed it impossible to create an objective measure of how 'musical' or 'creative' improvised melodies or rhythms were. Rather, we designed our behavioral measures to assess reliability of task performance, and whether that performance differed between groups.

#### Assessment of rhythmic freedom (comparison of Rhythmic Improvisation versus Metronome conditions): interpress interval variability

To assess rhythmic freedom in the Rhythmic Improvisation conditions compared to the Metronome conditions, we quantified interpress 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 interpress 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 preinstructed 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 prelearned 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 and Patterns/Metronome), and predicted a low percentage of unique note sequences here, given that subjects were instructed to play the same prelearned patterns in both Patterns subconditions.

### *Imaging data analysis*

Structural and functional 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. From the musician group, 11 out of 60 runs total across 12 subjects (18.3%) were removed, and one subjects' data were excluded entirely as a result of excessive head motion. In addition, four runs (each from a different subject) were excluded from the musician group due to equipment problems. We thus evaluated a total of 45 runs across 12 subjects in the musician group (75% of experimental runs acquired, excluding the one subject whose data were excluded entirely). From the nonmusician group, 11 out of 60 runs total across 12 subjects (18.3%) were removed due to excessive head motion, and three subjects' data were excluded entirely. In addition, six runs were excluded from the nonmusician group due to equipment problems (two runs from one subject, and one run each from four different subjects). We thus evaluated a total of 43 runs across twelve subjects in the nonmusician group (71.7% of experimental runs acquired, excluding the three subjects whose data were removed entirely).

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, general linear model. Paired sample *t*-tests were conducted to compare the main effects of melodic freedom (Melodic Improvisation vs. Patterns) and rhythmic freedom (Rhythmic Improvisation vs. Metronome) between groups.

The statistical maps resulting from these comparison were initially thresholded at $p<0.001$, uncorrected, and were subsequently corrected for multiple comparisons using cluster-size thresholding (Forman et al., 1995; Goebel et al., 2006). In this method, an initial voxel-level (uncorrected) threshold is set (in the present study, $p<0.001$). Then, thresholded maps are submitted to a whole-slab correction criterion based on the estimate of the map's spatial smoothness and on an iterative procedure (Monte Carlo simulation) for estimating cluster-level false-positive rates. After 1000 iterations, the minimum cluster size that yielded a cluster-level false-positive rate ($\alpha$) of .01 (1%) was used to threshold the statistical maps. In other words, this method calculates the size that a cluster would need to be (the cluster threshold) to survive a correction for multiple comparisons at a given statistical level. Only activations whose sizes meet or exceed the cluster threshold are allowed to remain in the statistical maps.

## Results

### *Behavioral results*

#### *Assessment of rhythmic freedom: interpress interval variability*

As expected, we demonstrated a main effect of rhythmic freedom across both groups [$F_{(1,22)}=73.657$, $p<0.0001$]. There was no significant interaction of rhythmic freedom and group [$F_{(1,22)}=0.434$ $p=0.517$]. Thus, subjects were more rhythmically free in Rhythmic Improvisation conditions when no metronome was present, and the two groups performed equivalently on this measure. There was also a main effect of melodic freedom across groups [$F_{(1,22)}=38.493$, $p<0.0001$], but no interaction of melodic freedom and group [$F_{(1,22)}=1.345$, $p=0.259$]. The interaction of melodic and rhythmic freedom was also found to be nonsignificant [$F_{(1,22)}=0.939$, $p=0.343$]. Finally, there was no significant three-way interaction of melodic freedom, rhythmic freedom, and group [$F_{(1,22)}=0.030$, $p=0.864$]. The main effect of melodic freedom could indicate that subjects tended to play more melodically freely when they were also allowed rhythmic freedom. Whatever the cause of this effect, it did not differ between groups.

#### *Assessment of melodic freedom: variety of note combinations*

As expected, there was a main effect of melodic freedom across groups [$F_{(1,22)}=81.767$, $p<0.0001$]. There was no interaction of melodic freedom and group [$F_{(1,22)}=0.838$, $p=0.370$]. These results demonstrate that both groups were similarly more melodically varied in their Improvisation conditions as compared to Patterns conditions and that both groups similarly adhered to playing the preinstructed patterns in Patterns conditions. There was no significant main effect of rhythmic freedom across groups [$F_{(1,22)}=0.017$, $p=0.897$], nor was there a significant interaction of rhythmic freedom and group [$F_{(1,22)}=0.258$, $p=0.616$]. The interaction of melodic and rhythmic freedom was found to be nonsignificant [$F_{(1,22)}=4.060$, $p=0.056$]. There was a significant three-way interaction of melodic freedom, rhythmic freedom, and group [$F_{(1,22)}=5.510$, $p=0.028$]. Post-hoc tests revealed an interaction of rhythmic and melodic freedom in the group of musicians alone [$F_{(1,11)}=6.257$, $p=0.029$] (as a result of the variety of note combinations being marginally greater in the Melodic Improvisation/Metronome condition than in the Melodic Improvisation/Rhythmic Improvisation condition [$t_{(11)}=2.2$, $p=0.051$]), whereas the nonmusicians group showed no such interaction [$F_{(1,11)}=.115$, $p=0.741$]. Thus, the three-way interaction can be explained by a small interaction of melodic and rhythmic freedom in the musician group and a lack thereof in the nonmusician group.

#### *Assessment of melodic freedom: percent of unique sequences*

As expected, there was a significant main effect of melodic freedom across groups [$F_{(1,22)}=765.834$, $p<0.0001$]. There was no significant interaction of melodic freedom and group [$F_{(1,22)}=0.018$, $p=0.895$]. Thus, both groups exhibited similar degrees of melodic novelty in Melodic Improvisation conditions. There was no significant main effect of rhythmic freedom across groups [$F_{(1,22)}=0.182$, $p=0.674$], nor was there a significant interaction of rhythmic freedom and group [$F_{(1,22)}=4.126$, $p<0.054$]. The interaction of melodic and rhythmic freedom was also found to be nonsignificant across groups [$F_{(1,22)}=1.593$, $p=0.220$]. A three-way interaction of melodic freedom, rhythmic freedom, and group was found to be significant [$F_{(1,22)}=5.091$, $p=0.034$]. Post-hoc *t*-tests revealed that this interaction can be explained by insignificant but opposing trends in differences between Melodic Improvisation/Rhythmic Improvisation and Melodic Improvisation/Metronome between groups (nonmusicians: $[t_{(11)}=1.213, p=0.250]$, musicians: $[t_{(11)}=-2.008, p=0.070]$; i.e., nonmusicians had a marginally higher percent uniqueness in Melodic Improvisation/Metronome as compared to Melodic Improvisation/Rhythmic Improvisation, whereas musicians showed a marginal difference in the opposite direction). Most relevant for this measure, however, was the strongly significant main effect of melodic freedom on the percent of unique sequences, and the fact that this effect did not differ between groups.

### *Number of key presses*

The number of key presses was assessed to make sure that the amount of motor activity was roughly the same across conditions and between groups. There was no significant main effect of melodic freedom across groups $[F_{(1,22)}=1.218, p=0.282]$, nor was there an interaction of melodic freedom and group $[F_{(1,22)}=.042, p=0.839]$. There was a very small main effect of rhythmic freedom across groups $[F_{(1,22)}=4.359, p=0.049]$, but no interaction of rhythmic freedom and group $[F_{(1,22)}=2.534$, p .126]. This indicates that both groups played slightly more notes when no metronome was present, but that this did not differ significantly between groups. There were no significant interactions between melodic and rhythmic freedom $[F_{(1,22)}=3.280, p=0.084]$ or between melodic freedom, rhythmic freedom, and group $[F_{(1,22)}=.233, p=0.634]$ for this measure.

In sum, there was a main effect of rhythmic freedom on the interpress interval variability, indicating that all subjects were more rhythmically free in Rhythmic Improvisation conditions than when they played with the metronome. There was a main effect of melodic freedom on both variety of note combinations and percent of unique sequences, indicating that all subjects were more melodically free in Melodic Improvisation conditions than when they played patterns. None of these behavioral measures showed significant differences between groups.

### *fMRI results*

There was a single difference between groups in the brain imaging data: for the main effect of melodic freedom (the contrast of Melodic Improvisation conditions versus Patterns conditions), a deactivation of the right temporoparietal junction (rTPJ) was found in the musician group (40, –39, 24; 546 voxels) (Fig. 2), with no significant activity in this region in the nonmusician group. There was no difference between groups with respect to rhythmic freedom (Rhythmic Improvisation conditions compared to Metronome conditions).

To further examine the group differences in the rTPJ for melodic improvisation, one-sample *t*-tests were conducted on the mean beta weights of all voxels in this region to assess whether this activation in each of the four experimental conditions differed significantly from baseline (rest) in each group. In order to ensure that these *t*-tests were corrected for multiple comparisons, Bonferroni corrections were applied at $p<0.05$. At four comparisons per group, this required a significance threshold of $p<0.0125$ (i.e., 0.05 divided by 4). In the nonmusicians, none of the activations in the rTPJ was found to be significant in this analysis (Patterns/Metronome $[t=1.900, p=0.084]$, Patterns/Rhythmic Improvisation $[t=1.914, p=0.082]$, Melodic Improvisation/Metronome $[t=2.509, p=0.029]$, Melodic Improvisation/Rhythmic Improvisation $t=2.953, p=0.065]$). In the musician group, two of the conditions were found to have significant deactivation in the rTPJ (Melodic Improvisation/Metronome $[t=-4.261, p=0.001]$, Melodic Improvisation/Rhythmic Improvisation $[t=-3.877, p=0.003]$), while two deactivations were not found to survive Bonferroni correction (Patterns/Metronome $[t=-1.796, p=0.100]$ and Patterns/Rhythmic Improvisation $[t=-2.811, p=0.017]$). The significant deactivations in the two conditions of Melodic Improvisation are thus consistent with the group difference for melodic freedom but not rhythmic freedom in the rTPJ.

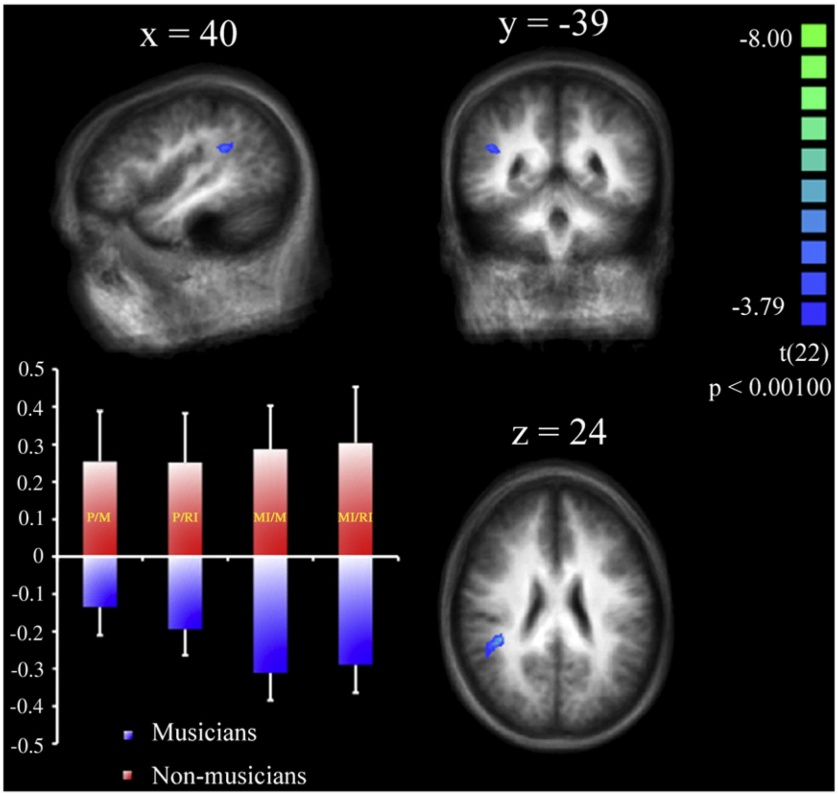

**Fig. 2.** fMRI results of the comparison between groups for the main effect of melodic freedom. This figure demonstrates the region of deactivation in the right temporoparietal junction (40, –39, 24; 546 voxels) in the musician group from sagittal, coronal, and axial views (clockwise from upper left) at $p<0.001$, uncorrected (corrected $p=0.01$ at the cluster level). The bar graph in the lower left corner demonstrates the deactivation in the musician group (in blue) and the activation in the nonmusician group (in red) for each of the four tasks (P/M = Patterns/Metronome, P/RI = Patterns/Rhythmic Improvisation, MI/M = Melodic Improvisation/Metronome, MI/RI = Melodic Improvisation/Rhythmic Improvisation).

## Discussion

In this study, we used improvisatory tasks to examine the neural correlates of the spontaneous generation of novel auditory–motor sequences in trained musicians as compared to nonmusician control subjects. The main effect of melodic freedom demonstrated a strong difference between musicians and nonmusicians in the right temporoparietal junction (henceforth rTPJ), while the main effect of rhythmic freedom did not reveal any activation differences between the two groups. More specifically, the rTPJ was found to be significantly deactivated in conditions of melodic improvisation as compared to baseline in the group of musicians, while the nonmusicians were not found to have any significant activation in this region as measured by fMRI (i.e., the one-sample *t*-tests reported above show that the activation of this region in the nonmusician group was not found to differ significantly from baseline in any of the four conditions, although the trend in the nonmusician group was toward activation). This area appears to be very close to the same region deactivated by musicians in our previous study (the right angular gyrus [45, −46, 27]).

While we had hypothesized that differences would likely be found in the frontal regions involved in generation and selection of novel motor sequences (e.g., inferior frontal gyrus, anterior cingulate cortex, dorsal premotor cortex), we did not predict that the main difference would be in degree of deactivation of a parietal region, nor that the difference would be for melodic improvisation but not rhythmic improvisation, nor that the frontal areas listed above would show no differences between groups. In what follows, after reviewing relevant literature on the purported role of the rTPJ and its deactivation in various cognitive tasks, we propose an explanation for the relevance of expertise-related deactivation of this region during improvisation. We then discuss possible explanations for the lack of group differences during rhythmic improvisation and in the frontal areas seen in our previous study of musicians alone.

The rTPJ is thought to be part of a ventral attentional network for bottom-up stimulus-driven processing (for reviews, see Corbetta and Shulman, 2002; Corbetta et al., 2008). Brain imaging results have supported the hypothesis that this region is important for reorienting attention when behaviorally relevant stimuli in any sensory modality are detected (Downar et al., 2000, 2001, and 2002; Kincade et al., 2005; Serences et al., 2005; Corbetta and Shulman, 2002; Corbetta et al., 2008). Deactivation of this region has been postulated to occur in response to top-down signals during goal-driven behavior so as to inhibit attentional shifts toward task-irrelevant stimuli that could cause decrements in performance (Shulman et al., 2003; Todd et al., 2005; for a review, see Corbetta et al., 2008). These top-down signals are thought to serve a filtering function, allowing only task-relevant stimuli to activate the rTPJ, and preventing a reorienting to task-irrelevant stimuli (Corbetta et al., 2008). In support of such theories of rTPJ function, increasing deactivation of this region has been found to correlate with more successful task performance in target detection (Shulman et al., 2007) and visual short-term memory (Chee and Chuah, 2007), as well as faster reaction times when processing large numbers of objects as opposed to smaller numbers (Ansari et al., 2007).

Although deactivation of the rTPJ has been correlated with improved task performance in these contexts, the deactivation of this region as a function of expertise revealed in the present paper is, to our knowledge, a novel finding. The deactivation of the rTPJ cannot be critical for the invention of novel motor sequences: despite a lack of deactivation in this region, nonmusicians achieved a level of novelty in melodic improvisation equivalent to that of the musician group, as evidenced by the lack of difference between the two groups in the percent of unique melodic sequences generated during the melodic improvisation conditions. In light of the prior work on the rTPJ reviewed above, we propose two related (and not mutually exclusive) possibilities for why musicians would demonstrate substantial deactivation of this region during improvisation while nonmusicians do not show any significant change in activity: training-induced changes in goal-directed attention and/or shifts toward a more top-down cognitive strategy.

When improvising, musicians are in a goal-driven state of invention, and, at least in the case of our experiment, the pursuit of novelty. It is thus important for their attention not to be distracted by irrelevant stimuli (e.g., in this experiment, scanner noise, errors in intended performance, etc.). The deactivation of the rTPJ region in experienced musicians suggests that their expertise may allow them to enter a more focused attentional state during performance of this task. Moreover, while the deactivations in the rTPJ in the musician group were statistically significant only for conditions involving melodic improvisation, visual inspection of Fig. 2 shows that a trend toward deactivation is seen even with rhythmic improvisation alone (Patterns/Rhythmic Improvisation) and to a lesser degree, with no improvisation at all (Patterns/Metronome). This suggests that musicians are entering a different state of attentional focus than nonmusicians as soon as they engage in even the simple act of playing, and that this effect is particularly heightened during melodic improvisation. Widespread deactivations during the performance of a previously memorized piece of music have been theorized to play a similar role in that context (Parsons et al., 2005). Sustained attention is indeed thought to be a critical cognitive process for creativity (Dietrich, 2004). Thus, one interpretation of the present finding is that musicians may have been more focused and/or goal driven in their task performance, whereas nonmusicians, because of lack of experience, may have been less so.

Beyond the general possibility of a more focused goal-driven attentional state, a more specific potential interpretation of the musicians' deactivation of the rTPJ during improvisation is that they strategized in a more top-down fashion, conceiving of and/or planning their improvised melodies as 5-note groups, and thus inhibiting any sort of stimulus-driven response to what they played while they planned their next improvised sequence. Nonmusicians, lacking musical experience, may have been more dependent on stimulus-driven information (i.e., auditory and sensory feedback) during melodic improvisation. This is consistent with the proposal of a recent fMRI study in which musicians' and nonmusicians' brain activity were compared during tasks of rhythmic synchronization, showing overlapping but distinct neural substrates between the two groups (Chen et al., 2008). These authors postulate a model in which musicians use a top-down strategy based on their prior knowledge of musical structure, whereas nonmusicians, without such knowledge, are relegated to bottom-up processing. Our results may indicate a similar training-induced shift toward a top-down processing strategy in improvisation. Such a strategy has also been described in a recent EEG study of the imagery of improvised dance in professionals versus novices (Fink et al., 2009b). In this study, increased alpha synchronization in right temporoparietal and parietooccipital areas in professional dancers as compared to novices was revealed, which the authors interpreted as reflecting top-down inhibition to prevent interference from task-irrelevant information during creative thinking. Top-down inhibition of stimulus-driven attention is also thought to correlate with novel idea generation during creative problem solving in the verbal domain (Fink et al., 2009a). Thus, such top-down inhibition may be an important component of creative thought across domains.

If the rTPJ is more deactivated in musicians through a top-down mechanism, this raises the question as to what brain region(s) is/are the source of this inhibition. It is thought that such inhibitory signals may come from the frontal eye fields, intraparietal sulcus, prefrontal cortex, anterior cingulate cortex, and/or the anterior insula (for a review, see Corbetta et al., 2008). Although we did not see any differences in activation in any of these regions at our selected, corrected threshold, we did find greater activation of the anterior cingulate cortex (Talairach coordinates: 4, 19, 21) in musicians as compared to nonmusicians during melodic improvisation at a more liberal threshold of $p < 0.005$, uncorrected. Thus, the ACC may be responsible for the top-down inhibition of the rTPJ in musicians in our experiment, consistent with the role of this region in cognitive control reviewed by Corbetta et al., 2008. It may be the case that such top-down modulatory signals occur prior to the deactivation of the rTPJ, a possibility that could be assessed in future studies using event-related design paradigms.

As noted above, we found a difference between groups for the main effect of melodic but not rhythmic freedom. The invention of novel melodic sequences may have thus required more top-down organizational processing than the invention of rhythms in the context of our task design. We speculate that one possible explanation for the presence of a group difference in the rTPJ for melodic improvisation and a lack of group differences in rhythmic improvisation could be as follows: In our experiment, there were only five pitch choices with which to work when improvising melodies, whereas there were potentially infinite durational possibilities when improvising rhythms. Thus, striving for ways of organizing novel melodic combinations of a limited number of elements could have required more effort, intention, and top-down attention to structure in the musician group as opposed to playing rhythmically freely.

In our previous study examining the neural correlates of the same tasks in musicians alone (Berkowitz and Ansari, 2008), we revealed a number of areas whose activity was modulated by melodic and rhythmic freedom that were not found to be significantly differentially activated between the musicians and the nonmusicians of the present study (see Introduction). There are several possible interpretations for the lack of significant differences in activation of any of these regions aside from the rTPJ between musicians and nonmusicians as measured by fMRI in the present study, despite the large differences in the characteristics of the two groups of subjects with respect to musical experience. First, it is possible that the neural activity associated with the general mechanisms subserving sequence generation, selection, and execution is not modulated by experience, whereas only the degree of top-down, goal-directed attention influencing these processes is altered by increasing expertise. Second, it is possible that similar levels of activity in these regions may not represent the same processes. For example, activity in dPMC has been shown to be increased with increasing complexity of a motor task in nonmusicians but not in musicians, whose brain activity is not significantly affected by the degree of motor sequence complexity in executed sequences (Meister et al., 2005). It is thus possible that the lack of observable significant differences in the dPMC in the present comparison could reflect the effect of increasing motor complexity in nonmusicians but more generativity-related function in musicians.

## Conclusions

In the present study, we explored whether there were expertise-related differences in brain activity during musical improvisation when musicians were compared with nonmusicians. Contrary to our prediction that differences would occur in more frontal regions, our results demonstrated that trained musicians deactivate the right temporoparietal junction with increasing melodic freedom, whereas nonmusicians showed no significant changes in brain activity in the same region despite behaviorally matched performance. These results are consistent with previous work demonstrating that deactivation of the rTPJ occurs in goal-directed states requiring top-down inhibition to prevent stimulus-oriented distraction during task performance (for a review, see Corbetta et al., 2008). Furthermore, our results corroborate the importance of such processes in creative thought proposed for both verbal tasks (Fink et al., 2009a) and in dance imagery (Fink et al., 2009b), and may provide support for a possible role of the rTPJ in creativity as has been described in other nonmusical domains as has been proposed by Samco et al. (2005), Aghababyan et al. (2007), and Fink et al. (2009b). Improvising musicians appear to exert more top-down attentional control than nonmusicians performing the same task, indicating a difference in cognitive strategy shaped by years of experience. Training-related changes in the musical mind thus go beyond regions involved in purely auditory and motor aspects of task performance, extending to higher levels of cognitive control as well, a finding that has also emerged in other recent studies of music cognition (Gaab et al., 2006; Chen et al., 2008).

The present study provides further evidence that musical tasks represent an excellent modality for the study of domain-general cognitive processes such as top-down attentional control. Future studies could more directly examine these processes by parametrically varying the need for top-down organization of motor sequence output for improvised, learned, and/or visually or auditorily presented sequences. Furthermore, nonmusicians could be trained on improvisation tasks to see if this experience changes their cognitive strategy and resultant functional brain activity, as was observed in a study of pitch memory by Gaab et al. (2006), which demonstrated training-induced functional plasticity in that context. Such future studies could provide further insights into the neural correlates of attention and creative thought and their roles during musical performance, as well as their modulation by training and expertise.

## Acknowledgments

This research was generously supported by a graduate student research award from the Harvard Mind/Brain/Behavior Initiative and by additional support from the Dartmouth Brain Imaging Center. We are grateful to Bibek Dhital, Alyssa Scott, and Ian Lyons for their assistance with the experimental setup, subject recruitment, and data analysis. We thank also Tim Ledlie for assistance in the analysis of the behavioral data, and Fiery Cushman for useful discussion regarding the analysis of the behavioral data.

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