

Jazz Drummers Recruit Language-Specific Areas for the Processing of Rhythmic Structure

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Rhythm is a central characteristic of music and speech, the most important domains of human communication using acoustic signals. Here, we investigated how rhythmical patterns in music are processed in the human brain, and, in addition, evaluated the impact of musical training on rhythm processing. Using fMRI, we found that deviations from a rule-based regular rhythmic structure activated the left planum temporale together with Broca’s area and its right-hemispheric homolog across subjects, that is, a network also crucially involved in the processing of harmonic structure in music and the syntactic analysis of language. Comparing the BOLD responses to rhythmic variations between professional jazz drummers and musical laypersons, we found that only highly trained rhythmic experts show additional activity in left-hemispheric supramarginal gyrus, a higher-order region involved in processing of linguistic syntax. This suggests an additional functional recruitment of brain areas usually dedicated to complex linguistic syntax processing for the analysis of rhythmical patterns only in professional jazz drummers, who are especially trained to use rhythmical cues for communication.

Keywords: auditory processing, fMRI, music, neuroplasticity, training

Introduction

Language and music are prominent examples of human communication via acoustic signals. In both faculties, a structure based on complex rules characterizes the respective acoustic sequences (Patel 2003) that can convey meaning using either linguistic or musical cues (Meyer 1956).

Besides harmony and melody, rhythm is one of the main structural components in western popular and jazz music. The basic element of any rhythm is a pulse (Sadie and Tyrell 2001), which is a recurring articulation (or sound) in the flow of musical time (Sadie and Tyrell 2001). A distinct number of regularly spaced pulses can be grouped together and stressed differently to form the so-called “meter” (e.g., 2/4 or 3/4, or a “March” or a “Waltz”). It provides a framework or grid that allows the listener to establish a temporal expectancy with regards to future acoustic events. Dividing the time between the pulses by an integer multiple of 2 or 3, placing additional acoustic events either together with the pulses of the regular meter or in the resulting time grids, and stressing events differently are all means of variations used to create a metrical rhythm (see Fig. 1 for an example), which can include different hierarchical levels (Drake et al. 2000). Such an arrangement of discrete elements into regular temporal sequences

according to a set of governing principles is here referred to as rhythmic structure. Moreover, such a regular rhythm is often enriched by syncopations, which are an important stylistic device mostly in jazz and classical music. Syncopation means the emphasis of an acoustic event within the regular time grid, which is (according to the hearing expectation established by the regular rhythm) usually not stressed, thus creating a deviation from musical expectancy, but still following the underlying rhythmic structure on a more complex level ((Sadie and Tyrell 2001); see “syncopated deviation” in Fig. 1B,C). In contrast, an acoustic event that is completely unrelated to the underlying time grid constitutes a musically “incorrect deviation” violating the rhythmic structure (incorrect deviation in Fig. 1D, see also Supplementary audio files for sound examples).

Violations of the expected musical structure in the harmonic or melodic domain are known to evoke event-related potentials mainly in frontal or temporal regions (Maess et al. 2001; Miranda and Ullman 2007), as measured using electroencephalography or magnetoencephalography (MEG). Interestingly, similar activations can be observed when subjects are exposed to violations related to language structure (Friederici and Kotz 2003) suggesting that the analysis of organizing principles of language and music takes place in overlapping brain areas (Friederici et al. 2000; Koelsch et al. 2002, 2005; Koelsch 2009), at least when harmonic or melodic aspects of music are concerned. In addition, there is a behavioral interference between musical and linguistic structure processing (Fedorenko et al. 2009; Slevc et al. 2009). As language and music are probably the most important means of human communication that are based on a rule-based arrangement of acoustic signals, it is thus conceivable that the brain uses shared resources for analysis of such rule-based organization in both domains. Accordingly, common neural substrates for processing hierarchically structured sequences in music and language have been suggested (Patel 2003), whereas others have emphasized the domain specificity of music processing, at least when tonal aspects of music are concerned (Peretz and Coltheart 2003). This debate not only concerns the “higher-level” structural analysis of the respective rule-based acoustic sequences, and some recent evidence suggests both commonalities and differences of the cortical representations of music and speech stimuli on a more general level (Rogalsky et al. 2011; Schirmer et al. 2012).

Previous research exploring the neural substrates of rhythm processing using neuroimaging found a strong

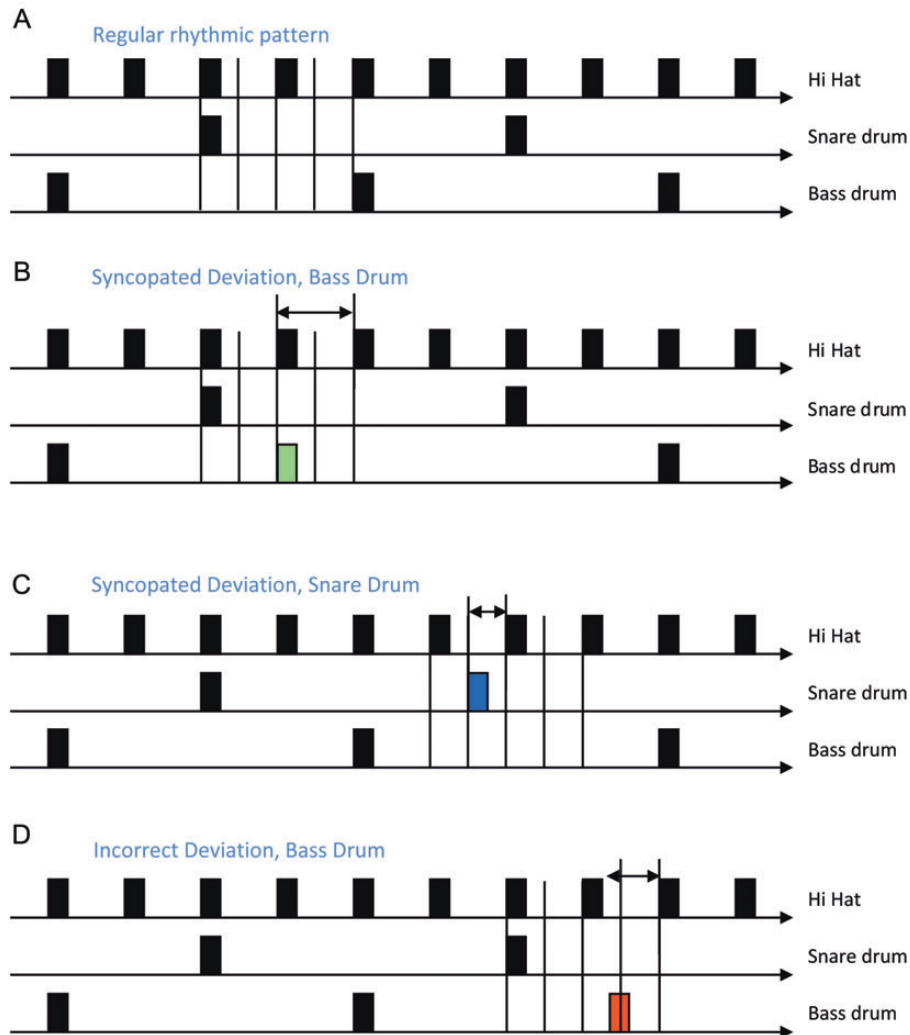


Figure 1. Schematic representation of the regular rhythmic pattern, and illustration of syncopated and incorrect deviations. In the basic rhythm (A), the hi-hat plays 1/8 notes, bass drum and snare drum play 1/2 notes (shifted 1/4 note in relation to each other), establishing a regular or metrical rhythmic pattern (indicated by vertical lines). (B–D) Examples of rhythmic variations: in (B), an early bass drum beat occurs together with the previous hi-hat beat (1/8 note earlier compared with the regular pattern, syncopated deviation), in C an early snare drum beat occurs exactly in between 2 hi-hat beats (shifted by an 1/16 note compared with A). These are examples for early beats that are musically correct (syncopated deviations). In D, an early bass drum beat is occurring with no relation to the time grid established by the underlying metrical rhythm (incorrect deviation). See also Supplementary audio files for sound examples.

involvement of brain regions usually implicated in motor tasks such as the basal ganglia (Grahn and Rowe 2009), (pre-) motor cortices (Chen et al. 2008; Bengtsson et al. 2009; Grahn and Rowe 2009) or cerebellar structures (Chen et al. 2008; Grahn and Rowe 2009) during the perception of musical rhythms, in addition to activity in auditory cortices. However, these studies mainly focused on the rhythm's tactus, that is, the perceptually prominent aspect of a rhythmic pattern to which most people choose to tap to when they listen to music (Parncutt 1994).

Here, we were interested to study which brain areas are involved in detecting deviations from temporal expectancies based on the analysis of rhythmic structure. Similar to the approach used by Maess et al. (2001) to localize the neural underpinnings of harmonic structure analysis in music, we thus exposed our subjects ($n = 22$) to a regular rhythmic sequence in a 2/4 m to establish a temporal or rhythmic expectancy of future events. However, this sequence was interspersed with

syncopated deviations (that constitute a form of deviation of the regular pattern, which is, however, governed by a more complex or higher-order structural principle, see syncopated deviations in Fig. 1B,C), or incorrect deviations (i.e., completely irregular drum beats with no relation to the underlying metrical rhythm (see incorrect deviations in Fig. 1D)). This enabled us to compare brain responses to rhythmic deviations that are either related to the underlying metrical rhythm (i.e., they are correct in a musical sense) with those that violate the underlying rhythmic structure completely. We hypothesized that, similar to violations of complex harmonic structure in music (Maess et al. 2001), violations of a rule-based rhythmic structure activate regions usually involved in the processing of linguistic structure.

To avoid perceptual interactions with the “beat” usually associated with conventional pulsed gradient sequences with our experimental stimuli, we used continuous-sound fMRI optimized for studying the auditory system (Seifritz et al. 2006)

and especially suited for the investigation of the processing of temporal aspects of sounds (Herdener et al. 2010), to identify brain structures involved in processing of rule-based rhythmic organization in music.

The focus of our study, however, was to evaluate the impact of musical training on rhythmic structure analysis. It has been argued that deviations of musical expectancy are used for musical communication (Meyer 1956; Huron 2001). Especially in jazz (when compared with other music styles such as western classical or pop music), improvisations are very common during performances and are often characterized by deviations from previously established rhythmic patterns and represent a means of spontaneous communication and expression of musical ideas during the interplay among musicians. This form of musical communication, however, still follows a set of (more complex) governing principles, and it requires a considerable amount of training to acquire the skills necessary for this musical «conversation». Thus, we compared the brain responses to syncopated deviations or incorrect deviations in rhythmical experts that experienced an intensive training of rhythmical skills (i.e., professional jazz drummers) versus nonexperienced persons (i.e., musical laypersons). We expected a differential pattern of neural activity in response to rhythmic deviations in experts as a result of extensive training (see also (Munte et al. 2002) for a review about functional plasticity in the musician's brain). More specifically, we hypothesized that left-hemispheric areas usually involved in language processing (Zatorre and Binder 2000; Fadiga et al. 2009) might also serve the analysis of rhythmic structure in jazz drummers who are used to communicate by rhythmic cues.

Materials and Methods

Subjects

We investigated 22 healthy male persons (age 20–50 years) with no history of neurological or audiological disorders. The study has been approved by the local ethics committee, and all subjects provided written informed consent prior to participation.

Inclusion criteria for professional jazz drummers were 1) professional training at a music college or university and several years of experience in playing jazz, or 2) at least 5 years of experience as a professional drummer in jazz music.

Subjects were considered as musical layperson (in the rhythm domain), if they either never played an instrument at all, or if they never played a percussion instrument and did not play any other instruments during the last 5 years.

Behavioral Testing of Musical Skills

To behaviorally assess basic temporal sound processing facilities, subjects performed a standardized test measuring musical abilities after functional imaging, which required the detection of small deviances in short melodies in a forced choice task (the Advanced Measures of Music Audiation [AMMA] test by Gordon [1998]).

Additionally, a second test to assess the rhythmic abilities was performed on all subjects (rhythm subtest of the Seashore Test [Carl Emil Seashore: Measures of Musical Talent 1939]).

Stimuli and Experimental Design

Stimuli were programmed in Pro Tools with drum sounds of the instrument plug-in “Strike” (Avid Technology, USA) using 3 instruments usually included in a typical drum set (i.e., bass drum, snare drum, hi-hat). We refer to any single sound of each of these 3 instruments as “beat.” A regular 2/4 rhythm and quarter-note pulse is established by

a bass drum beat on “1” and a snare drum beat on “2,” played at 100 bpm. Syncopated deviations are created by shifting the drum beats of 1 of these 2 instruments either a half or a quarter of the time interval between 2 pulses, that is, we created 4 different syncopated deviations (snare beats shifted either by 1/8 or 1/16 note, and bass beats shifted either by 1/8 or 1/16 note; see Fig. 1 for examples). Incorrect deviations are created by shifting the drum beats produced by either a snare or a bass drum to a point in the time grid that is not an integer multiple of the time between 2 pulses, and is thus not following any rhythmical structure, that is, we created 2 different incorrect deviations (incorrect snare beats, incorrect bass beats; see Fig. 1 for examples). Additionally, the third instrument (hi-hat) is placed on “1” and “2” and helps establishing the quarter-note pulse. Furthermore, it is also played exactly in between 2 pulses. This way, it is improving the temporal orientation of the listener by creating a sort of “sub-pulse” (see Fig. 1; see also Supplementary Files for sound examples). The hi-hat pattern continues throughout the whole experiment without any alteration. Variations from the regular rhythmic pattern (syncopated or incorrect deviations by either the bass drum or the snare drum) occurred on average every 19 s (jittered between 16 and 22 s), according to a classic event-related design, allowing the BOLD signal to return to baseline level prior to each successive event.

Stimuli were digitally recorded using ProTools (Avid Technology) as a wav-file (44.1 kHz, 24 bit), played from an Apple Notebook, and presented to the subjects in mono via MR-compatible headphones (Commander XG, Resonance Technologies) at comfortable sound levels. During the experiment, subjects were instructed to focus their attention on a silent cartoon movie (La Linea, Osvaldo Cavandoli, KSM, Germany) that was presented simultaneously to the acoustic stimulation on a back projection screen placed at the end of the scanner's magnet bore viewed via a mirror system. To control that subjects focused their attention to the visual input, they had to answer 5 questions related to the movie content after scanning. Furthermore, the movie was occasionally interrupted by a brief (500 ms) presentation of geometric symbols (triangles, squares, pentagons; 13 events within the whole run), and subjects were asked to count the number of triangles occurring within the experiment. The occurrence of these symbols was timed in a way that it was randomly jittered with the restriction that it was at least separated by 6.5 s from the acoustic events of interest, to avoid interferences of BOLD responses related to visual or acoustic inputs, respectively. This way, we ensured that the processing of the rhythmic pattern was not in the focus of attention, and were able to exclude an attentional bias between groups for the effects of interest.

Data Preprocessing

Image time series were processed using the software package Brain Voyager QX 2 (Brain Innovation, The Netherlands).

For each subject, the first 4 echoplanar images were discarded to allow for magnetization signal full saturation and all the remained scans were realigned to the first included volume scan one using a Levenberg–Marquadt algorithm optimizing 3 translation and 3 rotation parameters on a resampled version of each image. The resulting head motion-corrected time series were then corrected for the different slice scan times using an interpolation procedure and then filtered in the temporal domain. For temporal filtering, a high-pass filter with cutoff to 6 cycles was used to reduce linear and nonlinear trends in the time courses. Using the results of the image registration with 3D anatomical scans, the functional image time series were, then, warped into Talairach space and resampled into 3-mm isotropic voxel time series. Finally, to perform a group-level analysis, the resampled volume time series were spatially filtered (smoothing) using a 6-mm full-width-at-half-maximum Gaussian kernel.

Statistical Analysis

The variance of all image time series was estimated voxel-wise according to a random effects convolution-based general linear model (GLM) analysis (Friston et al. 1995; Friston et al. 1999). Six “event-type” predictors encoding the responses to the 4 different types of syncopated deviations (shifted by 1/8 or 1/16 note and either played

with the bass or the snare drum), the 2 types of incorrect deviations completely unrelated to the regular rhythmic pattern (played by bass or snare drum), and 1 “block-type” predictor of no interest encoding the response to the regular rhythmic pattern against a baseline of no auditory stimulation (confound) were defined using the double-gamma function (Friston et al. 1998) as hemodynamic input function for the linear convolution.

For each subject and each voxel included in the slab of imaging, the 7 “beta” weights of the 7 regressors were estimated according to a GLM fit–refit procedure, which ensured a correction of residual serial correlation in the error terms according to a first-order autoregressive model (Bullmore et al. 1996).

To draw population-level inferences from statistical maps, the 6 beta estimates for the predictors of interest at each voxel entered appropriate *t*-tests with subjects as random observations to evaluate the main effects of rhythmic variations across all subjects (random effects analysis, (Friston et al. 1999)).

To test for group differences, the beta estimates for the predictors of interest at each voxel also entered a second-level analysis of variance (random effects ANOVA), and 2 2-way ANOVA tables were prepared with one within subject factor (including either the 4 levels of syncopations or the 2 levels of false beats) and 1 between-subject factor (musicians vs. musical laypersons). Group differences were evaluated by contrasting the respective beta estimates across groups using a *t*-statistic.

All statistical maps were overlaid on the “average” Talairach-transformed anatomical scan derived from the anatomical images of all subjects. In order to localize the significant effects on the average anatomy, a threshold of $P < 0.01$ (corrected for multiple comparisons using a false discovery rate [FDR] approach; (Genovese et al. 2002)) was applied to the *t*-map representing the main effects across groups. For linear contrasts across conditions or across groups, we accepted an initial (uncorrected) voxel-level threshold of $P = 0.001$, and then applied a cluster-level correction approach (Forman et al. 1995, see also (Etkin et al. 2004)) which protected against false positives at 5% (corrected for multiple comparisons) and defined the corresponding minimum cluster size to apply.

Results

We presented 2 types of rhythmic variations to subjects with a widely different background of musical training (12 professional jazz drummers and 10 musical laypersons, all right handed; see also Table 1 for detailed subject characterization and behavioral measures of rhythmic expertise). More specifically, a regular 2/4 rhythm as programmed on a synthesizer (using a snare drum, a bass drum and a hi-hat and played at 100 beats per minute [bpm], Fig. 1) was presented that was interspersed by either syncopated deviations (beats that deviate from the musical expectancy by emphasizing a usually unstressed location in the time grid, but still related to the regular rhythmic structure), or by musically incorrect

Table 1

Subject characterization

	Musicians mean (SD)	Nonmusicians mean (SD)	<i>t</i> -Test
Age (years)	31.17 (7.29)	27.6 (5.44)	n.s. ($P = 0.23$)
Begin musical training at Age of (years)	8.42 (1.89)	n.a.	
Average number of hours per week spent on musical training (over the past 5 years)	21.5 (14.55)	n.a.	
AMMA score (rhythm/tonal)	33.08 (4.66)/ 30.67 (5.17)	28.5 (3.04)/ 26.50 (3.26)	$P = 0.016$ / $P = 0.041$
Seashore score	29.33 (0.75)	26.1 (2.3)	$P = 0.002$

beats (that are not related to the otherwise regular rhythmic structure, Fig. 1).

First of all, we observed that the occurrence of syncopated deviations, evaluated as main effects in the whole group of studied subjects, elicited a significant hemodynamic response in the posterior superior temporal gyrus (STG) of the right hemisphere ($P < 0.01$, FDR corrected; Table 2), whereas incorrect deviations (i.e., completely rhythmically unrelated beats) induced activations on posterior STG of both hemispheres ($P < 0.01$, FDR corrected; Table 2). Then, the differential contrast between syncopated and incorrect deviations was performed, to detect all possible regions that are specifically sensitive to violations of rhythmic structure. This contrast revealed significant differences in favor of incorrect deviations in left posterior STG and bifrontal inferior frontal gyrus, corresponding to Brodmann area (BA) 44 (i.e., Broca’s area and its right-hemispheric homolog; $P < 0.05$, cluster level corrected over the entire brain; Fig. 2; for additional clusters see Table 2).

Subsequently, we compared BOLD responses to syncopated or incorrect deviations between groups of rhythmic experts (professional jazz drummers) and musical laypersons. When comparing activity induced by syncopated beats, we found differential activity in the supramarginal gyrus (SMG) of the left hemisphere (BA 40, $x = -51$, $y = -45$, $z = 29$), with enhanced activation in the rhythmic experts only ($P < 0.05$, whole-brain cluster level corrected; Fig. 3A). When comparing the activity induced by incorrect deviations, we also found enhanced activity in musicians, in right insula (BA 13, $x = 37$, $y = 6$, $z = -1$) and, again, in left SMG ($x = -57$, $y = -48$, $z = 21$) at $P < 0.05$ (cluster level corrected over the entire brain; Fig. 3B), suggesting a specialization for the processing of both types of rhythmic variations in left SMG in professional drummers compared with musical laypersons. A further inspection of BOLD signal time courses in left SMG revealed that only rhythmic experts show activation in this region in response to deviations from a regular rhythmic pattern, whereas laypersons did not exhibit any specific response to deviations of rhythmic structure at this higher level of auditory processing (Fig. 3C).

Taken together, we show that secondary and adjacent association areas of auditory cortex represent deviations from a regular rhythmic pattern, with right posterior STG

Table 2

Brain regions activated by deviations of the regular rhythmic patterns

Brain region	Brodman area	Tal coordinates	Cluster size (mm ³)	<i>t</i> Value (average)
Response to syncopated deviations				
Right superior temporal gyrus (STG)	22	59, -35, 11	1444	6.69
Response to incorrect deviations				
Right STG	22	55, -34, 10	3108	5.98
Left STG	22	-54, -36, 11	2639	6.33

The table lists brain areas that are activated by either syncopated deviations, or by incorrect deviations (thresholded at $P < 0.01$, FDR corrected). Brain regions and Brodmann areas were labeled by using the Talairach Client (www.talairach.org). Note that syncopated and incorrect deviations both activate the same right-hemispheric area comprising posterior STG, while only the later additionally activate corresponding left-hemispheric regions (see also Fig. 2 for a differential contrast). Comparing activity to syncopated or incorrect deviations did not reveal differences between musicians and musical laypersons at this level of the auditory neuraxis (see also Fig. 3).

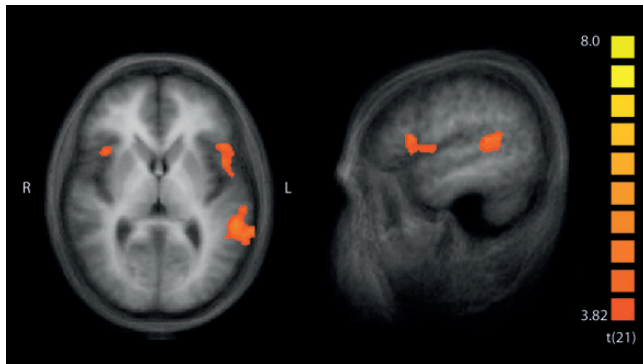


Figure 2. Brain regions processing violations of rhythmic structure in music. (A) differential contrast ($P < 0.05$, cluster level corrected) between activity related to syncopated and incorrect deviations revealed a network comprising left-hemispheric auditory cortices ($x = -57$, $y = -40$, $z = 8$) and bifrontal regions corresponding to Broca's area ($x = -46$, $y = 11$, $z = 11$) and its right-hemispheric homolog ($x = 40$, $y = 15$, $z = 9$), areas also involved in the syntactic analysis of language and harmonic syntax in music (slices shown at $z = 6$ (left) and $x = -50$ (right); for more details see also Table 3).

involved in the processing of syncopated deviations that are related to the rhythmic structure and, in addition, left posterior STG and bifrontal regions being more engaged in the detection of incorrect deviations in the temporal domain. Moreover, a higher order left-hemispheric area (left SMG) shows differential activation for rhythmic variations depending on musical expertise or training.

Discussion

Our results demonstrate that processing of rhythmic patterns involves posterior belt or parabelt areas (Seifritz et al. 2002; Rauschecker and Scott 2009) of human auditory cortex in both hemispheres. More specifically, syncopated deviations that are related to the regular rhythmic pattern are preferentially processed in right-hemispheric areas, whereas beats that show no temporal relation to the otherwise regular rhythmic patterns additionally evoke enhanced activity in homologous regions of the left hemisphere, and, moreover, in bifrontal regions corresponding to Broca's area and its right-hemispheric homolog. Evaluating the impact of musical expertise on rhythmic processing, we found that left SMG shows significant functional differences between professional jazz drummers and musical laypersons: only the professional jazz drummers show activation in this region elicited by deviations from the regular rhythmic pattern. This activity is strongest for incorrect deviations. Syncopated deviations, however, also induce activity in this region in the rhythm experts, whereas laypersons do not respond.

The area posterior to primary auditory cortex (Table 2) that is activated by rhythmic variations in both jazz drummers and musical laypersons has been previously suggested to play an important role for integrating sequential auditory events, the formation of echoic memory traces, and the detection of temporal changes in sound patterns (Mustovic et al. 2003; Kircher et al. 2004; Herdener et al. 2007; Herdener et al. 2009). Our findings are also consistent with prior studies reporting the analysis of longer-term time structures in posterior temporal lobe areas (Griffiths et al. 1999). Also the right-hemispheric dominance of activity to changes in temporal sound patterns

as observed in our study in response to syncopated deviations has been reported previously in response to more simple acoustic patterns based on isochronous intervals without rhythmical cues (Mustovic et al. 2003; Herdener et al. 2007; Herdener et al. 2009). Noteworthy, incorrect deviations of the rhythmic structure, as contrasted to syncopated deviations, lead to an additional activation of the homologous region in the left hemisphere, suggesting hemispheric differences in the processing of rhythmic structure (Table 2; see also (Kester et al. 1991; Schuppert et al. 2000; Samson et al. 2001; Zatorre

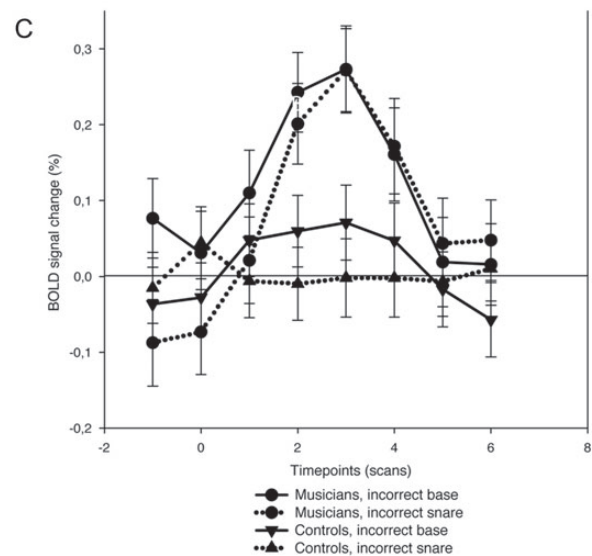
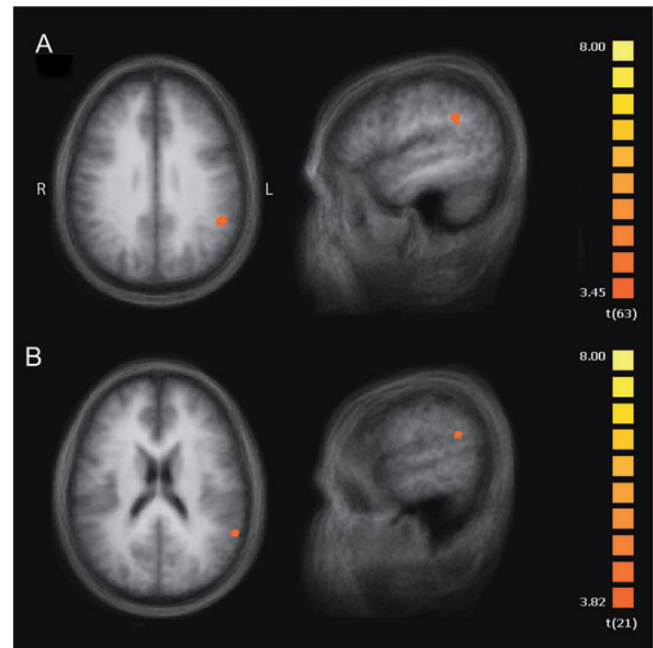


Figure 3. Differential processing of rhythmic structure in jazz drummers and musical laypersons. Comparing activity to either syncopated (A; at $z = 30$; $x = -48$) or incorrect deviations (B; at $z = 20$ and $x = -57$) across groups reveals differential involvement of left supramarginal gyrus (ISMG) in the analysis of rhythmic structure in professional musicians and controls ($P < 0.05$, cluster level corrected) with enhanced activation of ISMG in rhythmic experts only. (C) illustrates the BOLD time courses in response to incorrect deviations in ISMG (as shown in B) for both groups. Note also the consistency for BOLD activity induced by incorrect deviations either due to false beats of the snare or the bass drum within groups.

Table 3

Brain regions sensitive to violations of rhythmic structure

Brain region	Brodman area	Tal coordinates	Cluster size (mm ³)	t Value (average)
Right inferior parietal lobe	40	49, -46, 42	702	4.30
Right inferior frontal gyrus/insula	44/13	40, 15, 9	432	4.67
Right cerebellum	—	6, -63, -3	918	5.73
Left cingulate gyrus	31	-3, -45, 33	810	4.38
Left precuneus	7	-23, -74, 47	405	4.23
Left superior parietal lobe	7	-37, -67, 44	648	4.26
Left inferior frontal gyrus	44	-46, 11, 11	2835	5.27
Left superior/middle temporal gyrus	22	-57, -40, 8	6075	4.47

Only clusters with >15 functional voxels are reported; all clusters $P < 0.05$ (cluster level corrected).

Clusters are reported that show enhanced BOLD activity to incorrect deviations compared with syncopated deviations (i.e., a violation of rhythmic syntax).

et al. 2007)). Syncopated deviations, which constitute a shift of a beat within the temporal grid but following the regular structure of the rhythm, evoke more right-lateralized activity, while incorrect deviations with no relation to the underlying rhythmical time grid additionally activate left-hemispheric auditory areas. In contrast to a previous MEG study investigating rhythmic processing in musicians and nonmusicians (Vuust et al. 2005), we did not observe differential activations in response to rhythmic variations at the level of auditory core, belt, or parabelt regions for experts and nonexperts.

Both language and music are human universals and consist of hierarchically structured sound sequences. It has been suggested that the human brain uses shared resources to analyze the complex patterns characteristic for the sound sequences in both domains (Patel 2003; Koelsch and Siebel 2005). More specifically, it has been argued that the arrangement of basic structural elements (like words or tones) within such a sequence is guided by a set of rules across different hierarchical levels in both domains. In language, this can refer to formation of words from letters or syllables, the subsequent arrangement of phrases, or sentences, and is generally referred to as linguistic syntax. In music, such rules guide, for example, the combination of individual tones to chords, chord progressions, and musical keys, or the temporal arrangement of acoustic events to build up time intervals, meter, or rhythm. These rules or organizational principles are implicitly extracted by experienced listeners, and deviations from these rule-based patterns within a sequence are readily detected. Owing to these similarities, the structure in music based on a set of governing principles has been referred to as syntax, although such analogies have been discussed controversially (Lehrdahl and Jackendorf 1983; Swain 1997; Patel 2008). However, previous neuroimaging studies revealed that violations of harmonic structure in music is processed in the same areas as violations of linguistic syntax (Maess et al. 2001; Friederici and Kotz 2003; Fadiga et al. 2009). In addition, there is a behavioral interference between musical and linguistic structure processing (Fedorenko et al. 2009; Slevc et al. 2009). These findings support the view of similar principles of syntactic organization in language in music that are analyzed by shared brain resources.

Contrasting the responses to incorrect deviations in the rhythm domain to those evoked by syncopated ones, we found enhanced activity induced by violation of rhythmic

structure not only in left-hemispheric STG, but also in 2 frontal areas corresponding to Broca's area and its right-hemispheric homolog (Fig. 1 and Table 3). Thus, not only musical structure in the harmonic domain is represented in these regions (see (Maess et al. 2001) for very similar findings using chord sequences including violations of harmonic structure). By demonstrating the involvement of these regions also in the analysis of rhythmic patterns, our results suggest a more general role for these areas in music processing. This further supports the notion that Broca's area and its right-hemispheric homolog are less domain (or language) specific than previously thought (Zatorre et al. 1992), and are capable of processing rule-based acoustic information, or syntax, in the harmonic and rhythmic faculties in music, and in language (Koelsch 2005; Fadiga et al. 2009).

Besides investigating the processing of rhythmic structure in general, we were especially interested in differences of musical syntax representation related to musical expertise. Musicians have been proposed as a suitable model to study functional plasticity as a result of training (Munte et al. 2002; Kraus and Chandrasekaran 2010). For example, functional changes have been observed in musical experts at the level of auditory brainstem (Musacchia et al. 2007), sensory, and motor cortices (Elbert et al. 1995; Schneider et al. 2005) or in the hippocampus region (Herdener et al. 2010). Here, we found differential responses to deviations from the regular rhythmic patterns across groups in the left SMG. This brain region is anatomically connected with Broca's and Wernicke's area within left-hemispheric language network (Catani et al. 2005) and plays an important role in higher-order language processing (Price 2010). More specifically, it is activated by violations of more complex syntactic rules in language or by increased linguistic syntactic complexity. For example, this region is active when subjects listen to sentences with grammatical errors (Raettig et al. 2010); it also shows enhanced activity for sentences with increased syntactical complexity (Friederici et al. 2009; Richardson et al. 2010). Noteworthy, activity in this region is also enhanced by semantic complexity (Obleser and Kotz 2010). It seems that increasing difficulty in speech comprehension leads to an enhanced recruitment of left SMG (Friederici et al. 2009; Hickok et al. 2009; Obleser and Kotz 2010; Raettig et al. 2010; Richardson et al. 2010). Here, we found activity in this region in response to increased syntactical complexity or syntactic incongruities of rhythmic cues in the professional jazz drummers only.

Thus, musical experts seem to rely on the same neural resources during the processing of syntactic violations in the rhythm domain that the brain usually uses for the evaluation of linguistic syntax. Enhanced activity in left SMG in jazz drummers could reflect the attempt to attribute a meaning to increasingly complex rhythmical cues (i.e., syncopations and false beats) (Meyer 1956), analogous to the recruitment of this area with increasing complexity or difficulty of comprehension for linguistic tasks (for review see Price 2010). In contrast, musical laypersons did not show activity in this region in response to syncopations or false beats. We thus suggest that musical training can result in a functional recruitment of brain areas that have been hitherto mainly attributed to the processing of language. We therefore hypothesize that the ability of jazz drummers to communicate via rhythmic cues is associated with functional plasticity of higher-order left-hemispheric brain regions that usually serve the analysis of language.

Our observation of changes of the functional properties in a brain region usually dedicated to linguistic processing in highly trained rhythmical experts might also have some clinical impact and could motivate further research to use musical training as a tool to improve symptoms in language disorders like, for example, dyslexia as previously proposed (Overy 2003; Overy et al. 2003; Kraus and Chandrasekaran 2010), given that deficits of rhythmic timing might be crucial for the difficulties in speech perception observed in these patients (Goswami et al. 2002; Overy 2003; Overy et al. 2003) and for the development of reading skills (Dellatolas et al. 2009).

Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>.

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Notes

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References

- Bengtsson SL, Ullen F, Ehrsson HH, Hashimoto T, Kito T, Naito E, Forssberg H, Sadato N. 2009. Listening to rhythms activates motor and premotor cortices. *Cortex*. 45:62–71.
- Bullmore E, Brammer M, Williams SC, Rabe-Hesketh S, Janot N, David A, Mellers J, Howard R, Sham P. 1996. Statistical methods of estimation and inference for functional MR image analysis. *Magn Reson Med*. 35:261–277.
- Catani M, Jones DK, ffytche DH. 2005. Perisylvian language networks of the human brain. *Ann Neurol*. 57:8–16.
- Chen JL, Penhune VB, Zatorre RJ. 2008. Listening to musical rhythms recruits motor regions of the brain. *Cereb Cortex*. 18:2844–2854.
- Drake C, Penel A, Bigand E. 2000. JSTOR: Music perception: an interdisciplinary journal. 18(1), 1–23. *Music Perception*.
- Dellatolas G, Watier L, Le Normand M-T, Lubart T, Chevrie-Muller C. 2009. Rhythm reproduction in kindergarten, reading performance at second grade, and developmental dyslexia theories. *Arch Clin Neuropsychol*. 24:555–563.
- 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.
- Etkin A, Klemenhagen KC, Dudman JT, Rogan MT, Hen R, Kandel ER, Hirsch J. 2004. Individual differences in trait anxiety predict the response of the basolateral amygdala to unconsciously processed fearful faces. *Neuron*. 44:1043–1055.
- Fadiga L, Craighero L, D’Ausilio A. 2009. Broca’s area in language, action, and music. *Ann N Y Acad Sci*. 1169:448–458.
- Fedorenko E, Patel A, Casasanto D, Winawer J, Gibson E. 2009. Structural integration in language and music: evidence for a shared system. *Mem Cognit*. 37:1–9.
- Forman SD, Cohen JD, Fitzgerald M, Eddy WF, Mintun MA, Noll DC. 1995. Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): use of a cluster-size threshold. *Magn Reson Med*. 33:636–647.
- Friederici AD, Kotz SA. 2003. The brain basis of syntactic processes: functional imaging and lesion studies. *Neuroimage*. 20(Suppl 1): S8–17.
- Friederici AD, Makuuchi M, Bahlmann J. 2009. The role of the posterior superior temporal cortex in sentence comprehension. *Neuroreport*. 20:563–568.
- Friederici AD, Wang Y, Herrmann CS, Maess B, Oertel U. 2000. Localization of early syntactic processes in frontal and temporal cortical areas: a magnetoencephalographic study. *Hum Brain Mapp*. 11:1–11.
- Friston KJ, Fletcher P, Josephs O, Holmes A, Rugg MD, Turner R. 1998. Event-related fMRI: characterizing differential responses. *Neuroimage*. 7:30–40.
- Friston KJ, Holmes AP, Poline JB, Grasby PJ, Williams SC, Frackowiak RS, Turner R. 1995. Analysis of fMRI time-series revisited. *Neuroimage*. 2:45–53.
- Friston KJ, Holmes AP, Worsley KJ. 1999. How many subjects constitute a study? *Neuroimage*. 10:1–5.
- Genovese CR, Lazar NA, Nichols T. 2002. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *Neuroimage*. 15:870–878.
- Gordon EE. 1998. Introduction to research and the psychology of music (1998 Edition). GIA Publications, Chicago.
- Goswami U, Thomson J, Richardson U, Stainthorp R, Hughes D, Rosen S, Scott SK. 2002. Amplitude envelope onsets and developmental dyslexia: a new hypothesis. *Proc Natl Acad Sci USA*. 99:10911–10916.
- Grahn JA, Rowe JB. 2009. Feeling the beat: premotor and striatal interactions in musicians and nonmusicians during beat perception. *J Neurosci*. 29:7540–7548.
- Griffiths TD, Johnsrude I, Dean JL, Green GG. 1999. A common neural substrate for the analysis of pitch and duration pattern in segmented sound? *Neuroreport*. 10:3825–3830.
- Herdener M, Esposito F, di Salle F, Boller C, Hilti CC, Habermeyer B, Scheffler K, Wetzel S, Seifritz E, Cattapan-Ludewig K. 2010. Musical training induces functional plasticity in human hippocampus. *J Neurosci*. 30:1377–1384.
- Herdener M, Esposito F, di Salle F, Lehmann C, Bach DR, Scheffler K, Seifritz E. 2007. BOLD correlates of edge detection in human auditory cortex. *Neuroimage*. 36:194–201.
- Herdener M, Lehmann C, Esposito F, di Salle F, Federspiel A, Bach DR, Scheffler K, Seifritz E. 2009. Brain responses to auditory and visual stimulus offset: shared representations of temporal edges. *Hum Brain Mapp*. 30:725–733.
- Hickok G, Okada K, Serences JT. 2009. Area Spt in the human planum temporale supports sensory-motor integration for speech processing. *J Neurophysiol*. 101:2725–2732.
- Huron D. 2001. Is music an evolutionary adaptation? *Ann N Y Acad Sci*. 930:43–61.
- Kester DB, Saykin AJ, Sperling MR, O’Connor MJ, Robinson IJ, Gur RC. 1991. Acute effect of anterior temporal lobectomy on musical processing. *Neuropsychologia*. 29:703–708.
- Kircher TT, Rapp A, Grodd W, Buchkremer G, Weiskopf N, Lutzenberger W, Ackermann H, Mathiak K. 2004. Mismatch negativity responses in schizophrenia: a combined fMRI and whole-head MEG study. *Am J Psychiatry*. 161:294–304.
- Koelsch S. 2009. Music-syntactic processing and auditory memory: similarities and differences between ERAN and MMN. *Psychophysiology*. 46:179–190.
- Koelsch S. 2005. Neural substrates of processing syntax and semantics in music. *Curr Opin Neurobiol*. 15:207–212.
- Koelsch S, Gunter TC, Cramon DYV, Zysset S, Lohmann G, Friederici AD. 2002. Bach speaks: a cortical “language-network” serves the processing of music. *Neuroimage*. 17:956–966.
- Koelsch S, Gunter TC, Wittfoth M, Sammler D. 2005. Interaction between syntax processing in language and in music: an ERP Study. *J Cogn Neurosci*. 17:1565–1577.
- Koelsch S, Siebel WA. 2005. Towards a neural basis of music perception. *Trends Cogn Sci*. 9:578–584.
- Kraus N, Chandrasekaran B. 2010. Music training for the development of auditory skills. *Nat Rev Neurosci*. 11:599–605.

- Lehrdahl F, Jackendorf R. 1983. A generative theory of tonal music. Cambridge, MA, USA: MIT Press.
- Maess B, Koelsch S, Gunter TC, Friederici AD. 2001. Musical syntax is processed in Broca's area: an MEG study. *Nat Neurosci.* 4:540–545.
- Meyer LB. 1956. *Emotion and meaning in music*. Chicago (IL): The University of Chicago Press.
- Miranda RA, Ullman MT. 2007. Double dissociation between rules and memory in music: an event-related potential study. *Neuroimage.* 38:331–345.
- Munte TF, Altenmuller E, Jancke L. 2002. The musician's brain as a model of neuroplasticity. *Nat Rev Neurosci.* 3:473–478.
- Musacchia G, Sams M, Skoe E, Kraus N. 2007. Musicians have enhanced subcortical auditory and audiovisual processing of speech and music. *Proc Natl Acad Sci USA.* 104:15894–15898.
- Mustovic H, Scheffler K, di Salle F, Esposito F, Neuhoff JG, Hennig J, Seifritz E. 2003. Temporal integration of sequential auditory events: silent period in sound pattern activates human planum temporale. *Neuroimage.* 20:429–434.
- Obleser J, Kotz SA. 2010. Expectancy constraints in degraded speech modulate the language comprehension network. *Cereb Cortex.* 20:633–640.
- Overy K. 2003. Dyslexia and music. From timing deficits to musical intervention. *Ann N Y Acad Sci.* 999:497–505.
- Overy K, Nicolson RI, Fawcett AJ, Clarke EF. 2003. Dyslexia and music: measuring musical timing skills. *Dyslexia.* 9:18–36.
- Parncutt R. 1994. A perceptual model of pulse salience and metrical accent in musical rhythms. *Music Percept.* 11:409–464.
- Patel AD. 2003. Language, music, syntax and the brain. *Nat Neurosci.* 6:674–681.
- Patel AD. 2008. *Music, language, and the brain*. New York: Oxford University Press.
- Peretz I, Coltheart M. 2003. Modularity of music processing. *Nat Neurosci.* 6:688–691.
- Price CJ. 2010. The anatomy of language: a review of 100 fMRI studies published in 2009. *Ann N Y Acad Sci.* 1191:62–88.
- Raettig T, Frisch S, Friederici AD, Kotz SA. 2010. Neural correlates of morphosyntactic and verb-argument structure processing: an fMRI study. *Cortex.* 46:613–620.
- Rauschecker JP, Scott SK. 2009. Maps and streams in the auditory cortex: nonhuman primates illuminate human speech processing. *Nat Neurosci.* 12:718–724.
- Richardson FM, Thomas MS, Price CJ. 2010. Neuronal activation for semantically reversible sentences. *J Cogn Neurosci.* 22:1283–1298.
- Rogalsky C, Rong F, Saberi K, Hickok G. 2011. Functional anatomy of language and music perception: temporal and structural factors investigated using functional magnetic resonance imaging. *J Neurosci.* 31:3843–3852.
- Sadie S, Tyrell J. 2001. *The new grove dictionary of music and musicians*. London: Macmillan.
- Samson S, Ehrle N, Baulac M. 2001. Cerebral substrates for musical temporal processes. *Ann N Y Acad Sci.* 930:166–178.
- Schirmer A, Fox PM, Grandjean D. 2012. On the spatial organization of sound processing in the human temporal lobe: a meta-analysis. *Neuroimage.* 63:137–147.
- Schneider P, Sluming V, Roberts N, Scherg M, Goebel R, Specht HJ, Dosch HG, Bleeck S, Stippich C, Rupp A. 2005. Structural and functional asymmetry of lateral Heschl's gyrus reflects pitch perception preference. *Nat Neurosci.* 8:1241–1247.
- Schuppert M, Munte TF, Wieringa BM, Altenmuller E. 2000. Receptive amusia: evidence for cross-hemispheric neural networks underlying music processing strategies. *Brain.* 123(Pt 3):546–559.
- Seifritz E, di Salle F, Esposito F, Herdener M, Neuhoff JG, Scheffler K. 2006. Enhancing BOLD response in the auditory system by neurophysiologically tuned fMRI sequence. *Neuroimage.* 29:1013–1022.
- Seifritz E, Esposito F, Hennel F, Mustovic H, Neuhoff JG, Bilecen D, Tedeschi G, Scheffler K, di Salle F. 2002. Spatiotemporal pattern of neural processing in the human auditory cortex. *Science.* 297:1706–1708.
- Slevc LR, Rosenberg JC, Patel AD. 2009. Making psycholinguistics musical: self-paced reading time evidence for shared processing of linguistic and musical syntax. *Psychon Bull Rev.* 16:374–381.
- Swain JP. 1997. *Musical languages*. New York: WW Norton and Company.
- Vuust P, Pallesen KJ, Bailey C, van Zuijlen TL, Gjedde A, Roepstorff A, Ostergaard L. 2005. To musicians, the message is in the meter pre-attentive neuronal responses to incongruent rhythm are left-lateralized in musicians. *Neuroimage.* 24:560–564.
- Zatorre RJ, Binder JR. 2000. Functional and structural imaging of the human auditory system. In: Toga A, Mazziotta J, editors. *Brain mapping: the systems*. pp. 365–402. Los Angeles (CA): Academic Press.
- Zatorre RJ, Chen JL, Penhune VB. 2007. When the brain plays music: auditory-motor interactions in music perception and production. *Nat Rev Neurosci.* 8:547–558.
- Zatorre RJ, Evans AC, Meyer E, Gjedde A. 1992. Lateralization of phonetic and pitch discrimination in speech processing. *Science.* 256:846–849.