

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 con-

nected 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

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 non-musicians and musicians, they were chosen from the result of a conjunction analysis of the following contrast performed on the tapping conditions: $1/3(\text{MS} + \text{MC} + \text{NM}) - \text{silence}$.

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 [$t_s(6, 44) = 1.66, p = .85$].

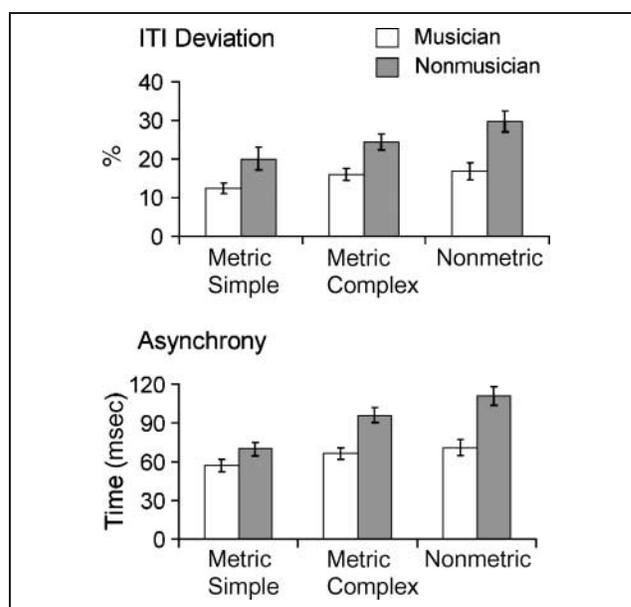


Figure 3. Percent ITI deviation and asynchrony measures for musicians and nonmusicians plotted across rhythm type. Data are reported as mean \pm SE.

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

Region	Nonmusicians Covariation		Musicians Covariation	
	(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	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.

^aRegions commonly recruited in nonmusicians and musicians, as revealed by the conjunction analysis.

^bRegions 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 metricity 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 %

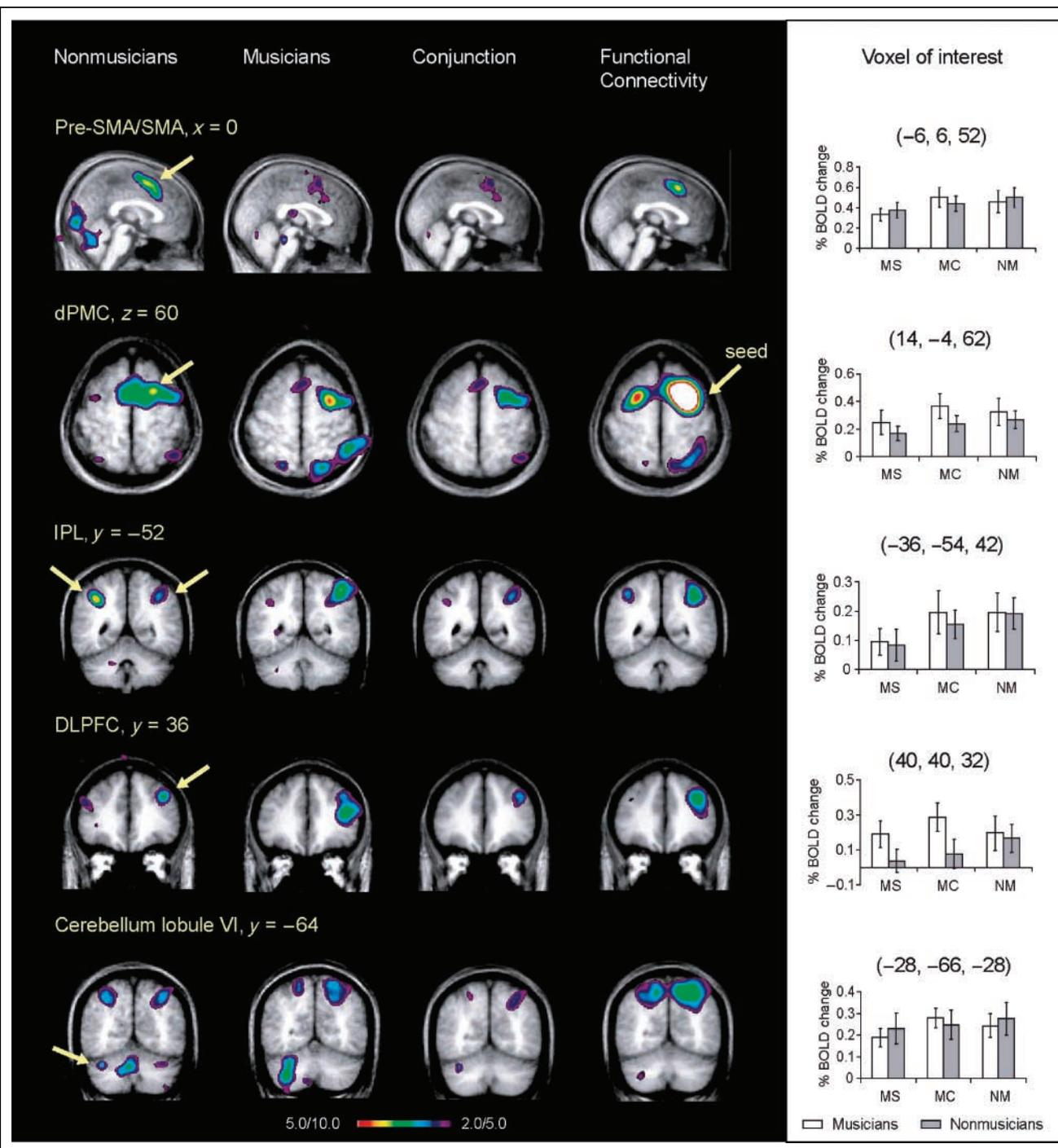


Figure 4. Brain regions modulated by temporal complexity. Results are shown for the covariation analysis for nonmusicians (column 1), musicians (column 2), and their conjunction (column 3). Regions where neural activity correlates with that of the dorsal premotor cortex (seed voxel) are shown in column 4 (Functional connectivity). Graphs in column 5 represent VOI analyses where the % BOLD signal change is plotted across rhythmic type for nonmusicians and musicians. Data are reported as mean \pm 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

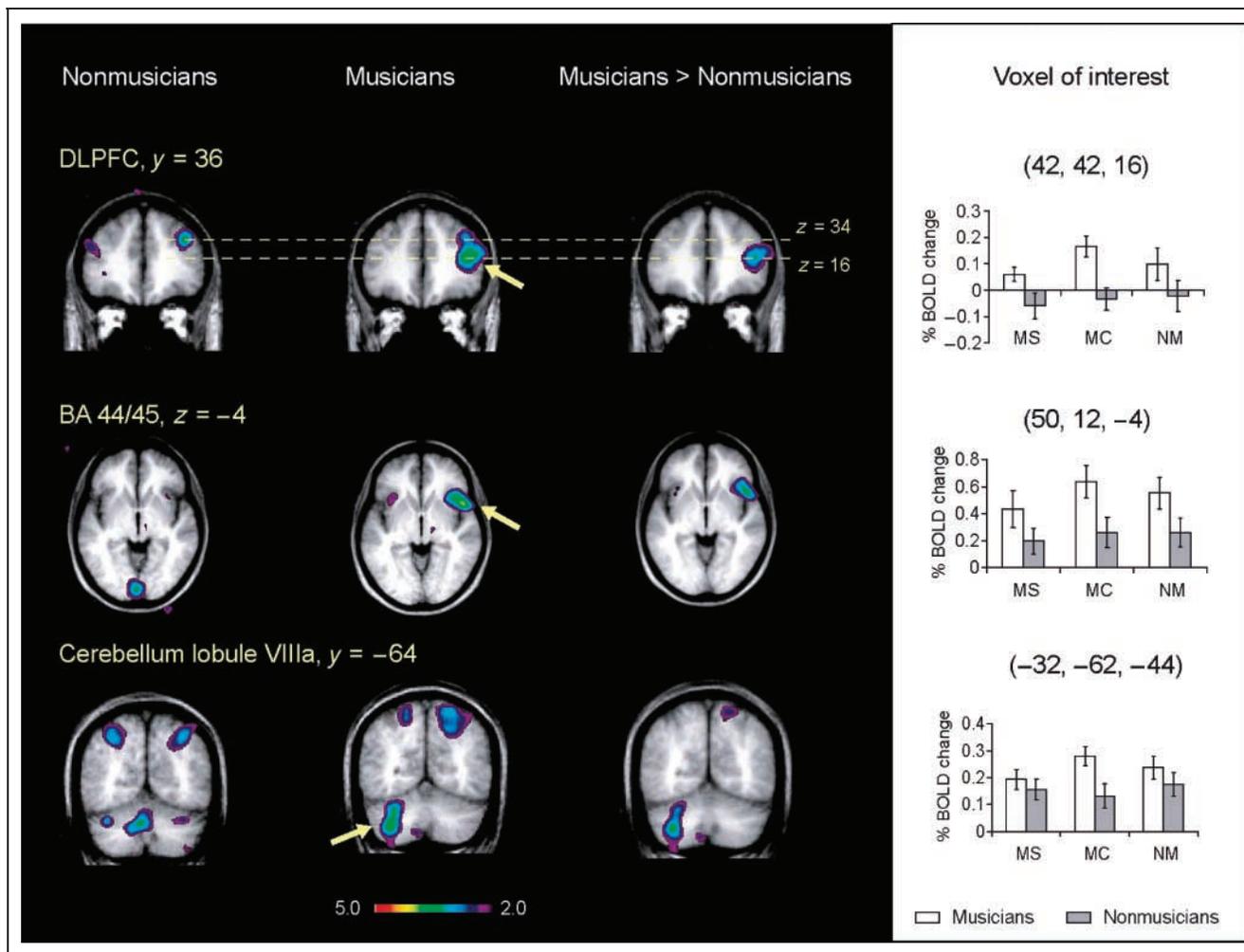


Figure 5. Differences between musicians and nonmusicians. Results are shown for the covariation analysis for nonmusicians (column 1), musicians (column 2), and the group contrast musicians > nonmusicians (column 3). Note that musicians recruit two peaks in the dorsolateral prefrontal cortex (DLPFC; dashed 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 \pm 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	(<i>x</i> , <i>y</i> , <i>z</i>)	<i>t</i>
<i>Seed: dPMC (24, 2, 60)</i>		
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 VIIa	(-32, -64, -44)	3.40
<i>Seed: PT (66, -28, 16)</i>		
dPMC		
Nonmusicians	(34, -14, 58)	3.98
Musicians	(30, -14, 74)	3.41
	(-34, -14, 66)	3.57
<i>Seed: PT (-46, -34, 18)</i>		
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.

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