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Left Hemispheric Lateralization of Brain Activity During Passive Rhythm Perception in Musicians

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ABSTRACT

The nature of hemispheric specialization of brain activity during rhythm processing remains poorly understood. The locus for rhythmic processing has been difficult to identify and there have been several contradictory findings. We therefore used functional magnetic resonance imaging to study passive rhythm perception to investigate the hypotheses that rhythm processing results in left hemispheric lateralization of brain activity and is affected by musical training. Twelve musicians and 12 nonmusicians listened to regular and random rhythmic patterns. Conjunction analysis revealed a shared network of neural structures (bilateral superior temporal areas, left inferior parietal lobule, and right frontal operculum) responsible for rhythm perception independent of musical background. In contrast, random-effects analysis showed greater left lateralization of brain activity in musicians compared to nonmusicians during regular rhythm perception, particularly within the perisylvian cortices (left frontal operculum, superior temporal gyrus, inferior parietal lobule). These results suggest that musical training leads to the employment of left-sided perisylvian brain areas, typically active during language comprehension, during passive rhythm perception. Anat Rec Part 288A:382–389, 2006.

Key words: rhythm; functional magnetic resonance imaging; perisylvian; auditory cortex

Rhythmic patterns have served as a cornerstone for musical expression and composition throughout history, regardless of instrumentation, musical genre, or culture of origin (Sessions, 1950). The development of functional neuroimaging techniques has allowed unprecedented access into the neural processing of auditory stimuli, even those as abstract as music. The majority of imaging research into the neural correlates of music perception thus far has focused on perception of pitch or tonal elements, while fewer studies have examined rhythm (Zatorre et al., 1994; Griffiths et al., 1999; Halpern and Zatorre, 1999; Janata et al., 2002). We define rhythm here as the organization of relative durations of notes and rests within a musical pattern (Peretz, 1990). Despite the relative lack of attention that rhythm has received, it nevertheless forms the temporal foundation of music and is arguably the most fundamental of all musical elements.

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In order to investigate the effect of musical training on rhythm perception and to clarify previous reports regarding hemispheric specialization, we used functional magnetic resonance imaging to determine how musical training affects neural processing of rhythm. We had two main hypotheses. First, there would be commonalities in the way both musicians and nonmusicians process rhythm. This hypothesis is based on the fact that musicians and nonmusicians alike are able to perceive musical rhythms. Even musically naive subjects (e.g., children) respond to rhythmic impulses (Demany et al., 1977; Trehub and Thorpe, 1989; Sansavini et al., 1997; Nazzi et al., 1998; Bahrick and Lickliter, 2004), suggesting that there is a basic neural architecture for rhythm perception that is independent of training.

The second hypothesis is that musicians would show increased left hemispheric activity in comparison to nonmusicians, even during passive rhythm perception. The second hypothesis is based on the argument that extensive training in music should lead to a heightened degree of analytical processing of music, which is known to favor left hemispheric mechanisms (Vollmer-Haase et al., 1998; Evers et al., 1999; Marinoni et al., 2000). We propose that this distinction is present even during processing of a relatively impoverished presentation of an isolated musical element (i.e., rhythm) with minimal emotional impact. This would support the notion that hemispheric lateralization for musical processing is affected by training at very basic levels, and not only during perception of musically rich stimuli (e.g., a symphonic movement).

Localization of Rhythm Perception

Early studies of musical processing in untrained individuals suggested right hemispheric specialization for tonal music (Peretz, 1985; Halpern and Zatorre, 1999; Perry et al., 1999). By comparison, the locus for rhythmic processing has been more difficult to identify, with several contradictory findings. Although lesion studies suggested left hemispheric dominance for rhythm perception (Sherwin and Efron, 1980; Robin et al., 1990), other studies showed definite right hemispheric contributions (Peretz, 1990; Kester et al., 1991; Penhune et al., 1999; Samson, 2003).

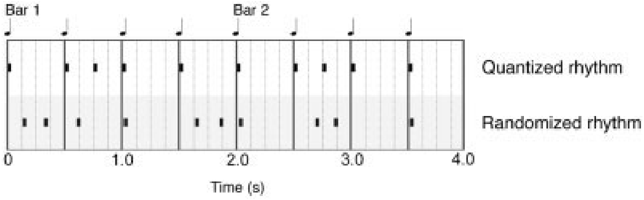

Fig. 1. Schematic representation of the differences between quantized and randomized rhythm stimuli. A 4-sec excerpt is shown. All notes had identical duration, loudness, and timbre and differed only by the temporal placement of their onset. Hence, the only differences between conditions were the degree of regularity or randomness of the rhythmic pattern. All stimuli were presented as pseudorandomized blocks (30 sec) of rhythm separated by rest intervals (30 sec), presented over 6 min.

These apparent inconsistencies may be a result of the disparate approaches that have been taken to study rhythm, with several factors contributing to the diversity of findings. Musical rhythms take place on the scale of seconds, thereby limiting the applicability of studies that have examined fine-grained temporal perception on the scale of milliseconds (Griffiths et al., 1998; Liegeois-Chauvel et al., 1999). Other studies of rhythm have also included aspects of pitch, melody, and timbre, making it difficult to isolate those neural elements responsible for rhythm alone (Platel et al., 1997). The fact that melodies have their own inherent rhythmic structure further obscures these issues. Additionally, many studies of rhythm have examined motor aspects of rhythm production (Krampe et al., 2000; Desain and Honing, 2003; Patel et al., 2005). While motor issues are obviously crucial to a broad understanding of rhythm processing, it is important to separate perceptual and productive aspects of rhythm, as they appear to implicate different (if overlapping) neural subsystems (Desain and Windsor, 2000). The impact of musical training on hemispheric specialization has also contributed to some of the confusion, as both anatomical and functional differences have been found in musicians' brains (Bever and Chiarello, 1974; Schlaug et al., 1995; Keenan et al., 2001; Ohnishi et al., 2001; Jongsma et al., 2004).

The effects of paradigm design on functional lateralization, particularly regarding the use of active vs. passive tasks, cannot be ignored. In electrophysiologic studies of speech comprehension, the use of an active task was found to increase left-sided activity and diminish right-sided activity within the temporal cortex in comparison to a passive task (Poeppel et al., 1996). That is, requiring a subject to perform a computational or judgmental task, despite providing a potentially informative behavioral index, may produce biases in brain activation that have more to do with the nature of the superimposed task rather than the actual perceptual stimuli themselves (Stephan et al., 2003). Since listening to music is generally a passive experience in that listeners are not required to make decisions on the basis of the perceived stimuli, an active task paradigm may not accurately reflect the neural processing typically involved in musical rhythm processing.

For this study, we prepared rhythmic stimuli in which all melodic elements were eliminated, allowing examination of the brain's responses to rhythm alone. A paradigm that contrasted complete rhythmic regularity against complete irregularity was utilized. We generated a perfectly quantized, or regular, rhythm as the test condition. For the control condition, the onset of each note was offset by the addition of randomness to the quantized rhythm, such that there was neither perceptual, predictable, or mathematical regularity, while the total number, loudness, and duration of notes remained constant (Fig. 1). To minimize the effects of task-based perception, which might induce additional left-lateralized activity, we chose a completely passive listening task. To minimize the possibility of increased analytical processing in response to a highly complex (or musically rich) stimulus, we intentionally employed an extremely simple, monotimbral percussive rhythm that could be easily reproduced by both musicians and nonmusicians alike.

MATERIALS AND METHODS

Subjects

We recruited 12 musicians and 12 nonmusicians for this study. In each group, there were nine males and three females. Musicians (mean age, 31 ± 6.52) were considered to have begun their musical training during childhood and played a musical instrument formally for more than 15 years, in addition to playing professionally. Nine of the 12 musicians were recruited from the Peabody Conservatory of Music (Baltimore, MD). The other three, recruited for their extensive musical experience, had all performed professionally prior to their enrollment in the study. Nonmusicians (mean age, 34 ± 14.9) had no formal musical background or aptitude beyond primary school and cultural exposure (e.g., radio, television) and played no musical instruments. All subjects had normal hearing and were right-handed. After explaining the nature and possible consequences of the study, informed consent was obtained for all subjects according to the guidelines set forth by the National Institutes of Health (NIH). The research protocol was approved by the institutional review board of the NIH.

Rhythm Stimuli

All rhythms were programmed and presented using the ES2 software synthesizer within the Emagic Logic Pro 6 sequencing environment on an Apple Powerbook G4 computer (Apple, Cupertino, CA). A snare drum sound of fixed loudness, duration, and timbre was chosen as the core auditory unit for all rhythms. To eliminate the effects of tonal perception, the programmed drum sound had a broadband frequency spectrum. Rhythms were presented at 120 beats/min in 4:4 time signature and were presented as either strictly quantized to fall exactly on the downbeat (test condition), or temporally randomized in terms of note onset such that no rhythmic regularity existed (Fig. 1). Intrarhythmic randomization was achieved by applying a random temporal filter (maximum range from −500 to 500 msec) to the onset of each note. After randomization, any overlapping notes were adjusted temporally to ensure that the total number of notes was identical for quantized and randomized rhythms, and that all notes could be discretely identified.

Scanning Procedure

All studies were performed at the Functional Magnetic Resonance Imaging Facility at the NIH. Functional imaging data were acquired using a 3 Tesla whole-body scanner (GE Signa; General Electric Medical Systems, Milwaukee, WI) using a standard quadrature head coil and a gradient-echo EPI sequence. The scan parameters were as follows: TR = 2,000 msec, TE = 30 msec, flip angle = 90°, 64 × 64 matrix, field of view = 220 mm, 26 parallel axial slices covering the whole brain, 6 mm thickness. Four initial dummy scans were acquired during the establishment of equilibrium and discarded in the data analysis; 180 volumes were acquired for each subject. In addition to the functional data, high-resolution structural images were obtained using a standard clinical T1-weighted sequence.

The subjects lay supine in the scanner without mechanical restraint. Subjects listened to rhythmic patterns presented in a block-design paradigm using nonferromagnetic electrostatic earphones (Stax, Saitama, Japan), with additional ear protection to minimize background scanner noise. Volume was set to a comfortable listening level that could be easily heard over the background scanner noise. Blood oxygen level-dependent imaging (BOLD) was used to measure functional activity. Stimuli were presented in one 6-min run that contained pseudorandomized blocks of rhythms (30 sec) separated by rest intervals (30 sec). Subjects were instructed to close their eyes and remain motionless while listening to all rhythms. The subjects were monitored to ensure that they did not tap their feet or hands throughout the scanning session.

Statistical Analysis

BOLD images were acquired and then preprocessed in standard fashion, with spatial realignment, normalization, and smoothing (9 mm kernel) of all data using SPM99 software (Wellcome Trust Department of Imaging Neuroscience, London, U.K.). Fixed- and random-effects analyses were performed using the threshold of $P < 0.001$ uncorrected. Contrast analyses were performed across both groups and all conditions. Normalized volume coordinates from SPM99 were converted from Montreal Neurological Institute coordinates to Talairach coordinates for specific identification of regions of activity. Three-dimensional renderings and axial slice representations were constructed from contrast maps generated by SPM99 and MRIcro (University of Nottingham, Nottingham, U.K.).

RESULTS

All data were processed using SPM99 (Wellcome Trust Department of Imaging Neuroscience). We performed analyses of commonalities (conjunctions) and differences (contrasts) in activation patterns of musicians and nonmusicians to both quantized and random rhythmic sequences. Fixed-effects analyses were used to create conjunction maps of activity common to both musicians and nonmusicians within a given condition, represented by [Musicians − Rest] + [Nonmusicians − Rest], referred to hereafter as [M + NM]. Random-effects analyses were used to compare differences between all groups and conditions. Contrast analyses revealed unambiguous differences between rhythm processing in musicians and nonmusicians, as well as group-specific differences between processing of quantized and random stimuli. These differences are reflected in the contrasts [Musicians − Rest] − [Nonmusicians − Rest}, referred to hereafter as [M − NM]; [Nonmusicians − Rest] − [Musicians − Rest], referred to hereafter as [NM − M]; and [Quantized Rhythms − Rest] − [Randomized Rhythms − Rest], referred to hereafter as [Quantized − Randomized].

Conjunction Analysis

The [M + NM] conjunction analysis during quantized rhythm blocks (Table 1, upper section) revealed bilateral activation of primary and secondary auditory cortices in the superior temporal gyrus (STG) and strongly right-lateralized activation throughout the frontal operculum, including the pars orbitalis, pars triangularis, and pars opercularis. Left-sided ventral supramarginal gyrus (SMG) and right-sided superior frontal gyrus (SFG) activity was also found. These areas of activation are rendered three-dimensionally in Figure 2 (top), with representative axial slices shown in the bottom panel.

Contrast Analysis of Musicians-Nonmusicians

The [M − NM] contrast shows activity that was relatively greater in musicians than in nonmusicians during quantized rhythm perception. This contrast was characterized by robust activation of perisylvian cortices—bilat-

TABLE 1. Anatomic regions, MNI coordinates, and intensity t-score of local maxima for conjunction and contrast analyses between musicians and non-musicians

MUSICIANS + NONMUSICIANS	Left Hemisphere				Right Hemisphere				
	Location (mm)			t-score	Location (mm)			t-score	BA
Region	*x*	*y*	*z*		*x*	*y*	*z*		
Superior Temporal									
TTG	−45	−24	12	4.03	45	−25	10	5.77	41
STG	−51	−33	12	10.64	57	−30	11	9.27	42
STG/STS	−54	−18	0	13.45	57	−21	0	14.38	22
STG	−48	−33	6	12.84	48	−33	6	10.55	22
Inferior Parietal									
Ventral SMG	−60	−48	27	3.48	—	—	—	—	40
Frontal Operculum									
Pars orbitalis	—	—	—	—	57	27	−1	3.17	47
Pars triangularis	—	—	—	—	54	25	6	3.30	45
Pars opercularis	—	—	—	—	48	9	27	3.02	44
Prefrontal									
SFG	—	—	—	—	3	0	69	3.73	6

MUSICIANS − NONMUSICIANS	Left Hemisphere				Right Hemisphere				
	Location (mm)			t-score	Location (mm)			t-score	BA
Region	*x*	*y*	*z*		*x*	*y*	*z*		
Middle Temporal									
Anterior MTG	−60	−39	−15	4.23	63	−42	−12	3.87	21
Mid MTG	−63	−39	−3	3.15	—	—	—	—	21
Inferior Parietal									
AG	−36	−66	33	4.06	48	−60	36	3.47	39
Dorsal SMG	−48	−54	48	3.12					40
Frontal Operculum									
Pars orbitalis	−45	42	−3	3.38	—	—	—	—	47
Pars opercularis	−60	9	24	3.34	—	—	—	—	44
Dorsal pars opercularis	−48	6	30	3.42	—	—	—	—	44/6
Prefrontal									
Ventral MFG	−27	60	12	4.12	—	—	—	—	10
Dorsal MFG	−51	9	45	3.50	—	—	—	—	9/6
SFG	−3	36	54	3.71	—	—	—	—	8

NONMUSICIANS − MUSICIANS	Left Hemisphere				Right Hemisphere				
	Location (mm)			t-score	Location (mm)			t-score	BA
Region	*x*	*y*	*z*		*x*	*y*	*z*		
Superior Temporal									
TTG/STG	−39	−39	12	3.81	45	−33	18	5.1	41/42
Inferior Parietal									
Ventral SMG	—	—	—	—	42	−36	27	3.58	40
Superior Parietal									
Precuneus	—	—	—	—	15	−57	45	4.09	7
Occipital									
Cuneus/Striate	−12	−75	9	4.13	—	—	—	—	17/18
Frontal Motor									
Precentral Gyrus	−33	−12	42	3.99	45	−12	30	3.88	4/6
Subcortical									
Globus Pallidus/Putamen	−27	−18	−3	4.29	—	—	—	—	—

eral activation of the anterior middle temporal gyrus (MTG), and strongly left lateralized activation of the frontal operculum, middle MTG, and inferior parietal lobule (IPL; both angular gyrus and SMG; Table 1, middle section). Prefrontal cortices, encompassing both the superior frontal gyrus (SFG) and left middle frontal gyrus (MFG), were activated as well. The perisylvian activations are rendered three-dimensionally with a volume cutout centered around the sylvian fissure in Figure 3 (top), revealing activity of the left frontal operculum, MTG, and IPL. Representative axial slices are shown in Figure 4 (top). During randomized rhythm presentations, the [M − NM] contrast revealed significant activations only in the left superior temporal gyrus.

Contrast Analysis of Nonmusicians-Musicians

The [NM − M] contrast shows activity that was relatively greater in nonmusicians than musicians for quan-

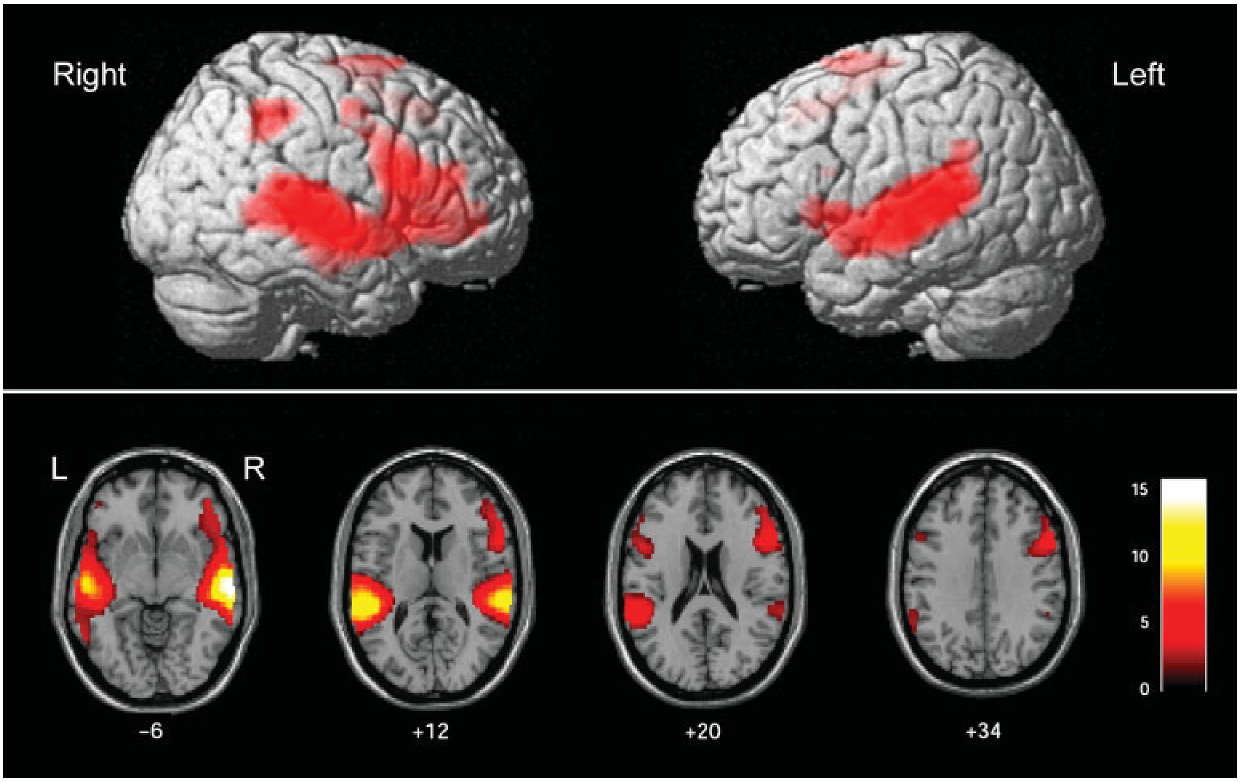

Fig. 2. Conjunction analysis reveals a common network for rhythm processing in musicians and nonmusicians. **Top:** Three-dimensional mapping of brain activity common to musicians and nonmusicians when listening to a simple quantized rhythm. Right frontal opercular, bilateral transverse temporal gyrus, and bilateral superior temporal gyrus activations are seen. **Bottom:** Representative axial slices [numbers indicate z-axis plane of section (in mm) above or below anterior commissure-posterior commissure line] showing a predominance of right-sided activity in the frontal operculum. Scale bar shows intensity of activation (*t*-score). L, left; R, right.

tized rhythm perception. For this contrast, the spread of activation was more evenly distributed. No perisylvian language areas were activated for [NM − M] (Table 1, lower section). Portions of Heschl's gyrus, STG, and planum temporale were more active, with right-sided predominance in nonmusicians. Bilateral activation of precentral gyrus and left globus pallidus was also seen. Representative axial slices are shown in Figure 4 (bottom).

Contrast Analysis of Quantized-Randomized Rhythms

The [Quantized − Randomized] contrast reveals activity that was greater during stimulus blocks of regular (quantized) rhythms than during randomized rhythm blocks. For musicians, a random-effects analysis of contrasts between [Quantized − Randomized] rhythms revealed greater activity in left hemisphere perisylvian areas as well, including the left frontal operculum and MTG—approximately the pattern seen for [M − NM] processing of quantized rhythms. Figure 3 (bottom) shows fitted response curves for voxels representing the left frontal operculum (pars orbitalis and pars opercularis), left MTG, and left supramarginal gyrus for a fixed-effects analysis. The fitted curves reveal greater activity in these perisylvian regions for quantized (red) vs. randomized (blue) rhythm perception within musicians. Within these regions, the opercular and middle temporal regions showed more robust findings, while the supramarginal gyrus showed less robust findings. The left angular gyrus showed contrasting findings, with slightly increased activity during randomized vs. quantized rhythm perception. Nonmusicians revealed no suprathreshold activity in any of these areas. No differences were seen within musicians for [Quantized − Randomized] rhythms in right MTG.

Rest Intervals/Scanner Noise

During the rest condition, the presence of scanner noise (which itself is a repetitive, rhythmic sound) introduced a potential confound to the study. Contrasts analysis of explicitly modeled rest conditions revealed no differences between musicians and nonmusicians during rest intervals, despite the presence of ongoing scanner noise in the background. All differences between musicians and nonmusicians were only seen during the presentation of rhythmic stimuli.

DISCUSSION

The conjunction analysis between musicians and nonmusicians (Fig. 2) highlights a basic network for the processing of quantized rhythms that is activated in both musicians and nonmusicians, which may reflect an innate musical competence that is independent of training. The findings of right frontal opercular activation in both mu-

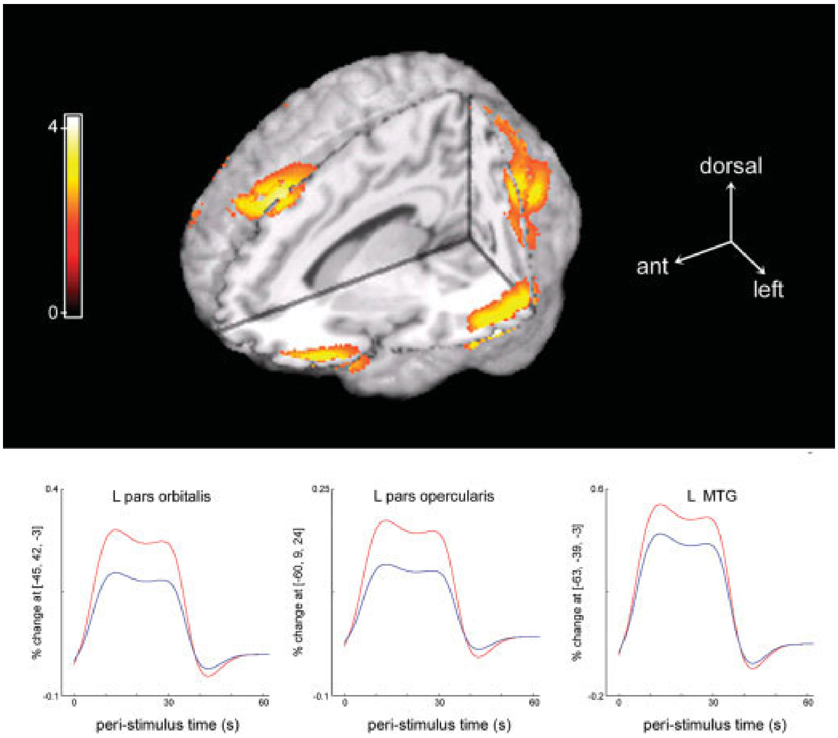

Fig. 3. Left perisylvian language areas are active in musicians during passive quantized rhythm perception. **Top:** Three-dimensional rendering with cutout volume centered around sylvian fissure of [Musician − Nonmusician] contrast during quantized rhythm perception. The contrast analysis reveals activation in perisylvian language areas (left frontal operculum, middle temporal gyrus, and inferior parietal lobule) and left prefrontal cortex. Scale bar shows intensity of activation (*t*-score). **Bottom:** Fitted response curves for musicians listening to quantized vs. randomized rhythms. The curves show percentage changes in mean signal activity (y-axis) over peristimulus time (x-axis) within voxels of interest (given in MNI coordinates) selected from the contrast of [Musicians − Nonmusicians] during quantized rhythm perception. Responses to quantized rhythms (red) and randomized rhythms (blue) are shown for left frontal operculum (pars orbitalis and pars opercularis) and middle temporal gyrus. MTG, middle temporal gyrus; L, left; ant, anterior.

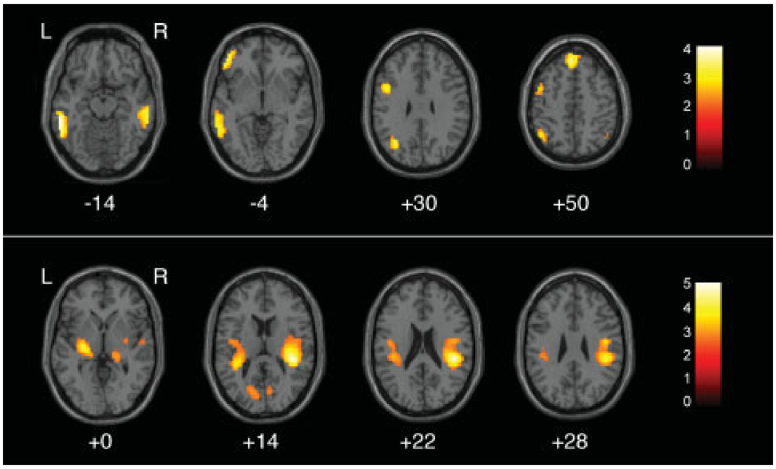

Fig. 4. Nonmusicians do not exhibit left lateralization of brain activity during passive rhythm perception. Functional activation maps revealed by a random-effects analysis of contrasts between musicians and nonmusicians listening to quantized rhythms. **Top:** [Musicians − Nonmusicians]. Representative axial slices reveal left-sided predominance in musicians of perisylvian region activity, including frontal operculum, middle temporal gyrus, and inferior parietal lobule. **Bottom:** [Nonmusicians − Musicians]. Axial slices reveal right-sided distribution in nonmusicians without activation of perisylvian language areas. Scale bars show intensity of activation (*t*-score). L, left; R, right.

sicians and nonmusicians clarifies previous results regarding right hemispheric contributions to rhythm processing (Peretz, 1990; Kester et al., 1991; Penhune et al., 1999), implying a fundamental role of this region in rhythmic tasks. Furthermore, additional musical training does not lead to a decrease in right-sided activity for regular rhythm processing, but rather the recruitment of additional areas. This finding supports the first hypothesis proposed in this article, that there should be common areas active in both musicians and nonmusicians during rhythm processing.

Nonmusicians showed greater right-lateralized activation within the auditory cortices (STG/TTG) and parietal regions than musicians. Nonmusicians also showed greater activity in right-sided globus pallidus and bilateral precentral gyrus, suggesting preferential recruitment of motor regions during quantized rhythm perception in the musically untrained. This activation in motor regions was present despite the fact that the task was passive and isolated to perception alone, and that no visible movement (such as foot or finger tapping) was observed during scanning. These findings imply a basic, training-independent link in nonmusicians between rhythmic auditory input and neural systems responsible for motor control, with an emphasis on right-sided neural mechanisms. Musicians, in comparison, appeared to dissociate incoming rhythmic input from motor responses relative to nonmusicians and instead utilized an analytic mode of processing concentrated in the left hemisphere.

Our findings support the hypothesis that formal musical training may lead to left-lateralized activity during passive rhythm perception. Musicians showed selective activation of heteromodal association cortices lateralized to the left during passive quantized rhythm perception. Furthermore, within musicians as a group, the perisylvian language areas had relatively greater hemodynamic responses during quantized rhythms in comparison to randomized rhythms. Decreasing the statistical threshold for significance (e.g., $P < 0.01$) revealed activation of perisylvian cortices in musicians even during randomized rhythm presentation, suggesting that these areas are fundamentally important in musicians during temporal pattern analysis, and that increasing the rhythmic regularity of a pattern enhances the use of these regions. This network of regions—anterior and middle MTG, IPL, and frontal operculum—constitutes the perisylvian language system. Indeed, the distribution of perisylvian activations seen in musicians is strikingly congruent with that identified in studies of language comprehension at the sentential and narrative levels (Papathanassiou et al., 2000; Xu et al., 2005).

As human forms of communication and expression, music shares several similarities with language (Maess et al., 2001; Zatorre et al., 2002; Koelsch et al., 2004). It has been suggested that, like language, there is a universal musical grammar—a set of formal rules that govern musical expression—instantiated in the human brain (Lerdahl and Jackendoff, 1983). Indeed, some authors have proposed the notion of a distinct "musical syntax," although the rules and the universality of these rules have been difficult to define (Bernstein, 1976). Spoken languages have a readily apparent rhythmic flow that contributes to phrasing, prosody, and cadence (Patel et al., 1998; Patel and Daniele, 2003). The art form of poetry, with its emphasis on verse, meter, and stanza structure, represents perhaps the most sophisticated union between language and rhythm (Jones, 1997; Lerdahl, 2001).

Yet beyond the obvious rhythmic patterns that characterize both musical and verbal utterances, there may be deeper parallels that account for a more robust relationship between language and rhythm in musicians (Liberman and Prince, 1977). Rhythm possesses generative features much like language does—the capacity to produce an infinite range of permutations from a finite set of elements—paralleling the combinatorial features of phonology and syntax (Selkirk, 1984; Fitch and Hauser, 2004). The hierarchical organization of rhythmic structure obeys rules that mirror those of metrical phonology. At a syntactic level, meter provides a contextual musical grammar, within which an infinite number of possible rhythmic sequences can be derived, much as phrase structure grammar permits a limitless range of syntactic constructions (Longuet-Higgins and Lee, 1984). These parallels between deeper aspects of rhythm and language suggest that rhythm processing might be linked to left hemisphere language mechanisms in the musically trained.

In a neuroimaging study of six subjects attempting to reproduce auditory rhythms, it was found that hemispheric lateralization for rhythm processing depends on mathematical intervallic properties of the rhythm, and that integer-based rhythms were easier to reproduce than noninteger-based rhythms (Sakai et al., 1999). Although the paradigm in this study differed (an active paradigm was used with an explicitly modeled period of working memory), the authors found left-sided hemispheric lateralization in nonmusicians for integer-based rhythms. Taken together, our findings support the notion that integer-based rhythms (which were also quantized and easier to reproduce) lead to relatively greater activity within the left hemisphere. However, we found that this left lateralization was pronounced only in the musically trained, and that this activity was centered in the perisylvian language cortices.

While it may be argued that the perisylvian language areas may subserve multiple processing functions (i.e., both language and rhythm perception in the musically trained), it is notable that nonmusicians did not show similar findings even when processing identical auditory stimuli—similar to the situation in which one hears the sounds of a foreign language yet misses linguistic structure (Belin et al., 2000, 2002; Davis and Johnsrude, 2003). Our results suggest one possible interpretation to account for the increased activation of language areas in musicians during passive rhythm perception: within the context of fundamental commonalities between the generative nature of rhythm and language, as well as between the hierarchical structure and recursive properties of rhythm, metrical phonology, and phrase structure grammar—properties that may become implicitly evident after extensive musical training.

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