# Moving on Time: Brain Network for Auditory–Motor Synchronization is Modulated by Rhythm Complexity and Musical Training

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## Abstract

■ Much is known about the motor system and its role in simple movement execution. However, little is understood about the neural systems underlying auditory–motor integration in the context of musical rhythm, or the enhanced ability of musicians to execute precisely timed sequences. Using functional magnetic resonance imaging, we investigated how performance and neural activity were modulated as musicians and nonmusicians tapped in synchrony with progressively more complex and less metrically structured auditory rhythms. A functionally connected network was implicated in extracting higher-order features of a rhythm's temporal structure, with the dorsal premotor cortex mediating these auditory–motor interactions. In contrast to past studies, musicians recruited the prefrontal cortex to a greater degree than nonmusicians, whereas secondary motor regions were recruited to the same extent. We argue that the superior ability of musicians to deconstruct and organize a rhythm's temporal structure relates to the greater involvement of the prefrontal cortex mediating working memory. ■

## INTRODUCTION

The ability to synchronize movements to a musical rhythm is a powerful but commonplace phenomenon: Most people will spontaneously tap their feet or nod along to the beat of a tune. In highly trained musicians, this skill reaches extraordinary levels, allowing a performer to execute complex movements with high temporal precision. Although a great deal is known about the motor system's involvement in simple movement execution, little is understood about the neural systems underlying auditory–motor integration in the context of musical rhythm. In particular, it is unknown whether these systems are sensitive to the higher-order temporal structure contained in a musical rhythm, nor is it clear what underlies the enhancement of this capacity in musicians. In the present study, we use functional magnetic resonance imaging (fMRI) to investigate the neural mechanisms that underlie synchronization to varying levels of rhythm complexity, and we explore how these mechanisms are altered as a function of training that allows musicians to excel in timing movements to complex rhythms.

A rhythm can be defined as a pattern of time intervals demarcated by sensory and/or motor events. Although movement synchronization is better to auditory than visual rhythms (Patel, Iversen, Chen, & Repp, 2005), little is understood about the neural substrates and mechanisms of these auditory–motor interactions. The ability to accurately reproduce and to synchronize to musical rhythm is dependent upon the temporal structure of the sequence, that is, the manner in which intervals of time marked by musical beats are organized (Essens & Povel, 1985). Metrical rhythms, where sequences can be subdivided into equal intervals of time, are better reproduced than nonmetrical rhythms, where sequences cannot be evenly partitioned in time (Grahn & Brett, in press; Essens & Povel, 1985). Thus, metrical rhythms may perhaps facilitate the ability to accurately encode, recall, and execute movement sequences because events can be temporally organized into smaller, chunked units, with each event falling in time with the temporal grid of an internally generated clock (Povel & Essens, 1985).

The first goal of the present study is to parametrically manipulate the metrical structure of a rhythm in order to assess its behavioral and neural effect on movement synchronization and sequencing. In this study, we use the term synchronization in a general sense to convey the notion of the ability to time the onset of a motor response with the onset of an auditory event, and thus, the ability to reproduce rhythmic time intervals. Past studies have examined the neural correlates of movement synchronization to simple isochronous auditory rhythms (Pollok, Gross, & Schnitzler, 2006; Jancke, Loose, Lutz, Specht, & Shah, 2000; Rao et al., 1997). Others have parametrically manipulated physical aspects

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of movement as an index of sequence complexity, and as expected, showed corresponding increases in motor activity (Dhamala et al., 2003; Haslinger et al., 2002; Harrington et al., 2000; Boecker et al., 1998; Catalan, Honda, Weeks, Cohen, & Hallett, 1998; Sadato, Campbell, Ibanez, Deiber, & Hallett, 1996). However, these paradigms may not be sensitive in revealing neural effects of musical training. One study (Lewis, Wing, Pope, Praamstra, & Miall, 2004) investigated temporal complexity by progressively increasing the number of different time intervals in a rhythm, but no change in performance as a function of the complexity manipulation was found. These aforementioned studies have shown that the neural regions involved in sequence and temporal complexity include the supplementary and presupplementary motor areas (SMA and pre-SMA, respectively), the dorsal premotor cortex (dPMC), the dorsolateral prefrontal cortex (DLPFC), the superior parietal lobule, and the cerebellum. Further, some of these regions are also implicated in the perception of metrical and nonmetrical rhythms (Sakai et al., 1999), as well as metrical rhythm reproduction from memory (Bengtsson, Ehrsson, Forssberg, & Ullen, 2004, 2005). The present study aims to establish a direct brain–behavior relationship between performance changes due to sequence complexity and neural activity, and to show that increases in motor activity as a function of complexity can be related to the motor system's ability to organize temporally complex information.

A previous fMRI study conducted in our laboratory provides some evidence that the dPMC is involved in interactions between the auditory and motor systems during movement sequencing (Chen, Zatorre, & Penhune, 2006). In that study, we parametrically manipulated auditory features of a simple isochronous rhythm to increase its metric saliency. As saliency increased, so did activity in the dPMC and auditory cortex with, in addition, increasing functional connectivity between these regions. These findings suggest that auditory regions may interact with the dPMC to accurately time the synchronization of movements to sounds. At present, models of auditory–motor interactions involving the dPMC have been formulated based on studies of speech/vocalizations and auditory spatial processing (Warren, Wise, & Warren, 2005; Hickok & Poeppel, 2004). Thus, the present study aims to extend results from our previous investigation (Chen et al., 2006) and thereby expand current knowledge about auditory–motor interactions.

Studying musicians can allow us to examine how the brain changes in response to a focused and long-term training regime that is specific to the execution of intricately timed movement sequences. Synchronization to (Kincaid, Duncan, & Scott, 2002), and reproduction of, metrical (Drake, 1993; Franek, Mates, Radil, Beck, & Poppel, 1991; Smith, 1983) or nonmetrical (Watanabe, Savion-Lemieux, & Penhune, in press) rhythms is more accurate in musicians than nonmusicians. Furthermore, there is evidence for a greater cortical representation (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995) and gray matter concentration (Gaser & Schlaug, 2003) in motor-related regions of the brain for musicians. Finally, a number of studies have shown that compared to nonmusicians, musicians recruit smaller areas of activation in motor regions of the brain, such as the primary motor cortex, SMA, pre-SMA, premotor cortex, and cerebellum, suggesting that long-term training may result in a more efficient use of neural resources (Meister et al., 2005; Koeneke, Lutz, Wustenberg, & Jancke, 2004; Jancke, Shah, & Peters, 2000; Krings et al., 2000; Hund-Georgiadis & von Cramon, 1999). However, an important issue that arises from these studies is that no behavioral differences in measures of performance accuracy were demonstrated between the highly skilled musicians and subjects without musical training. This suggests that the dependent measures were not sensitive enough to detect differences, or that the simple unimanual movement sequences implemented in all of these studies were relatively easy for all participants to execute. In fact, the use of simple sequences to test for differences in musicians and nonmusicians, although relevant for examining carryover effects of long-term motor training to everyday skills, is unlikely an optimal paradigm to assess the specificity of musicianship. Thus, the paradigm developed for the present study uses a relatively complex rhythmic sequencing task that is specific to the skills a musician has acquired, and assesses whether this specificity is related to a particular pattern of neural activity different from that of nonmusicians.

The present fMRI study aims to advance our knowledge about movement sequencing, auditory–motor interactions, and musicianship. First, we assess how manipulation of rhythm complexity can influence movement synchronization and examine the neural correlates mediating this behavior. The second goal evaluates how performance and neural activity differ between musicians and nonmusicians when the tested motor sequencing task is specific to those with musical training. A novel paradigm was implemented by parametrically manipulating the temporal structure of a rhythmic sequence for three levels (metric simple [MS], metric complex [MC], nonmetric [NM]), such that they became more temporally complex, and thus, less metrically structured (Figure 1). It is also possible that the nonmetric sequence can have structure imposed on it and thus, one could consider this rhythm type to be ambiguous. Subjects always first listened to a rhythm, and then tapped in synchrony with it during the next trial (Figure 2). We predicted that percent correct across the three levels of complexity and between-subject groups would not differ, indicating that all sequences were globally well learned by all subjects: It was paramount to ensure that any neural effect seen was not

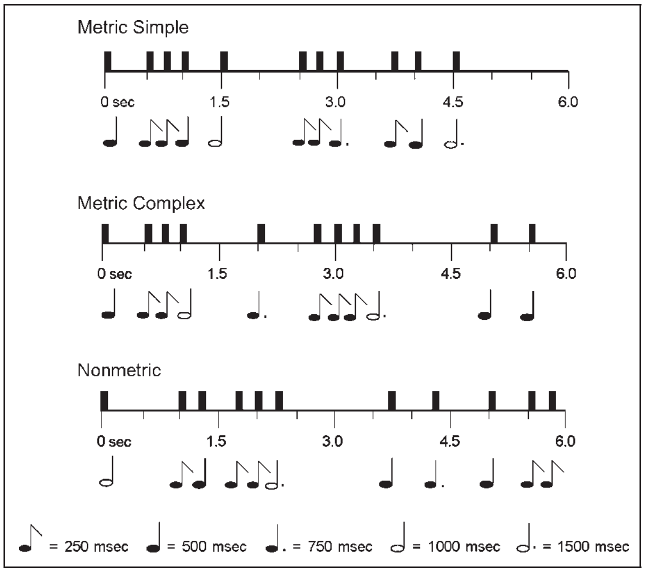

**Figure 1.** Schematic depiction of stimuli. Top row in each case shows the temporal sequence of events; bottom row shows the equivalent musical notation. All rhythms contained the same number and type of musical note durations, but arranged to create three levels of increasing metrical complexity: metric simple, metric complex, nonmetric.

due to general complexity, effort in movement execution, or differences in motor learning. Critically though, we predicted that at the level of response synchronization, performance would progressively decrease as sequence complexity increased and that musicians would be better at synchronizing their motor responses with the auditory cue than nonmusicians. Based on previous findings, we predicted the involvement of the SMA, pre-SMA, dPMC, DLPFC, and cerebellum in the sequencing of movements defined by temporal complexity. We also hypothesized that musicians should perform better than nonmusicians on our task and evaluated if this specialized subject group demonstrates a more efficient pattern of neural activity in motor-related regions of the brain, as has been suggested by previous studies.

## METHODS

### Subjects

Twelve nonmusicians and 12 musicians (balanced for sex) participated in the study after giving informed written consent for a protocol approved by the Montreal Neurological Research Ethics Review Board. All volunteers were right-handed and healthy with normal hearing. Nonmusicians ranged from 20 to 32 years of age (mean = 23.83 years), had no musical training, and were either pursuing an undergraduate degree or had already obtained one. Musicians ranged from 19 to 28 years of age (mean = 23.17 years) and were categorized as musicians based on several criteria which ensured that they were highly skilled. Musical training commenced early between the ages of 3 and 10 years (mean = 5.5 years), with private instruction continuing up to the time of testing and an average of 17.67 years of training. Subjects were either pursuing a Bachelor's degree in music or had already obtained one. Categories of instruments played included strings, percussion, piano, woodwinds and brass.

### Stimuli and Conditions

Subjects listened to and imitated three different auditory rhythms by tapping in synchrony on a computer mouse key with the index finger of the right hand (Figure 2).

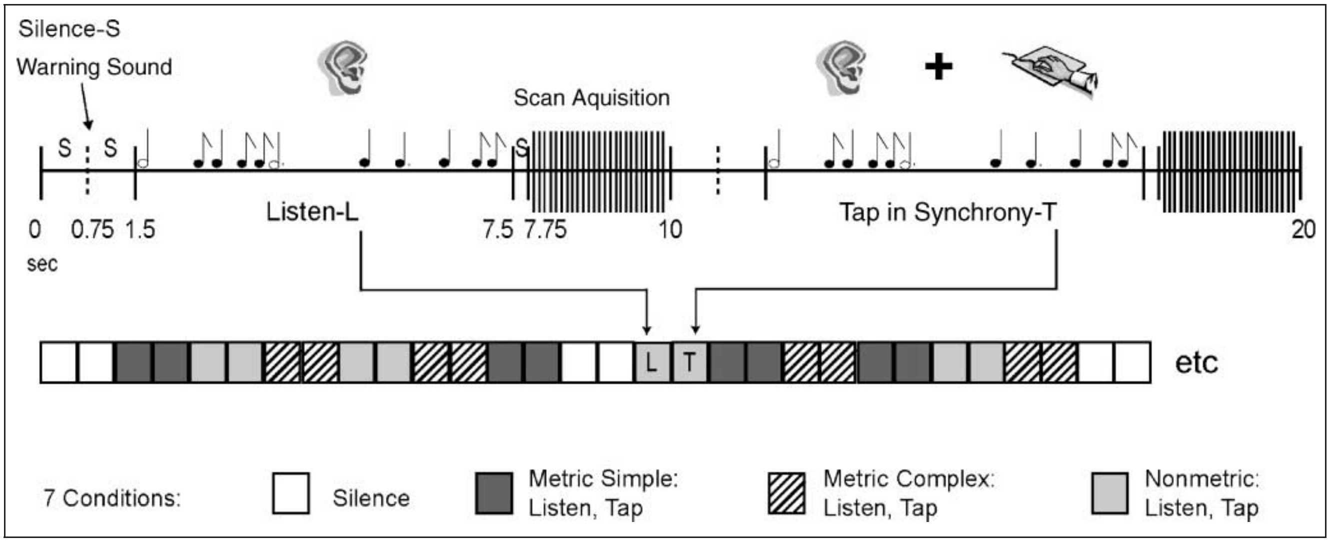

**Figure 2.** Representation of the fMRI sparse-sampling protocol. Each rhythm type was presented in a pair so that subjects first listened, then tapped with the same rhythm (only data for the tap trials were used for analysis). The three rhythm types were presented in a pseudorandom order, along with silence.

Each rhythm comprised 11 events (a woodblock sound), each 200 msec in duration. The interval following each sound was varied such that five different musical durations (onset-to-onset) would be created, each rhythm containing (in musical terminology): five eighth notes (each 250 msec), three quarter notes (each 500 msec), one dotted quarter note (750 msec), one half note (1000 msec), and one dotted half note (1500 msec). Thus, all rhythms were 6000 msec in duration with the same total number and type of notes, differing only in their temporal organization. This manipulation allowed us to create three rhythms with increasing metrical complexity (MS, MC, NM), based on rules of metric organization (Essens & Povel, 1985; Povel & Essens, 1985) (Figure 1). Pilot testing was first conducted on a separate group of 19 subjects in order to choose three rhythms from a sample of 12 that distinctly differed from each other with respect to complexity. There were a total of six test conditions as each rhythm type was associated with two tasks, ''listen'' and ''tap in synchrony.'' For listen trials, subjects only listened to the rhythms, without making any movements. During tapping trials, instructions were to tap as accurately as possible, synchronizing motor responses with each note of the rhythm (see Figure 2 for trial structure).

## Procedure

### *Prescan*

To minimize the potential confound of motor learning during fMRI scanning, subjects were familiarized with the three test rhythms 1 day prior to the scan session. First, to address any non-task-specific effects, six easy rhythms were presented, defined based on their composition of three-beat repeating motifs (as opposed to the test rhythms with no recurring pattern). Subjects listened during the first trial and tapped in synchrony for the subsequent three trials. Next, each of the three test rhythms was presented in a block of 20 trials, each block randomized for order across subjects. Subjects listened during odd-numbered trials and learned to tap in synchrony for even-numbered trials. Lastly, 12 trials were given at the end of this session where each of the three test rhythms was presented in two successive trials, pseudorandomized for order across subjects. Subjects listened during the first presentation and tapped in synchrony during the second presentation. Thus, the ''listen'' trial served as a prime for the ensuing ''tap in synchrony'' trial, ensuring that subjects knew which rhythm to tap to. This provided subjects with a preview of trial presentation during the fMRI session. Rhythms were presented at a comfortable intensity level through Sony headphones using Presentation software (version 0.8, from Neurobehavioral Systems) on a PC computer. Responses were made on the left mouse button using the right index finger and were recorded online.

### *Scan*

Subjects were first given a block of 12 trials for practice, similar to the last set of trials carried out during the prescan session. During scanning, two runs were completed, each of which contained the six test conditions plus a silent baseline, for a total of seven conditions. The three rhythms were pseudorandomized in pairs by type (as described above), for presentation order within each run and across subjects. Two silent trials of the same duration as the rhythm trials were interspersed every six paired trials. Subjects were instructed that the beginning of each run commenced with a ''listen'' trial that was followed by a ''tap in synchrony'' trial, after which they would continue alternating between these tasks, with silent rest brakes interspersed (Figure 2). In the present study, only the data from the ''tap in synchrony'' trials were analyzed. Rhythms were presented binaurally through Siemens MR-compatible pneumatic sound transmission headphones at a sound intensity of 75 dB SPL using Presentation on a PC computer. All conditions were performed with eyes closed, and tap responses (key onset and offset times) were collected online.

## fMRI Acquisition

Scanning was performed on a 1.5-T Siemens Sonata imager. High-resolution T1-weighted anatomical scans were collected for each subject (voxel size = $1 \times 1 \times 1$ mm$^3$, matrix size = $256 \times 256$). Ninety-nine frames were obtained for each of two runs in the functional T2*-weighted gradient echo-planar scans (14 frames per condition per run). Whole head interleaved scans ($n = 25$) were taken, oriented in a direction orthogonal to that of the Sylvian fissure (TE = 50 msec, TR = 10,000 msec, voxel size = $5 \times 5 \times 5$ mm$^3$, matrix size = $64 \times 64 \times 25$, FOV: 320 mm$^2$) (Figure 2). A single-trial sparse-sampling design (i.e., long TR) was used whereby scan acquisition occurred after each trial presentation. This ensured that the blood oxygenation level-dependent (BOLD) signal of the auditory stimuli would not be contaminated with the BOLD response of the acquisition noise (Belin, Zatorre, Hoge, Evans, & Pike, 1999). Furthermore, this paradigm avoids behavioral, and thus, neural interactions that may occur when auditory stimuli of a rhythmical nature are concurrently processed with the loud rhythmical scanner noise.

## Behavioral Analysis

A global measure of accuracy assessed overall performance and ensured that all subjects were able to perform the task. Subjects' tap onset for each sound in the rhythm sequence was compared to the stimulus onset; a tap was deemed correctly executed when it occurred within half the onset-to-onset interval before or after the stimulus onset. If more than one tap response fell within the same window of time, the first response was taken and the second was excluded. Therefore, this measure globally informs us whether subjects knew the sequence, but critically, is not informative about the timings of each action within the sequence. Performance related to the specific skill of sensorimotor integration was assessed using more sensitive measures of synchronization ability, the intertap interval (ITI) and asynchrony. These dependent variables are appropriately suited to evaluate differences between groups and rhythm types because they assess specific aspects of performance and precisely tap into the cognitive process of interest. The ITI measures the ability to reproduce time intervals between each event in a sequence; it is a measure of period matching. We calculated the deviation (in absolute value) of a subject's ITI relative to the actual onset-to-onset interval, as a percentage score (% ITI deviation); the greater the deviation, the poorer the performance. Asynchrony assesses the ability to time the onset of a motor response with the onset of a stimulus event; in another words, it is a measure of relative phase matching. For this measure, the absolute value of asynchrony was calculated because we were only interested in quantifying the amount of phase mismatch without regard for whether subjects were tapping ahead or lagging behind the stimulus event. Lastly, all dependent variables were calculated for each correct tap subjects made averaged across all trials for each rhythm type. After the experimental session, we also asked if subjects used any strategy to decode the rhythms, and thus, perform the task.

## fMRI Analysis

The first volume of each functional run was discarded. Images from each scan were then realigned with the third frame as reference, motion corrected using the AFNI software (Cox, 1996), and smoothed using a 12-mm full-width half-maximum isotropic Gaussian kernel. For each subject, both anatomical and functional volumes were transformed into standard stereotaxic space based on the MNI 305 template. Statistical analysis of fMRI data was based on the general linear model with correlated errors, performed using an in-house tool called fMRISTAT (www.math.mcgill.ca/keith/fmristat) (Worsley et al., 2002). Group statistical maps were generated for each contrast of interest using a mixed-effects model (Worsley et al., 2002).

To determine brain regions modulated by performance across the different levels of rhythm complexity, a covariation analysis was performed separately for each subject and then averaged for each group. Each individual subject's % ITI deviation score for each of the tapping conditions, averaged for each run, was used as the regressor variable. Thus, the parameter estimates represent the covariation of the BOLD response with increasing % ITI deviation. The $t$ statistical map assesses whether the slope of the regression line at each voxel is significantly different from zero. Positive $t$ statistics show voxels whose activity increases as performance decreases and negative $t$ statistics show voxels whose activity decreases as performance decreases. As a way to confirm the findings, and to quantify the changes in neural activity across conditions and between subject groups, the % BOLD signal change was extracted for voxels of interest (VOIs) from regions identified in this analysis, in each of the MS, MC, and NM tapping conditions, relative to silence, irrespective of the % ITI score. We also performed the above analyses using two other types of regressors: each subject's asynchrony score and a linear weighting of 1 to 3 that represented the rhythm complexity levels.

To determine brain regions commonly recruited by nonmusicians and musicians from the covariation analysis, a conjunction analysis was performed. The conjunction analysis was implemented using the minimum of the $t$ statistic obtained from the covariation contrast for each subject group (Friston, Penny, & Glaser, 2005). Thus, only those voxels from each contrast that survive a common threshold are considered significantly activated in the conjunction analysis.

To address differences in neural activity between musicians and nonmusicians, a group subtraction analysis was carried out on the data for the covariation analysis, using a fixed effects model. This contrast thus assesses differences in the slope of the regression line between subject groups. For example, positive $t$ statistics show neural regions that increase more in activity as performance decreases for musicians relative to nonmusicians. The % BOLD signal change was also extracted relative to silence at VOIs obtained from this analysis.

To ascertain that regions identified in the covariation contrast are engaged in a network, a functional connectivity analysis was performed across all subjects because this type of analysis allows one to determine how neural activity at one prechosen seed voxel correlates with all other voxels in the brain across time. In modeling functional connectivity, the effects of the stimulus are accounted for, and data from the seed voxel are added as another confound to be solved for in the general linear model: $Y_{ij} = X_i\beta_{1j} + R_i\beta_{2j} + \varepsilon$, where $Y_{ij}$ is the voxel value at each frame $i$, for each voxel $j$; $X$ contains the explanatory variables; $\beta$ represents the parameter estimates; $R$ represents data from the seed voxel; and $\varepsilon$ represents the error term. Slice timing correction is also implemented so that data from the seed voxel are resampled at the same frametimes and slicetimes as the fMRI data. The effect, standard deviation, and $t$ statistic are then estimated using fMRISTAT. The three tapping conditions (MS, MC, NM) used in the covariation analysis were inputted to the model for this analysis. Furthermore, the seed voxel was chosen from results of the conjunction analysis to ensure that it would be representative of both subject groups. This voxel was located in the dPMC and was statistically the highest peak obtained from the conjunction analysis.

Two additional functional connectivity analyses were performed for each subject group to specifically assess the temporal correlations between seed auditory regions with the dPMC. However, to ensure that the seed voxels would be common to the data set of both nonmusicians and musicians, they were chosen from the result of a conjunction analysis of the following contrast performed on the tapping conditions: 1/3(MS + MC + NM) − silence.

Peaks were evaluated using a general uncorrected value of $p < .0005$ (with particular focus on regions predicted a priori), that corresponded to a threshold of $t = 3.39$ for all analyses except the between-groups contrast where $t = 3.34$. Furthermore, because one goal of this study is to quantify similarities and differences in neural activation between musicians and nonmusicians, regions significantly activated in one subject group are also reported (if present) for the other. Anatomical localization of peak neural activity was classified using atlases (Schmahmann, Doyon, Toga, Petrides, & Evans, 2000; Duvernoy, 1991) and/or previously established criterion (Petrides, 2005; Picard & Strick, 2001; Westbury, Zatorre, & Evans, 1999).

## RESULTS

### Behavioral Results

We used a repeated measures analysis of variance (ANOVA) to compare behavioral performance for musicians and nonmusicians across three levels of rhythmic complexity (MS, MC, NM). As predicted, global accuracy did not differ between subject groups [$F(1, 22) = 0.74$, $p = .40$] (musicians: MS = 92%, MC = 91%, NM = 89%; nonmusicians: MS = 89%, MC = 87%, NM = 88%). Similarly, there was no main effect of accuracy across the three rhythm types [$F(2, 44) = 1.24, p = .30$] and no interaction effect [$F(2, 44) = 0.70$, $p = .51$]. However, critically, measures of synchronization ability revealed that musicians were significantly more accurate in reproducing rhythmic intervals and synchronous in timing tap responses, than nonmusicians [% ITI deviation: $F(1, 22) = 14.88, p < .001$; asynchrony: $F(1, 22) = 15.86, p < .001$] (Figure 3). Furthermore, there was a significant main effect for rhythm type [% ITI deviation: $F(2, 44) = 12.56$, $p < .0001$; asynchrony: $F(2, 44) = 49.37$, $p < .0001$], where accuracy for interval reproduction and synchrony decreased as rhythm complexity increased (Figure 3). No interaction effect was present for the % ITI deviation measure [$F(2, 44) = 1.99, p = .15$], However, a significant interaction was found for the asynchrony measure [$F(2, 44) = 12.03$, $p < .0001$]: Tukey's post hoc comparison indicated that the MC and NM rhythm types were not significantly different from each other in the musician group [$t_s(6, 44) = 1.66, p = .85$].

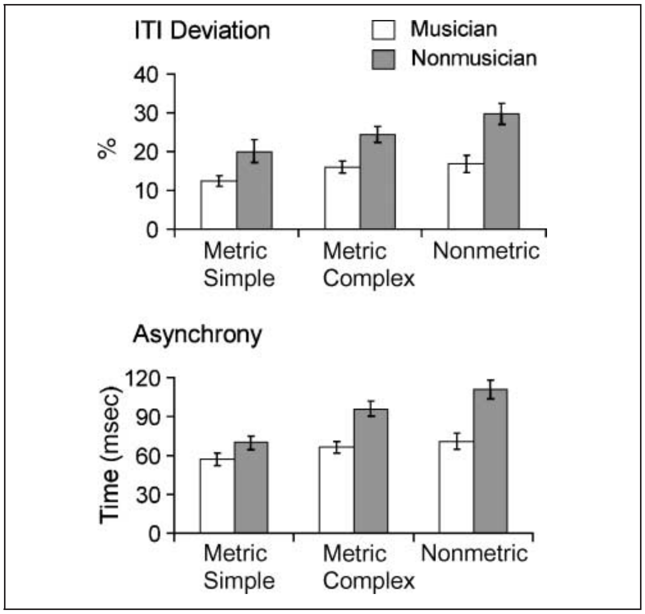

**Figure 3.** Percent ITI deviation and asynchrony measures for musicians and nonmusicians plotted across rhythm type. Data are reported as mean ± *SE*.

During debriefing, all musicians subjectively reported that they tried to fit the sequence with a metric structure, whereas nonmusicians reported chunking or grouping elements together.

### fMRI Results

*Covariation: Brain Regions Modulated by Temporal Complexity*

The results of the behavioral analyses demonstrated decreased synchronization ability as subjects tapped with increasingly complex rhythms. Therefore, % ITI deviation scores for each subject were regressed against neural activity across the three rhythm conditions to reveal brain regions whose activity was correlated with task performance. In nonmusicians, regions found to covary with increasing % ITI deviation scores included the following: pre-SMA, SMA, dPMC, ventral premotor cortex (vPMC), DLPFC, anterior cingulate cortex (ACC), inferior parietal lobule (IPL), thalamus, and cerebellum lobule VI (Table 1; Figure 4 where images are labeled under ''Nonmusicians''). In musicians, regions found to covary with changes in % ITI deviation across conditions were the same as those of nonmusicians (with the exception of the ACC), and in addition, the inferior frontal gyrus (BA 44/45) and cerebellum lobule VIIIa (Table 1; Figure 4 where images are labeled under ''Musicians''). These results were essentially identical to those using the asynchrony or stimulus regressors and are thus not reported to avoid redundancy. However, it is important to note that convergence of these data allows us to suggest that performance is linked

**Table 1.** Brain Regions Modulated by Temporal Complexity

| | *Nonmusicians Covariation* | | *Musicians Covariation* | |
|---|---|---|---|---|
| *Region* | *(x, y, z)* | *t* | *(x, y, z)* | *t* |
| Pre-SMA (BA 6)[a] | (−6, 6, 52) | 4.28 | (0, 4, 50) | 2.42 |
| | (2, 18, 48) | 3.98 | (4, 16, 56) | 2.84 |
| SMA (BA 6)[a] | (0, −2, 62) | 3.84 | (4, −2, 70) | 2.31 |
| dPMC (BA 6)[a] | (22, 4, 60) | 4.18 | (28, −2, 58) | 4.70 |
| | (14, −4, 62) | 4.10 | | |
| | (42, −6, 54) | 3.93 | | |
| vPMC (BA 6) | | | (42, −4, 46) | 3.99 |
| | (−30, −6, 44) | 3.76 | | |
| ACC (BA 32) | (2, 20, 44) | 4.04 | | |
| DLPFC (BA 9/46, 46) | (34, 50, 28) | 3.50 | (36, 50, 22) | 4.10 |
| Superior[a] | (40, 40, 32) | 3.50 | (40, 36, 34) | 2.92 |
| Inferior[b] | | | (42, 42, 16) | 3.95 |
| IFG (BA 44/45)[b] | | | (50, 12, −4) | 3.98 |
| IPL (BA 40)[a] | (38, −60, 54) | 3.23 | (46, −50, 54) | 4.25 |
| | (−36, −54, 42) | 4.45 | (−40, −52, 38) | 3.94 |
| Thalamus[a] | (10, −18, 4) | 3.23 | (10, −18, 16) | 3.94 |
| Cerebellum: lobule VI[a] | (−36, −66, −28) | 3.02 | (−28, −66, −28) | 3.39 |
| | (−8, −72, −26) | 3.57 | | |
| lobule VIIIa[b] | | | (−32, −62, −44) | 4.01 |

The stereotaxic coordinates of peak activations are given according to Talairach–MNI space, along with peak $t$ values significant at $p < .0005$, uncorrected. BA = Brodmann's area; Pre-SMA = presupplementary motor area; SMA = supplementary motor area; dPMC = dorsal premotor cortex; vPMC = ventral premotor cortex; ACC = anterior cingulate cortex; DLPFC = dorsolateral prefrontal cortex; IFG = inferior frontal gyrus; IPL = inferior parietal lobule.

[a] Regions commonly recruited in nonmusicians and musicians, as revealed by the conjunction analysis.

[b] Regions that show more neural activity for musicians than nonmusicians.

with rhythm complexity because brain activity varied in a similar manner both with stimulus- and subject-driven properties. Lastly, none of the a priori regions of interest demonstrated a significant negative correlation.

### *Conjunction: Brain Regions Similarly Recruited by Nonmusicians and Musicians*

Regions that were commonly modulated by metricality for both nonmusicians and musicians were determined by a conjunction analysis performed on data from the covariation analyses. Regions commonly activated included the dPMC and DLPFC (Table 1, Figure 4 where images are labeled under "Conjunction"). Although below threshold, the pre-SMA, SMA, IPL, and cerebellum lobule VI were also similarly recruited in nonmusicians and musicians (Table 1, Figure 4). These findings were confirmed by a between-subjects repeated measures ANOVA on the % BOLD signal change values, extracted for peaks obtained from the covariation contrasts. These results showed no significant differences in neural activity between nonmusicians and musicians for any of these regions (see graphs in Figure 4).

### *Subtraction: Differences between Musicians and Nonmusicians*

To determine how neural activity differed between nonmusicians and musicians in performance across rhythm complexity, a between-groups contrast was performed on the covariation data. The contrast musicians minus nonmusicians showed that neural activity in the following regions increased more as performance decreased in musicians: DLPFC (44, 38, 14), $t = 3.37$; Brodmann's area (BA) 44/45 (50, 14, −4), $t = 3.44$; cerebellar lobule VIIIa (−30, −62, −44), $t = 3.70$ (Figure 5 where images are labeled under "Musicians > Nonmusicians"). A between-subjects repeated measures ANOVA on %

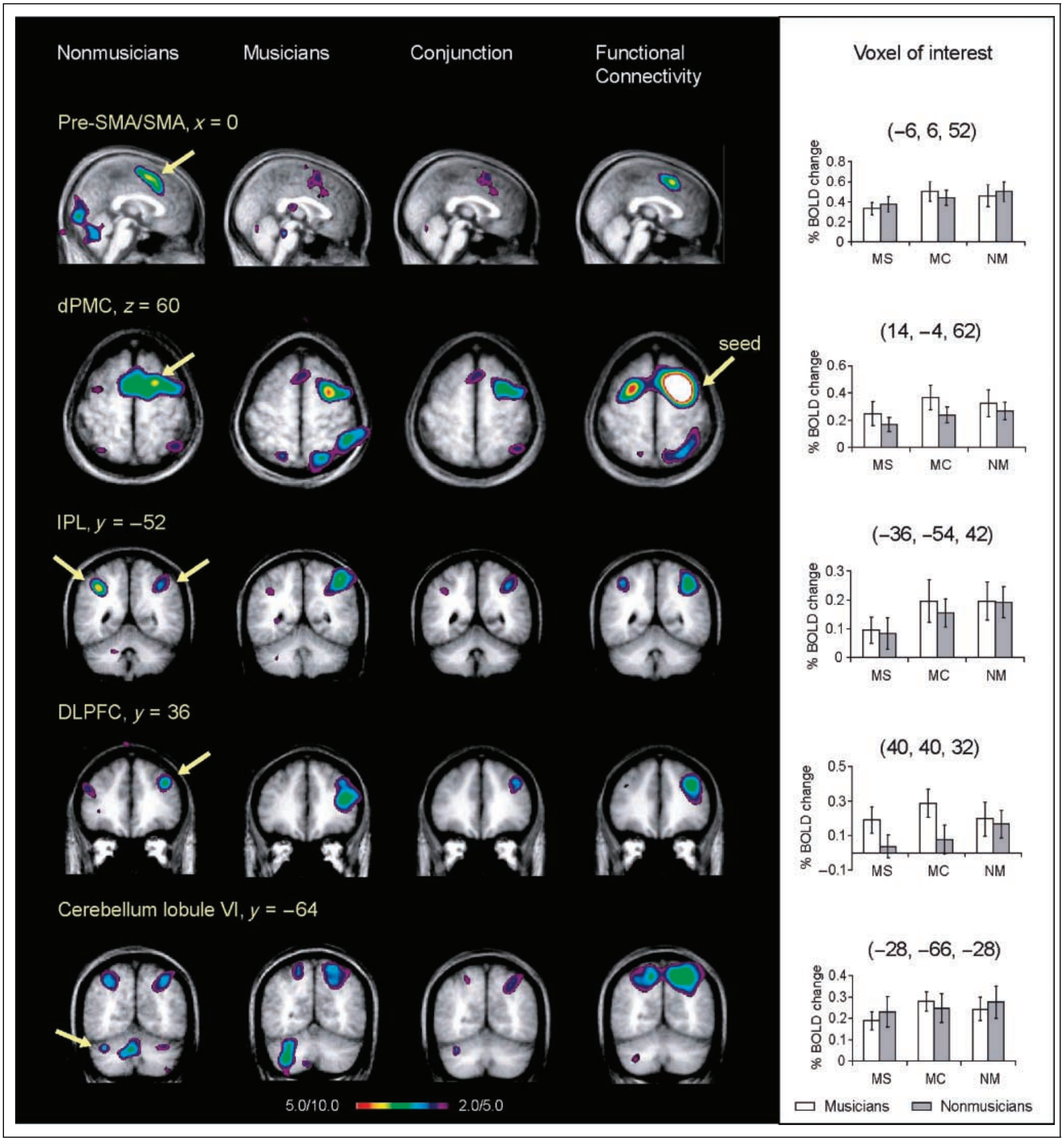

**Figure 4.** Brain regions modulated by temporal complexity. Results are shown for the covariation analysis for nonmusicians (column 1), musicians (column 2), and their conjunction (column 3). Regions where neural activity correlates with that of the dorsal premotor cortex (seed voxel) are shown in column 4 (Functional connectivity). Graphs in column 5 represent VOI analyses where the % BOLD signal change is plotted across rhythm type for nonmusicians and musicians. Data are reported as mean ± *SE*. Color bar represents *t* values: range 10.0–5.0 (range 10.0–3.0 for cerebellum) for functional connectivity images; range 5.0–2.0 for all other analyses. Pre-SMA/SMA = presupplementary motor area/supplementary motor area (row 1, sagittal view); dPMC = dorsal premotor cortex (row 2, horizontal view); IPL = inferior parietal lobule (row 3, coronal view); DLPFC = dorsolateral prefrontal cortex (row 4, coronal view); cerebellum (row 5, coronal view); MS = metric simple; MC = metric complex; NM = nonmetric.

BOLD signal change values obtained from VOI analyses at these peaks was also performed; results confirmed that musicians relative to nonmusicians demonstrated greater neural activity in the DLPFC [$F(1, 22) = 7.49$, $p < .05$] and a trend toward greater neural activity in BA 44/45 [$F(1, 22) = 3.90$, $p = .06$] (Figure 5). At the cerebellar peak in lobule VIIIa, there were no group differences [$F(1, 22) = 2.65$, $p = .12$], but a significant

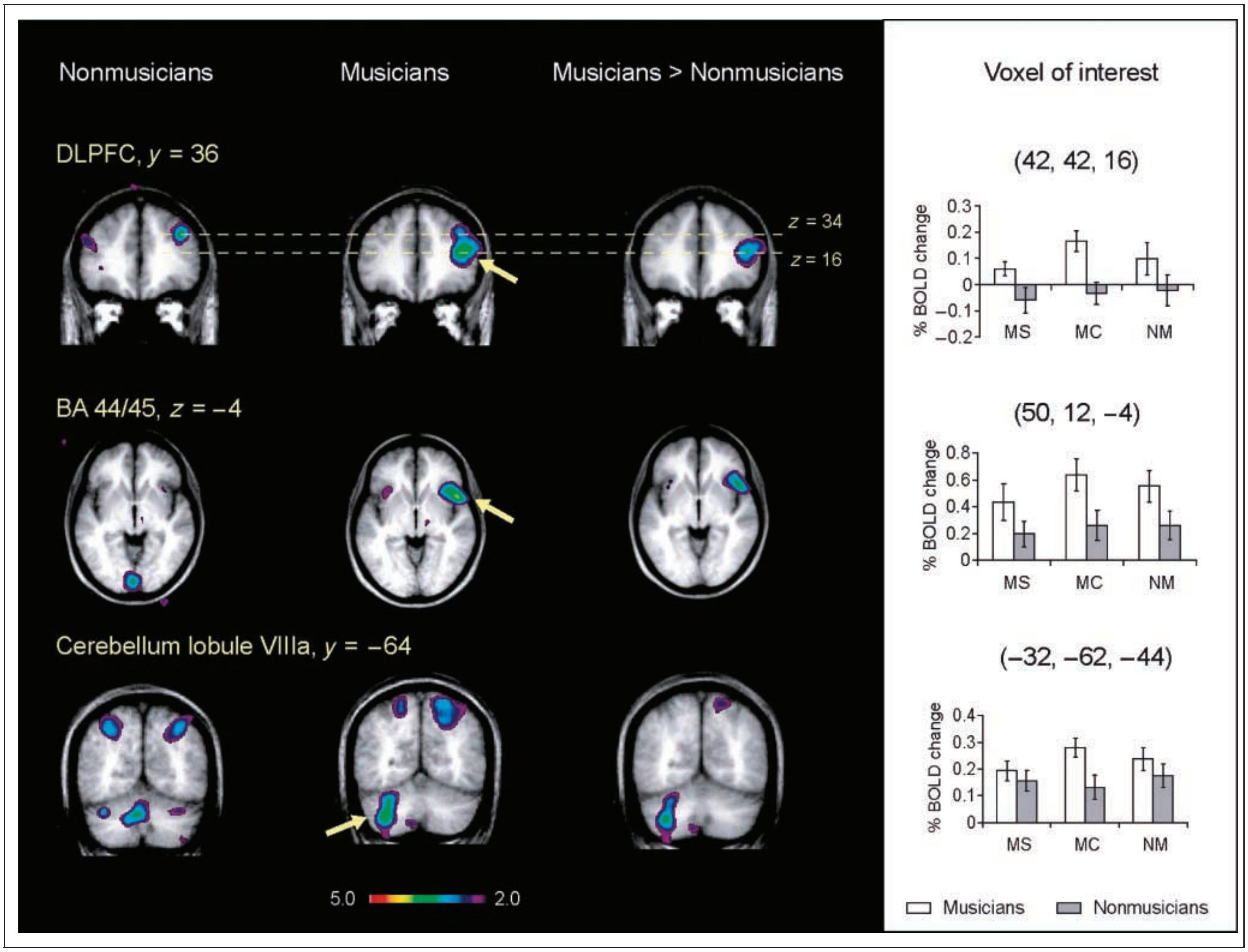

**Figure 5.** Differences between musicians and nonmusicians. Results are shown for the covariation analysis for nonmusicians (column 1), musicians (column 2), and the group contrast musicians > nonmusicians (column 3). Note that musicians recruit two peaks in the dorsolateral prefrontal cortex (DLPFC; dashed lines). Rows 1 and 3 in coronal view, row 2 in horizontal view. Graphs in column 4 represent VOI analyses where the % BOLD signal change is plotted across rhythm type for nonmusicians and musicians. Data are reported as mean ± *SE*. Color bar represents $t$ values; range 5.0–2.0 for all analyses. BA = Brodmann's area; MS = metric simple; MC = metric complex; NM = nonmetric.

interaction effect was present $[F(1, 44) = 5.03, p < .05]$ with greater signal change in the MC condition for musicians than for nonmusicians [Tukey's post hoc test; $t_s(6, 44) = 8.24, p < .01$], and a general trend in the same direction for the other rhythm conditions (Figure 5). The contrast nonmusicians minus musicians showed neural activity in the medial posterior cingulate gyrus (−6, −56, 16 and 4, −54, 20) and medial frontal BA 10 (0, 72, 10 and −4, 72, 8). More specifically, VOI analyses at these peaks revealed that nonmusicians demonstrated less deactivation (relative to silence) than musicians in these midline regions.

### *Functional Connectivity: Distributed Network for Metrical Rhythm Processing*

A functional connectivity analysis was performed for all subjects, using a right dPMC peak obtained from the conjunction analysis as a seed voxel. This analysis allowed us to confirm whether the regions identified from the covariation analyses were indeed functionally related. Regions that temporally correlated across time with the right dPMC voxel included the following: left dPMC, vPMC, pre-SMA, DLPFC, IPL, precuneus, thalamus, anterior insula/inferior frontal operculum, and cerebellum lobule VIIIa (Table 2; Figure 4 where images are labeled under ''Functional Connectivity'').

### *Functional Connectivity: Evidence for Auditory–Motor Temporal Coherence*

Based on the results from our previous study (Chen et al., 2006), which demonstrated functional connectivity between dPMC and secondary auditory regions, functional connectivity analyses were performed for each subject group exclusively to evaluate the temporal relationship

**Table 2.** Regions that Demonstrate Functional Connectivity with Seed Voxels in the Dorsal Premotor Cortex (dPMC) and Bilateral Planum Temporale (PT)

| *Region* | *(x, y, z)* | *t* |
|---|---|---|
| *Seed: dPMC (24, 2, 60)* | | |
| Pre-SMA (BA 6) | (4, 18, 50) | 9.42 |
| dPMC (BA 6) | (−22, 0, 62) | 9.62 |
| vPMC (BA 6) | (48, 8, 32) | 8.24 |
| | (−44, 0, 38) | 5.48 |
| DLPFC (BA 9/46, 46) | (38, 28, 36) | 9.58 |
| | (−36, 28, 34) | 6.69 |
| | (−32, 48, 8) | 3.64 |
| IPL (BA 40) | (44, −46, 44) | 8.69 |
| | (−38, −54, 50) | 6.52 |
| Precuneus (BA 7) | (14, −66, 52) | 7.11 |
| | (8, −40, 48) | 5.12 |
| | (−12, −66, 52) | 6.32 |
| Anterior insula/IFO | (−30, 18, 2) | 4.24 |
| Thalamus | (16, −6, 8) | 4.43 |
| Cerebellum: lobule VIIIa | (−32, −64, −44) | 3.40 |
| *Seed: PT (66, −28, 16)* | | |
| dPMC | | |
| Nonmusicians | (34, −14, 58) | 3.98 |
| Musicians | (30, −14, 74) | 3.41 |
| | (−34, −14, 66) | 3.57 |
| *Seed: PT (−46, −34, 18)* | | |
| dPMC | | |
| Nonmusicians | (20, −18, 54) | 3.95 |
| Musicians | (26, −10, 62) | 4.23 |
| | (36, −18, 54) | 4.55 |

The stereotaxic coordinates of peak activations are given according to Talairach–MNI space, along with peak *t* values, significant at $p < .0005$, uncorrected. BA = Brodmann's area; pre-SMA = presupplementary motor area; vPMC = ventral premotor cortex; DLPFC = dorsolateral prefrontal cortex; IPL = inferior parietal lobule; IFO = inferior frontal operculum.

between these regions in the present study. The seed auditory voxels were located in the planum temporale (66, −28, 16 and −46, −34, 18), at locations similar to the coordinates obtained from the previous study. Activity in the right auditory seed correlated with the right dPMC for nonmusicians, and bilaterally in this region for musicians (Table 2). The left auditory seed correlated with the right dPMC in both nonmusicians and musicians (Table 2).

## DISCUSSION

### Behavioral Results

A novel aspect of our study is that we parametrically manipulated rhythm complexity using an auditory–motor synchronization paradigm, and showed that the ability to accurately time actions with an auditory cue depends on how successfully one can deconstruct the temporal structure of the sequence. Global accuracy was no different across levels of rhythm complexity for both subject groups, indicating that the sequences were well-learned and that all subjects were able to perform the task adequately. Therefore, any interpretation derived from the neuroimaging data could not be attributed to task difficulty for example, but rather, to specific parameters of performance such as the ability to synchronize movements with an auditory cue. As predicted, both musicians and nonmusicians demonstrated a decreased ability to accurately reproduce rhythmic intervals, and increased asynchrony while tapping to rhythms that become progressively more complex; musicians also performed better than nonmusicians across all levels of rhythm complexity. It has been suggested that the superior performance of musicians stems from their ability to organize individual elements in a sequence within the context of the global temporal framework (Smith, 1983), a principle attributed to what is known as beat-perception in the field of music cognition. Thus, in conjunction with the subjective reports of our subjects, it is proposed that musicians use grouping strategies derived from higher-order knowledge of how musical time is structured, and this approach may consequently allow for a more accurate encoding of temporal information at each event in a sounded sequence. On the other hand, nonmusicians cannot use this type of top–down strategy, and thus, likely implement a bottom–up approach where individual elements in a sequence are grouped according to the Gestalt principle of temporal proximity; events that are close in time are chunked together (Bregman, 1999). This latter approach may hinder accurate encoding of temporal information at the event-by-event level, which would consequently result in an inferior ability to execute precisely timed movement sequences.

### Brain Regions Modulated by Temporal Complexity

We manipulated the temporal structure of an auditory rhythm as an index of sequence complexity in order to modulate the ability to synchronize movements with these rhythms. Each subject's performance was regressed against BOLD signal change, thus critically, allowing us to make specific conclusions about brain–behavior relationships. In both nonmusicians and musicians, neural regions that showed increasing BOLD signal change as a function of performance included the pre-SMA, SMA, dPMC, DLPFC, IPL, and cerebellum lobule VI. Importantly, the results of the functional connectivity analysis provide strong evidence for involvement of these regions in a related network; activity in the seed dPMC voxel was shown to temporally correlate across time with all other regions modulated by the task. Because the number of movements and their timings are identical for each rhythm, our results identify a specific network of areas involved in the organization and sequencing of temporally complex movements, relevant for intricate action plans required during music performance. The role of the pre-SMA and SMA in the temporal organization of movements (Tanji, 2001), such as sequence chunking (Kennerley, Sakai, & Rushworth, 2004), is highly relevant to the present study because the strategy employed by all subjects relied upon the parsing of sequences, whether via a bottom–up (for nonmusicians) or top–down (for musicians) approach as discussed previously. The cerebellum, on the other hand, may facilitate the precision of these timed movements (Penhune, Zatorre, & Evans, 1998; Ivry & Keele, 1989), and the DLPFC and IPL may be involved in a prefrontal–parietal network for auditory (Zatorre, Mondor, & Evans, 1999) and temporal (Lewis & Miall, 2003) attention to the encoding and synchronization of temporal events.

Current models of auditory–motor interactions have focused on the involvement of posterior auditory regions, and most of the data supporting these models come from studies of speech (Hickok & Poeppel, 2004), and/or more general auditory feature processing such as space (Warren et al., 2005). This study makes a specific contribution concerning the role of the dPMC in rhythm sequencing; we propose that it is involved in the interfacing of auditory information with motor action in order to produce temporally organized movements. Past literature has already shown that the dPMC is critically involved in the discrete selection of movements based on conditional rules; these higher-order rules are conveyed or prompted by a sensory stimulus (Passingham, 1985; Petrides, 1985), leading some to propose a role for the dPMC in indirect sensorimotor transformations (Hoshi & Tanji, 2006; Wise, di Pellegrino, & Boussaoud, 1996). In the present study, we have proposed that musicians select movements based on higher-order rules of metricality, and nonmusicians select actions based on the Gestalt principles, or rules of grouping by temporal proximity. Neural activity in the dPMC increased as the ability to select movements, and thus, to synchronize accurately with auditory cues became more difficult, suggesting that subjects may have relied more on the dPMC as a guide to integrate the auditory cues with action. In our previous study, it was also demonstrated that neural activity in the dPMC increased as auditory features of a rhythm guiding movement selection progressively conveyed information of a higher-order nature, such as metric salience (Chen et al., 2006). Our work further suggests that the temporal accuracy in the integration of these sensory-guided movements may be mediated by the dPMC. This proposal is in line with results from a transcranial magnetic stimulation study (Davare, Andres, Cosnard, Thonnard, & Olivier, 2006) that found that the dPMC is critically involved in the timing of a visuomotor task requiring the coordination of a grasp with a concurrent lift. Lastly, results from the functional connectivity analysis confirm involvement of the dPMC in auditory–motor interactions; activity in the planum temporale is temporally correlated with activity in the dPMC, findings that replicate results from our previous study (Chen et al., 2006). Thus, our findings support and extend current models of auditory–motor interactions by demonstrating a direct link between activity in the planum temporale and the dPMC, in a musically relevant task.

### Similarities and Differences in Neural Activity between Musicians and Nonmusicians

Having established the neural network involved in movement synchronization to auditory rhythms, we then further investigated whether this network differed in musicians who have had long-term practice on motor skills requiring fine sensorimotor coupling. Musicians were more accurate than nonmusicians at synchronizing motor responses with auditory cues, and neural activity in the pre-SMA, SMA, dPMC, and cerebellum lobule VI was similarly engaged in both subject groups across all conditions, as confirmed by the conjunction analysis. Furthermore, between-groups comparisons and VOI analyses did not reveal any differential neural activity in these motor-related areas. Our behavioral and neuroimaging findings are in contrast to previous studies comparing musicians and nonmusicians on unimanual motor sequencing tasks (Meister et al., 2005; Koeneke et al., 2004; Jancke, Shah, & Peters, 2000; Krings et al., 2000; Hund-Georgiadis & von Cramon, 1999). These studies have shown that musicians recruit a smaller network of neural activity in secondary motor regions and the cerebellum, and they have put forth the interpretation that this reduced activity is the result of a more efficient neural organization derived from their long-term training on motor skills. However, the findings in the present study suggest that, for a motor sequencing task requiring accurate synchronization of movements with sounds, secondary motor regions and cerebellar lobule VI are not differentially recruited. Instead, musicians recruit the DLPFC and BA 44/45 to a greater extent than nonmusicians, a finding we attribute to the superior ability of musicians to track, retrieve, manipulate, and thus, organize temporal information. The task utilized in this experiment relies upon an ability to sequence rhythmic events, a skill specific to training acquired by musicians. However, the tasks implemented in the previous studies tested basic motor abilities that nonmusicians and musicians alike possess (e.g., sequential finger–thumb opposition, tapping with one finger or each finger sequentially), which could thus account for the lack of performance difference between subject groups. Therefore, musicians may demonstrate a more ''efficient'' recruitment of motor neural regions, but only when the experimental tasks used are nonspecific to musicianship. We suggest that when a task is designed to tap into skills specific to musicianship, such as that used in the present study, then we are testing the ''competency,'' rather than ''efficiency,'' of the neural system in response to that task, and that musicians should activate neural regions specific to the tested skill. Similarly, studies have demonstrated enhanced recruitment of auditory regions in musicians compared to nonmusicians when the stimuli used are specific to musicianship (Schneider et al., 2002; Pantev et al., 1998).

The between-groups contrast also revealed one peak in lobule VIIIa of the cerebellum that showed more neural activity in musicians than nonmusicians for the metric complex condition, and a trend toward group differences in the same direction for the other conditions. Because this peak was located in the left cerebellar hemisphere, it is unlikely related to the mere act of motor execution that would recruit ipsilateral neural activity corresponding to right-finger tapping. Instead, one could hypothesize that musicians, by nature of their specific training, would demonstrate superior abilities in timing and error correction (Penhune et al., 1998), and general auditory discriminative processes (Petacchi, Laird, Fox, & Bower, 2005), roles attributed to the cerebellum that may be related to the greater gray matter cerebellar concentration in musicians than in nonmusicians (Gaser & Schlaug, 2003).

We argue that activity in the right DLPFC and right BA 44/45 is directly related to the behavioral advantage demonstrated by musicians because these regions were revealed by a group contrast of the covariation analysis, which itself, is a regression using each individual's behavioral score. Although nonmusicians recruited the DLPFC, musicians additionally recruited another DLPFC peak that was more inferiorly located. One could interpret this additional peak of activity as just an extension of its involvement in the prefrontal–parietal network related to temporal attention processing previously discussed. However, there is also an alternative interpretation when one considers the role of the DLPFC in conjunction with that of BA 44/45. The DLPFC and the ventrolateral prefrontal cortex (VLPFC), which includes BA 45, are critical nodes involved in a dorsal–ventral model of working memory function (Petrides, 2005). In this model, sensory information that is held in the posterior association cortices is actively retrieved by the VLPFC, and manipulation or monitoring of this information is mediated by the DLPFC. In the context of rhythmic sequencing, we propose that the VLPFC is involved in extracting the correct temporal information (i.e., beat duration) related to each of the 11 elements comprising the sequence, and that the DLPFC may be concomitantly involved in keeping track or monitoring which of the 11 temporal durations is the next in the sequence to be retrieved for movement synchronization. It has also been suggested that Broca's areas 44 and 45 are involved in a structured hierarchy of action selection, independent of temporal arrangement (Koechlin & Jubault, 2006), and could be involved in auditory–motor interactions (Lahav, Saltzman, & Schlaug, 2007). Neural activity in BA 44 may mediate the selection of simple action chunks, whereas BA 45 may be implicated in the superordinate organization of these simple action chunks (Koechlin & Jubault, 2006). As discussed previously, musicians have a priori knowledge about how rhythms are structured in time, and therefore, we propose use of a top–down strategy, whereby elements in a sequence are recoded into smaller chunks following the rules of metric organization. The enhanced ability to retrieve, monitor, and thus, chunk information confers a behavioral advantage for the musicians over nonmusicians and may be accounted for by greater neural activation in the DLPFC and VLPFC.

## Acknowledgments

We thank Marc Bouffard for consultations on the fMRI analysis and computer programming of the behavioral task, Evgueni Lapidous for implementation of an algorithm for behavioral data analysis, and the staff at the McConnell Brain Imaging Centre for their technical assistance. This work was supported by grants from the Canadian Institutes of Health Research, Natural Science and Engineering Research Council, and a McGill Major Fellowship to J. L. C.

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## REFERENCES

Belin, P., Zatorre, R. J., Hoge, R., Evans, A. C., & Pike, B. (1999). Event-related fMRI of the auditory cortex. *Neuroimage, 10,* 417–429.

Bengtsson, S. L., Ehrsson, H. H., Forssberg, H., & Ullen, F. (2004). Dissociating brain regions controlling the temporal and ordinal structure of learned movement sequences. *European Journal of Neuroscience, 19,* 2591–2602.

Bengtsson, S. L., Ehrsson, H. H., Forssberg, H., & Ullen, F. (2005). Effector-independent voluntary timing: Behavioural and neuroimaging evidence. *European Journal of Neuroscience, 22,* 3255–3265.

Boecker, H., Dagher, A., Ceballos-Baumann, A. O., Passingham, R. E., Samuel, M., Friston, K. J., et al. (1998). Role of the human rostral supplementary motor area and the basal ganglia in motor sequence control: Investigations with H2 15O PET. *Journal of Neurophysiology, 79,* 1070–1080.

Bregman, A. (1999). *Auditory scene analysis, the perceptual organization of sound.* Cambridge: MIT Press.

Catalan, M. J., Honda, M., Weeks, R. A., Cohen, L. G., & Hallett, M. (1998). The functional neuroanatomy of simple and complex sequential finger movements: A PET study. *Brain, 121,* 253–264.

Chen, J. L., Zatorre, R. J., & Penhune, V. B. (2006). Interactions between auditory and dorsal premotor cortex during synchronization to musical rhythms. *Neuroimage, 32,* 1771–1781.

Cox, R. W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research, 29,* 162–173.

Davare, M., Andres, M., Cosnard, G., Thonnard, J. L., & Olivier, E. (2006). Dissociating the role of ventral and dorsal premotor cortex in precision grasping. *Journal of Neuroscience, 26,* 2260–2268.

Dhamala, M., Pagnoni, G., Wiesenfeld, K., Zink, C. F., Martin, M., & Berns, G. S. (2003). Neural correlates of the complexity of rhythmic finger tapping. *Neuroimage, 20,* 918–926.

Drake, C. (1993). Reproduction of musical rhythms by children, adult musicians, and adult non-musicians. *Perception & Psychophysics, 53,* 25–33.

Duvernoy, H. M. (1991). *The human brain: Surface, three-dimensional sectional anatomy and MRI*. New York: Springer-Verlag.

Elbert, T., Pantev, C., Wienbruch, C., Rockstroh, B., & Taub, E. (1995). Increased cortical representation of the fingers of the left hand in string players. *Science, 270,* 305–307.

Essens, P. J., & Povel, D. J. (1985). Metrical and nonmetrical representations of temporal patterns. *Perception & Psychophysics, 37,* 1–7.

Franek, M., Mates, J., Radil, T., Beck, K., & Poppel, E. (1991). Finger tapping in musicians and nonmusicians. *International Journal of Psychophysiology, 11,* 277–279.

Friston, K. J., Penny, W. D., & Glaser, D. E. (2005). Conjunction revisited. *Neuroimage, 25,* 661–667.

Gaser, C., & Schlaug, G. (2003). Brain structures differ between musicians and non-musicians. *Journal of Neuroscience, 23,* 9240–9245.

Grahn, J. A., & Brett, M. (2007). Rhythm and beat perception in motor areas of the brain. *Journal of Cognitive Neuroscience, 19,* 893–906.

Harrington, D. L., Rao, S. M., Haaland, K. Y., Bobholz, J. A., Mayer, A. R., Binder, J. R., et al. (2000). Specialized neural systems underlying representations of sequential movements. *Journal of Cognitive Neuroscience, 12,* 56–77.

Haslinger, B., Erhard, P., Weilke, F., Ceballos-Baumann, A. O., Bartenstein, P., Grafin von Einsiedel, H., et al. (2002). The role of lateral premotor–cerebellar–parietal circuits in motor sequence control: A parametric fMRI study. *Brain Research, Cognitive Brain Research, 13,* 159–168.

Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: A framework for understanding aspects of the functional anatomy of language. *Cognition, 92,* 67–99.

Hoshi, E., & Tanji, J. (2006). Differential involvement of neurons in the dorsal and ventral premotor cortex during processing of visual signals for action planning. *Journal of Neurophysiology, 95,* 3596–3616.

Hund-Georgiadis, M., & von Cramon, D. Y. (1999). Motor-learning-related changes in piano players and non-musicians revealed by functional magnetic-resonance signals. *Experimental Brain Research, 125,* 417–425.

Ivry, R. B., & Keele, S. W. (1989). Timing functions of the cerebellum. *Journal of Cognitive Neuroscience, 1,* 136–152.

Jancke, L., Loose, R., Lutz, K., Specht, K., & Shah, N. J. (2000). Cortical activations during paced finger-tapping applying visual and auditory pacing stimuli. *Brain Research, Cognitive Brain Research, 10,* 51–66.

Jancke, L., Shah, N. J., & Peters, M. (2000). Cortical activations in primary and secondary motor areas for complex bimanual movements in professional pianists. *Brain Research, Cognitive Brain Research, 10,* 177–183.

Kennerley, S. W., Sakai, K., & Rushworth, M. F. (2004). Organization of action sequences and the role of the pre-SMA. *Journal of Neurophysiology, 91,* 978–993.

Kincaid, A. E., Duncan, S., & Scott, S. A. (2002). Assessment of fine motor skill in musicians and nonmusicians: Differences in timing versus sequence accuracy in a bimanual fingering task. *Perceptual and Motor Skills, 95,* 245–257.

Koechlin, E., & Jubault, T. (2006). Broca's area and the hierarchical organization of human behavior. *Neuron, 50,* 963–974.

Koeneke, S., Lutz, K., Wustenberg, T., & Jancke, L. (2004). Long-term training affects cerebellar processing in skilled keyboard players. *NeuroReport, 15,* 1279–1282.

Krings, T., Topper, R., Foltys, H., Erberich, S., Sparing, R., Willmes, K., et al. (2000). Cortical activation patterns during complex motor tasks in piano players and control subjects. A functional magnetic resonance imaging study. *Neuroscience Letters, 278,* 189–193.

Lahav, A., Saltzman, E., & Schlaug, G. (2007). Action representation of sound: Audiomotor recognition network while listening to newly acquired actions. *Journal of Neuroscience, 27,* 308–314.

Lewis, P. A., & Miall, R. C. (2003). Distinct systems for automatic and cognitively controlled time measurement: Evidence from neuroimaging. *Current Opinion in Neurobiology, 13,* 250–255.

Lewis, P. A., Wing, A. M., Pope, P. A., Praamstra, P., & Miall, R. C. (2004). Brain activity correlates differentially with increasing temporal complexity of rhythms during initialisation, synchronisation, and continuation phases of paced finger tapping. *Neuropsychologia, 42,* 1301–1312.

Meister, I., Krings, T., Foltys, H., Boroojerdi, B., Muller, M., Topper, R., et al. (2005). Effects of long-term practice and task complexity in musicians and nonmusicians performing simple and complex motor tasks: Implications for cortical motor organization. *Human Brain Mapping, 25,* 345–352.

Pantev, C., Oostenveld, R., Engelien, A., Ross, B., Robert, L. E., & Hoke, M. (1998). Increased auditory cortical representation in musicians. *Nature, 392,* 811–814.

Passingham, R. E. (1985). Premotor cortex: Sensory cues and movement. *Behavioral Brain Research, 18,* 175–185.

Patel, A. D., Iversen, J. R., Chen, Y., & Repp, B. H. (2005). The influence of metricality and modality on synchronization with a beat. *Experimental Brain Research, 163,* 226–238.

Penhune, V. B., Zatorre, R. J., & Evans, A. C. (1998). Cerebellar contributions to motor timing: A PET study of auditory and visual rhythm reproduction. *Journal of Cognitive Neuroscience, 10,* 752–765.

Petacchi, A., Laird, A. R., Fox, P. T., & Bower, J. M. (2005). Cerebellum and auditory function: An ALE meta-analysis of functional neuroimaging studies. *Human Brain Mapping, 25,* 118–128.

Petrides, M. (1985). Deficits on conditional associative-learning tasks after frontal- and temporal-lobe lesions in man. *Neuropsychologia, 23,* 601–614.

Petrides, M. (2005). Lateral prefrontal cortex: Architectonic and functional organization. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, 360,* 781–795.

Picard, N., & Strick, P. L. (2001). Imaging the premotor areas. *Current Opinion in Neurobiology, 11,* 663–672.

Pollok, B., Gross, J., & Schnitzler, A. (2006). How the brain controls repetitive finger movements. *Journal of Physiology (Paris), 99,* 8–13.

Povel, D. J., & Essens, P. J. (1985). Perception of temporal patterns. *Music Perception, 2,* 411–440.

Rao, S. M., Harrington, D. L., Haaland, K. Y., Bobholz, J. A., Cox, R. W., & Binder, J. R. (1997). Distributed neural systems underlying the timing of movements. *Journal of Neuroscience, 17,* 5528–5535.

Sadato, N., Campbell, G., Ibanez, V., Deiber, M., & Hallett, M. (1996). Complexity affects regional cerebral blood flow change during sequential finger movements. *Journal of Neuroscience, 16,* 2691–2700.

Sakai, K., Hikosaka, O., Miyauchi, S., Takino, R., Tamada, T., Iwata, N. K., et al. (1999). Neural representation of a rhythm depends on its interval ratio. *Journal of Neuroscience, 19,* 10074–10081.

Schmahmann, J. D., Doyon, J., Toga, A. W., Petrides, M., & Evans, A. C. (2000). *MRI atlas of the human cerebellum*. San Diego: Academic Press.

Schneider, P., Scherg, M., Dosch, H. G., Specht, H. J., Gutschalk, A., & Rupp, A. (2002). Morphology of Heschl's gyrus reflects enhanced activation in the auditory cortex of musicians. *Nature Neuroscience, 5,* 688–694.

Smith, J. (1983). Reproduction and representation of musical rhythms: The effect of musical skill. In D. R. Rogers & J. A. Sloboda (Eds.), *Acquisition of symbolic skills*. New York: Plenum.

Tanji, J. (2001). Sequential organization of multiple movements: Involvement of cortical motor areas. *Annual Review of Neuroscience, 24,* 631–651.

Warren, J. E., Wise, R. J., & Warren, J. D. (2005). Sounds do-able: Auditory–motor transformations and the posterior temporal plane. *Trends in Neurosciences, 28,* 636–643.

Watanabe, D., Savion-Lemieux, T., & Penhune, V. (2007). The effect of early musical training on adult motor performance: Evidence for a sensitive period in motor learning. *Experimental Brain Research, 176,* 332–340.

Westbury, C. F., Zatorre, R. J., & Evans, A. C. (1999). Quantifying variability in the planum temporale: A probability map. *Cerebral Cortex, 9,* 392–405.

Wise, S. P., di Pellegrino, G., & Boussaoud, D. (1996). The premotor cortex and nonstandard sensorimotor mapping. *Canadian Journal of Physiology and Pharmacology, 74,* 469–482.

Worsley, K. J., Liao, C. H., Aston, J., Petre, V., Duncan, G. H., Morales, F., et al. (2002). A general statistical analysis for fMRI data. *Neuroimage, 15,* 1–15.

Zatorre, R. J., Mondor, T. A., & Evans, A. C. (1999). Auditory attention to space and frequency activates similar cerebral systems. *Neuroimage, 10,* 544–554.