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# Dynamics of brain activity in motor and frontal cortical areas during music listening: a magnetoencephalographic study

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There are formidable problems in studying how 'real' music engages the brain over wide ranges of temporal scales extending from milliseconds to a lifetime. In this work, we recorded the magnetoencephalographic signal while subjects listened to music as it unfolded over long periods of time (seconds), and we developed and applied methods to correlate the time course of the regional brain activations with the dynamic aspects of the musical sound. We showed that frontal areas generally respond with slow time constants to the music, reflecting their more integrative mode; motor-related areas showed transient-mode responses to fine temporal scale structures of the sound. The study combined novel analysis techniques designed to capture and quantify fine temporal sequencing from the authentic musical piece (characterized by a clearly defined rhythm and melodic structure) with the extraction of relevant features from the dynamics of the regional brain activations. The results demonstrated that activity in motorrelated structures, specifically in lateral premotor areas, supplementary motor areas, and somatomotor areas, correlated with measures of rhythmicity derived from the music. These correlations showed distinct laterality depending on how the musical performance deviated from the strict tempo of the music score, that is, depending on the musical expression.

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# Introduction

Both music and language rely on form and tempo to capture and communicate cognitive and emotional schemata that can be shared by different people. Nowadays human communication is dominated by language, but the formal similarities and dissimilarities of music and language suggest that music predates language by a long time (Merker, 2000). In general, sound perception triggers brain processes at distinct cortical regions, often lasting just a few milliseconds. Music cognition and appreciation on the other hand require seconds for a musical phrase to be established: first, what might be called the 'primitive archetypes' of music syntax must be identified (Marcus et al., 2003), and then integrated within a wider unfolding (musical) context. Thus, music perception involves a wide spectrum of cerebral responses, from activations that dynamically reflect the time structure of the stimulus at the level of resolution of individual notes (i.e., at fine temporal scales), to activations whose dynamics track the most global contour of accumulating interest or tension (i.e., at coarse temporal scales). Ideally, we need to map cortical activations with good spatial accuracy and with temporal resolutions that extends from milliseconds to seconds to identify processes that might mirror the complex, hierarchical structural information present in a piece of authentic music. The formidable problems that such a study of brain processes entails has limited most earlier studies to contrasting congruent versus incongruent terminal notes in short note sequences. Motivated by these considerations, we used the exceptional temporal resolution and good spatial localization of magnetoencephalography (MEG) to analyze the neural activity elicited by the unfolding of a passage of authentic music in real time.

Early psychophysical studies (Dowling and Harwood, 1986; Fraisse, 1982; Handel, 1989) suggested that rhythmic information is more salient than pitch for music cognition. Tapping of feet and fingers to music is just the behavioral tip of a deep relationship between music perception and movement generation (Trevarthen, 1999). Tapping makes explicit the primacy of rhythm, and it is but one of the many manifestations of effortless induction of movement elicited by musical rhythm. Insights gained about internal representation of serial temporal pattern together with movements in synchrony with the musical rhythm have promoted a motor theory of musical rhythm perception (Seifert et al., 1995; Todd, 1992). More recent electrophysiological and pharmacological studies suggested that rhythmic *timing* might be accomplished by temporal pattern generators originating in the motor cortex (Arshavski et al., 1997) or temporally predictable changes in the activity of buildup cells in supplementary motor areas (SMA), which gradually increase their activity before movement (Matsuzaka et al., 1992). In addition, it has been suggested that the cerebellum plays an important role in motor timing (Ivry and Keele, 1989).

Neuroimaging studies of rhythm perception and reproduction also strengthened the hypothesis that the circuitry used for timing of brief intervals is likely to be located within the motor system,

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even in the absence of movement (Lewis and Miall, 2003). Two PET studies used auditory imagery for music and reported that SMA is specifically active in musical image generation (Halpern and Zatorre, 1999; Zatorre et al., 1996). Another PET study on music perception (Platel et al., 1997) reported significant hemodynamic responses in the left inferior Broca's area during detection of irregularities of interval lengths embedded into tone sequences. An fMRI study of sustained perceptual analysis of both auditory and visually presented rhythms revealed significant activations extending from the SMA and pre-SMA via the anterior and posterior banks of the superior and inferior precentral sulcus to the frontal operculum, including Broca's area and its right homologue (Schubotz et al., 2000).

In parallel, studies of brain-damaged patients revealed that rhythm processing could be selectively impaired without deficits in melody perception, suggesting the presence of a neural system



Fig. 1. (a) The basic structure of the motif. Line 1 shows the score musical motif. Line 2 shows the segmentation of the motif, melodic parts segments A + B, bars 4 3/4, and C + D, bars 4 1/4. Line 3 displays the groups of three notes (weak, weak, strong), and line 4 shows the individual note duration in performance. The mean duration ratio of each note in the segment is printed below the first bar of the corresponding segment. (b) The mean duration for segments A, B, and C in histogram form.

specialized for rhythm (Peretz and Kolinsky, 1993). This and other studies have searched for a coherent model of hemispheric asymmetry in rhythm processing, but as yet without success. Some studies concluded that the left cerebral hemisphere is mainly involved in rhythm processing (Gordon and Bogen, 1974; Mavlov, 1980; Polk and Kertesz, 1993), but others indicated that dysfunction of either the left or right hemispheres compromise tapping of rhythmic patterns from short musical pieces (Peretz, 1990; Peretz and Morais, 1980; Prior et al., 1990). Variability in the location and size of the lesions prevented pinpointing the neural structures responsible. A recent fMRI study (Sakai et al., 1999) has shed new light on the issue of rhythm perception, highlighting the inconsistency of stimulus material among previous studies of musical rhythm perception. The study used right-handed individuals and showed that the brain areas activated depended on the type of rhythm they were preparing to tap. Specifically, for rhythmical patterns with tones spaced evenly at integer ratios (1:2, 1:3), the left hemisphere areas, including the left premotor area (PMA) and the right cerebellum were mostly active, whereas for rhythms with tones spaced at complex ratios (such as 1:2.5), which were more difficult to memorize and tap out, a shift in areas to the right



Fig. 2. Different representations of the acoustical signal. (a) The acoustic signal (pressure change) of the musical motif is displayed on the upper line and an expanded copy of the yellow band of 650 ms is shown below. (b) Spectrotemporal representation of the yellow band in a. Colors relate to spectral energy. (c) The scalogram of the sound amplitude modulation of the first segment of the motif (segment A). Upper line shows the amplitude modulation (AM) as a function of time and the lower line shows the pseudocontinuous wavelet transform. (d) Schematic representation of embedding pairwise feature vectors in the similarity matrix. (e) and (f) show the rhythmogram and the self-similarity matrix of the acoustic signal, respectively. The matrices colors are proportional to the similarity measure at each pixel. In all parts of the figure where color is used to represent intensity, the level increases from green (lowest), yellow, red to blue (highest).





Fig. 3. Beat spectra of the segments A, B, and C.

hemisphere (including the right PMA) with bilateral activation of the cerebellum were noticed. These results offered an explanation for the psychological findings showing that the accuracy of reproducing even very simple temporal patterns is strongly influenced by the rhythmic structure of the sequences (Essens, 1986; Essens and Povel, 1985; Povel, 1981; Povel and Essens, 1985).

Neuroimaging studies with high temporal resolution of the recorded brain signals have used stimulus material consisting of short segments of sound patterns or fragments of musical pieces specifically composed or selected for the experiment. These fragments often terminated either in a congruous or in a 'harmonically', 'melodically', or 'rhythmically' incongruous note. The brain responses of musicians and nonmusicians, evoked by the end notes, were analyzed and compared as a function of the subject's familiarity with the melodies and the type of incongruity (Koelsch et al., 2000; Maess et al., 2001; Patel et al., 1998). The emphasis of those studies was on identifying isolated responses to musical violations rather than probing the responses evoked during processing the local and global attributes of an authentic musical piece.

Despite the increasing number of neuroimaging studies dealing with perception of sequencing and of music, and the acknowledgement of the strong connection between action (motor behavior) and perception, neither the expressive modulation of movement nor the dynamic aspects of music-as they are formalized in the musical score and as they are expressed by the performer and appreciated by the listener-were part of the analysis. In a previous work (Ioannides et al., 2002), we categorized the brain regions showing significant activations during authentic music listening according to the similarity between the spectral peaks of the sound envelope and those of individual regional brain activation curves. Based on those results, we suggested that the brain processes the musical attributes at different temporal scales in distributed and partially overlapping networks. The features of individual notes should also be analyzed in regions within and around the auditory cortex and motor areas, while 'higher-order patterns' formed by those features should be analyzed by networks distributed in the anterior part of the temporal lobes and frontal areas.

The present study specifically explores the neuronal correlates related to changes in rhythm elicited by a piece of authentic music. The approach entails considerable computational cost dictated by the recording and analysis of long duration MEG segments. We tested the hypothesis that during *listening* to authentic music, which maintains the tonal-harmonic relations of the stimulus material, temporal deviations (performance jitter produced as musical expression) of an agogic character will induce changes in the brain that could be captured by the MEG signal and highlighted by our analysis.

## Methods

#### Subjects, measurements, and stimuli

Five male, right-handed subjects, with no history of otological or neurological disorders and normal audiological status (air conduction hearing threshold lower than 10 dB) and no formal musical training, volunteered for the experiment. The Riken ethical committee granted ethical permission and subjects signed



Fig. 6. Representative instantaneous current density estimates for subject S5 in the cerebellum (a) left and (b) right.



Fig. 4. Representative instantaneous current density estimates for subject S5 showing activations at loci consistently identified in the study. (a) Activations in the right primary and secondary auditory cortices. (b) Activations in the left primary and secondary auditory cortices. (c,d) Activations in the posterior temporal–parietal junction. (e) Activations in the anterior middle and superior temporal gyri. (f) Activations in the parietal areas.



Fig. 5. Representative instantaneous current density estimates for subject S5 showing activations at loci consistently identified in the study. (a) Activations in the right somatomotor area. (b) Activations in the left somatomotor area. (c) Activations in the lateral premotor area. (d) Activations in the supplementary motor area. (e) Activations in the frontopolar cortex. (f) Activations in the orbitofrontal and ventrolateral prefrontal cortex.

a consent form after the procedures and purpose of the experiment had been explained to them. The MEG signals were recorded in a magnetically shielded chamber using the CTF whole head Omega system. During recordings, the subjects were seated comfortably with their head in the magnetometer. In low ambient illumination, they fixated a central point while the musical stimuli were binaurally delivered using echo-free plastic tubes. The music stimulus was a part of Frantz Liszt's Etudes d'exécution transcendante d'après Paganini, S.141-No. 5, performed in 1948 by a Russian pianist, Grigory Ginsberg. The stimulus material was selected because it was a solo piano piece with a moderate tempo, and definite rhythm. The whole composition lasted altogether for 2 min 50 s. The entire analysis reported in this paper is based on a single motif component lasting 10 s (Fig. 1a). This motif was selected because its different segments had small but distinct changes in the performance rhythm that could be objectively quantified by the degree of temporal deviations from the reference interval ratio (DRIR). The top line of Fig. 1a details the score with the timing and the rhythm. The timing (short-short-long pattern) and stress [weak-weak-strong or unstressed-unstressed-stressed pattern, i.e., anapest meter, articulated by the tenuto marking on the strong/stressed (third) beat on the score] defines the smallest rhythmic component, the three-note-based group, which is the driving force in the piece. The motif is divided into two parts, defined by their melodic narrative (question and answer) and harmonic structure (suspension in dominant at the second beat of the fifth bar). Each part is further segmented by its melodic contour. The temporal segments A and C consist of 12 notes made up of a repetition of coupled three notes linear descent (B to G# and G# to E). Segment B is again three-note based, but forms first a linear ascent by threefold steps (E to G#, F# to A, and G# to B) then a descent (A to F#). The last segment D starts in a linear ascent (E to G#) as was the case for segment B, but this time it is followed by a twofold descent, which leads the melody back to the tonic (A to F# and G# to E). It was important for the analysis that the piece was driven by the threenote-based group throughout and that the rhythmic and metrical values stayed the same in all segments. The interval ratio of the group component defined by the score is 1:1:2. However, subtle differences exist between the segments in the way they deviate from the scored reference interval ratio. The mean interval ratios in performance are shown in Fig. 1b: 1:1.2:2.0 in segment A, 1:1.3:2.4 in segment B, and 1:1.1:2.1 in segment C. That is, segment C corresponds best to the reference ratio of the score, segment A was close to it, and segment B was the most deviant. It is not clear if this deviation is due to the performer's artistic expression or to the limitation of his finger mobility. This melodic partitioning therefore reveals two switches in note duration ratios that occur during the musical motif: the first switch marks the transition from a close to metrical segment (segment A) to a segment characterized by higher DRIR (segment B), whereas the second switch marks the transition to segment C with the smallest DRIR. Hence, the music stimulus was sufficiently complex to test whether different brain regions could track various degrees of temporal DRIRs.

The top line of Fig. 2a illustrates the audio signal of the musical motif used in the experiment. The first segment of 650 ms from the signal (yellow band) is enlarged in the lower line, corresponding approximately to the first three notes in the musical score. The signal shape reveals the complexity of the

auditory stimulus: first, the sound onset of almost every note occurs before the sound of the previous note has died away; second, since the music notes are played in *chords* of two notes, two fundamental frequencies are mixed throughout the duration of each note, as shown by the presence of the two fundamental frequencies in the spectrotemporal representation of the first three chords (Fig. 2b).

The musical piece was unfamiliar to the subjects, who first listened inside the shielded room to the motif (nine bars) and then to the entire music composition. Finally, the subjects listened to 20 repetitions of the motif for the MEG recording used in the analysis. Specifically, the average signal derived from these recordings (20 presentations of the motif, each lasting for 14 s beginning 2 s before the onset of the 10-s-long motif and ending 2 s following its presentation) was used for the analysis reported in this paper. The earlier exposure to the



Fig. 7. Grand averaged ACVs from ROIs defined bilaterally. (a) Frontopolar cortex. (b) Orbitofrontal cortex. (c) Ventrolateral prefrontal cortex. (d) Medial prefrontal cortex.

entire musical piece acclimatized the subjects to the recording environment and helped by reducing the novelty effects of listening to unfamiliar music.

## Beat-tracking algorithm

We used a novel beat-tracking approach, intended to provide a robust characterization of the musical rhythm reflecting its perceptual expressiveness. The method does not require any prior knowledge of the tempo, or meter; instead, all the required information is automatically derived from the audio data. We detail the calculations required for analysis of the data in the Results section, with a brief description of its major processing steps, while a more detailed technical description is made available in Appendix A.

# MEG data analysis

The raw MEG data were low pass filtered using a fourthorder bidirectional Butterworth filter with a cutoff frequency of 100 Hz, to reduce the high-frequency noise. A notch filter at 50 Hz (second-order bidirectional Butterworth filter) removed the power line interference. The mean of a 2-s baseline recording before the stimulus onset was used to remove the steady baseline level. The subject's head position relative to the MEG sensors was measured by the localization of the center coordinates of three orthogonal coils on the nasion, left and right pre-auricular positions (see caption Table 1). The outline of the head was obtained using the Polhemus FASTRAK 3D Digitizer (Polhemus, Inc., Colchester, VT, USA) to allow the surface matching with the segmented skin surface from MRI data, and the accurate displays of superimposed functional and anatomical images (Fuchs et al., 1995). The current density throughout the brain was reconstructed using the CURRY 4.5 source localization software (Philips Res. Lab.), with a minimum L2 norm constraint for the currents and the L curve regularization, which avoided overfitting the remaining noise in the averaged data (Hämäläinen and Ilmoniemi, 1994). The head/brain compartments were semiautomatically segmented from MRI data by a fast 3D-region-growing algorithm (Wagner et al., 1995). Source reconstruction used a spherically shaped volume conductor model. Current estimates were computed at all latencies from 2 s before to 2 s after the stimulus onset. The source space was defined as a regular grid of points distributed in 34 parallel planes equally spaced at 5 mm, (the in-plane distance between points was also 5 mm in each direction). The sources were further constrained to be at least 3 mm inside the cerebrospinal fluid boundary. A magnetic coil quadrature of 9 points/coil was used to improve the accuracy of the forward problem. The source reconstruction used a diagonal location-weighting matrix for depth bias removal. For tracking the time course of the brain activations, the modulus of the current density estimate was integrated over spherically shaped volumes of interest (VOIs).



Fig. 8. Upper panels: VOIs definition for the SM1 (blue), SMA (green), and PMA (red) areas. The VOIs are displayed in lateral and top views for the same subject (S5) whose brain activation were shown in Figs. 5–7. Lower panels: Grand average (across subjects) of power density spectra are displayed for the different motor regions (red and blue colors are used for the left and right hemispheres, respectively). The power spectral density of the audio signal is shown in black color.

To test for interhemispheric differences in activity, we computed the asymmetry coefficients of the total signal power (denoted by P) derived from the activation curves (ACVs) from corresponding brain areas of the right and left hemispheres, and from the whole duration of the musical motif:

$$AC = \frac{P^{\text{right}} - P^{\text{left}}}{P^{\text{right}} + P^{\text{left}}} \times 100(\%)$$

To provide a coarse estimate of the periodicities that are present by the time course of the ACVs, the Fast-Fourier Transform, using a Hanning window, was applied to characterize globally the music signal and the regional activations by the characteristic peaks of the power spectrum density (PSD). While this comparison does not offer a precise characterization of the timing of transient responses to the note onsets, it does provide preliminary indications that activations in several brain regions generally track the major temporal patterns (periodicities) of the sound envelope. For a more robust characterization of these periodicities, the ACVs were processed the same way as the amplitude modulation component of the music signal, that is, they were parameterized by wavelet transformation followed by computation of their rhythmogram and beat spectra (see below). In this way, we isolated the attack onsets of the notes, and we used the beat spectrum as a more accurate measure, which did not depend on the *decay*, *sustained*, and *release* segments of the note. The algorithm therefore did not rely on any a priori assumptions about the signal morphology (which was highly unpredictable given the complexity of the stimulus). The algorithm also tested for the presence of self-similar, transient brain responses, which could be either responses to note onsets, or to the internally generated activations anticipating the music to come, or to a combination of these two mechanisms.

The degree of similarity between the rhythmicity of the music and regional brain activations was quantified by computing the correlation coefficients between the beat spectra of the musical motif and the beat spectra for each motor area separately. Matched-pairs t tests of the Fisher's z-transformed values of the correlation coefficients were used to test across subjects the significance of the variations in the correlation of the different musical segments.



Fig. 9. From ACVs to beat spectra. (a) ACVs from the right SM1 and PMA areas (subject S1), from segment A. The onsets of the notes are marked by black arrows. (b) The scalograms for SM1 (upper line) and PMA (lower line) ACVs in a. (c) The self-similarity matrix for SM1; the similarity measure at each pixel is encoded using the same color scale as in Fig. 2. (d) The beat spectra for the music signal, right SM1 and right PMA activations capturing the periodicity structure of the corresponding ACVs.

The first step of the beat tracking algorithm segregated the prominent rhythmical features of the musical motif by extracting the amplitude modulation (AM) component of the acoustic signal. The AM component was then parameterized using a pseudocontinuous wavelet transformation (see Appendix A). Fig. 2c illustrates the AM component of segment A (upper line) and its scalogram, that is, the magnitude of its wavelet representation (lower line). Singularities of the signal (sharp note 'attacks') are clearly marked by localized increases in the amplitude of the modulus of the wavelet transform coefficients over a wide range of frequencies. The scalogram reveals also the grouping of the anapestic rhythm of the musical group into short-short-long beats. In the next step, similarity measures between feature vectors (matrices) were computed from successive temporal windows of the AM scalogram (Fig. 2d and Appendix A). The distance measure was embedded in a two-dimensional similarity matrix that will be referred to henceforth as a rhythmogram. Fig. 2e illustrates the rhythmogram derived from the AM scalogram of the musical motif for its first segment A of 2.5 s. The regions of high self-similarity (note attacks, red/blue blobs) are clearly distinguished throughout this temporal segment. The rhythmogram provides a qualitatively different description of the data as compared with the similarity measures directly derived from the acoustic signal (Foote and Uchihashi, 2001). For comparison purposes, Fig. 2f shows the similarity measures derived directly from the audio signal of Fig. 1a. Regions of high self-similarity in this case (shown in blue color) reveal a periodicity of about 1.4 s (as determined by their shift from the main diagonal of the self-



Fig. 10. Single-subject beat spectra from motor regions and the music signal. (a) Subject S1. (b) Subject S4. (c) Subject S5. (d) Subject S2. Motif segment C is used for a and c and segment B for b and d. The beat spectrum of the music is shown together with the beat spectra of left SM1 and left PMA in a, left SMA and left PMA in b, c, and right SMA and right PMA in d.



Fig. 11. Mean correlation coefficients between the beat spectrum of the music segments A, B, and C and the corresponding beat spectra for SMA, Broca PMA, and SM1 in the left (blue-like color bars) and right (red-like color bars) hemisphere. For further explanation, see text.

similarity matrix), which is due to the repetition of the initial sixnotes pattern on the second part of segment A from the musical motif. This approach does not segregate the attack part of the notes, but it is rather sensitive to the frequencies of the notes' sounds. The areas of high self-similarity will extend proportionally to the duration of the notes, as could be noticed by comparing the corresponding patterns of the third note in each triad to the patterns of the first two notes. Furthermore, the onset of any second consecutive note of the same pitch as the previous one will not be distinguished, as self-similarity will be high for the whole duration of the two-note group when music is played in *legato* style. The beat spectrum derived from this similarity matrix will not be tightly coupled to the *tempo* unless adjacent notes share some common physical properties (either fundamental frequencies or harmonics).

The beat spectrum is calculated using the autocorrelation of the rhythmogram matrix (Foote and Uchihashi, 2001), and it is used to characterize the periodicity and relative strength of the musical beats. Beat spectra were separately computed for the three segments (A, B, C, 2.4 s each) of the musical motif, each of them starting from the onset of their first notes (Fig. 3). The last segment D was not considered for analysis, due to the strong nonstationarity caused by the progressive slowing down of the rhythm of its last three notes as the motif ends. The periodicities can be clearly assessed from the spectral peaks. They were different for the differences in the note durations of the different segments (Fig. 1b).

#### Source reconstruction results

Although the accuracy of the source reconstruction (in terms of spatial delineation of the brain areas) is not the primary goal of our study, nevertheless the identified regions merit some discussion. The head coordinate position of consistent current density maxima were computed for each subject and the areas that were consistently identified across subjects are summarized in Table 1. The coordinate system uses the left and right preauricular points and nasion to define Cartesian axes for each subject (see caption to Table 1). The results show that music perception involves widely distributed neural circuits in both hemispheres. Figs. 4-6 show

typical instantaneous activations of the superficial cortical surface and the cerebellum of one subject (S5) at different latencies throughout the musical motif. We stress that the analysis of the temporal properties of regional activations relies on measures of continuous modulation of activity rather than on individual latencies. The actual latency value relates to the onset of activity in a given area only for the immediate period (about 200 ms) following the onset of the motif. The later latencies in the figures were selected to show areas that were consistently activated during the 10-s-long presentation of the motif, at a time when interference from other areas was relatively weak.

Sites near the temporal-parietal junction were typically responsive soon after the stimulus onset (107–112 ms), first within and close by the primary and secondary auditory cortices of both hemispheres (Figs. 4a,b). Activity in the posterior temporalparietal junction was identified shortly after that (133–141 ms) across the supratemporal gyrus and planum temporale (Figs. 4c,d). The activations shown for the middle temporal and superior temporal gyri (Fig. 4e), as well as for the supramarginal and postcentral gyri and precuneus (Fig. 4f), were identified bilaterally much later (488–627 ms). Peaks of activity were also noticed bilaterally in brain areas anterior to the central sulcus.

Consistent focal maxima were observed bilaterally in somatomotor areas SM1 (Figs. 5a,b), PMA (Fig. 5c), and SMA (Fig. 5d). There were also consistent activations identified in orbitofrontal, middle prefrontal (Fig. 5e), frontopolar, and ventrolateral prefrontal cortex (Fig. 5f). Bilateral activations were also consistently identified in cerebellar regions (Fig. 6), which is in agreement with previous music perception investigations (Khorram-Sefat et al., 1997; Tillmann et al., 2003).

Table 1

Brain regions showing activation in response to the motif

Fig. 7 shows the grand averaged ACVs from frontal areas and allows interhemispheric comparisons between the strengths of their activations. These regions show very low frequency variations. The ACV amplitudes become generally higher when enough time has elapsed from the onset of the acoustic stimulus to allow the unfolding of the central representations of the musical surface and the building-up of a complex system of relations (tonal-harmonic and semantic). This requires the integration of the "cognitive primitives" over large temporal scales (in the order of seconds). These activations persist well beyond the offset of the musical motif and they are generally higher in the right hemisphere. The asymmetry coefficients computed separately for each subject were therefore tested for significant positive values (R > L) by using a one-tailed t test. The activations were higher in the right hemisphere in the frontopolar cortex (t = 2.18, P = 0.047), orbitofrontal cortex (t = 4.28, P = 0.006), and ventrolateral prefrontal cortex (t = 6.11, P = 0.0018). No significant interhemispheric difference was noticed on the activations from the medial prefrontal cortex (t = 0.85, P = 0.22).

# Temporal pattern representation in motor-related areas

The findings described above confirmed predictions of psychophysical studies, which suggested that activity in motorrelated areas, accompanies music perception. These psychophysical studies have also suggested that the same areas are particularly involved in the representation of the rhythmic dimension of music. The data-driven approach introduced previously was used to study the dynamic properties of the activation in motor-related areas and their relationship with the temporal patterns of musical

| Brain region                                  | Brodmann<br>area | Coordinates ( $\pm$ SD) |                  |                 |                  |                  |                 |
|-----------------------------------------------|------------------|-------------------------|------------------|-----------------|------------------|------------------|-----------------|
|                                               |                  | Left hemisphere         |                  |                 | Right hemisphere |                  |                 |
|                                               |                  | <i>x</i> (mm)           | <i>y</i> (mm)    | z (mm)          | <i>x</i> (mm)    | <i>y</i> (mm)    | z (mm)          |
| Primary and association auditory cortex       | 41, 42, 22       | 56.6 ± 3.9              | $-6.9 \pm 12.2$  | 49.6 ± 6.3      | $-62.9 \pm 5.4$  | $-7.64 \pm 12.9$ | 52.8 ± 3.0      |
| Supramarginal gyrus                           | 40               | $51.4 \pm 5.5$          | $-5.8 \pm 10.2$  | $82.8 \pm 11.5$ | $-55.1 \pm 8.8$  | $-5.1 \pm 12.6$  | 86.1 ± 11.2     |
| Temporal-parietal junction                    | 39, 40           | $55.5 \pm 3.6$          | $9.0 \pm 11.7$   | $66.5 \pm 4.6$  | $-58.9 \pm 2.4$  | $8.7 \pm 12.0$   | $73.3~\pm~7.8$  |
| Precuneus                                     | 7                | $22.6 \pm 4.1$          | $6.6 \pm 13.8$   | $107.3 \pm 4.9$ | $-31.4 \pm 8.8$  | $5.3 \pm 13.2$   | $104.6~\pm~5.3$ |
| Posterior central gyrus                       | 43, 4            | $55.5 \pm 3.8$          | $-25.2 \pm 8.1$  | $60.5 \pm 5.7$  | $-59.8 \pm 3.6$  | $-21.7 \pm 10.3$ | $63.6~\pm~7.3$  |
| Posterior middle temporal gyrus               | 21, 22           | $56.9 \pm 4.2$          | $13.1 \pm 5.6$   | $43.1 \pm 6.6$  | $-64.9 \pm 4.4$  | $8.9 \pm 7.7$    | $42.9~\pm~5.4$  |
| Anterior middle and superior<br>temporal gyri | 21, 38           | $56.0 \pm 5.0$          | $-15.2 \pm 7.6$  | $26.8~\pm~6.3$  | $-60.1 \pm 4.8$  | $-15.2 \pm 12.3$ | $26.6~\pm~6.4$  |
| Somatomotor cortex (SM1)                      | 4, 6             | $43.3 \pm 4.1$          | $-29.1 \pm 15.0$ | $86.0 \pm 6.5$  | $-47.6 \pm 3.9$  | $-27.1 \pm 15.6$ | $86.5 \pm 6.5$  |
| Dorsal motor cortex (SMA)                     | 6                | $8.7 \pm 5.7$           | $-32.7 \pm 14.3$ | $100.9 \pm 5.9$ | $-11.0 \pm 2.2$  | $-33.1 \pm 14.4$ | $100.8~\pm~5.9$ |
| Broca's premotor area (PMA)                   | 44, 45           | $47.0~\pm~2.2$          | $-52.3 \pm 12.0$ | $44.6 \pm 7.5$  | $-54.2 \pm 6.3$  | $-49.7 \pm 13.2$ | $42.7~\pm~4.3$  |
| Medial prefrontal cortex                      | 8, 9             | $30.6 \pm 6.6$          | $-69.7 \pm 2.0$  | $55.7 \pm 8.6$  | $-30.9 \pm 1.6$  | $-71.0 \pm 2.7$  | $56.7 \pm 8.4$  |
| Orbitofrontal cortex                          | 11               | $26.4~\pm~2.7$          | $-60.8 \pm 4.4$  | $12.3 \pm 7.9$  | $-32.3 \pm 4.5$  | $-61.9 \pm 3.6$  | $13.2 \pm 6.9$  |
| Ventrolateral prefrontal cortex               | 45, 47           | $43.3~\pm~2.6$          | $-53.4 \pm 7.5$  | $24.4 \pm 3.3$  | $-48.2 \pm 4.1$  | $-53.4 \pm 10.4$ | $27.2~\pm~3.2$  |
| Frontopolar cortex                            | 10               | $16.5 \pm 0.8$          | $-76.7 \pm 5.8$  | $20.9 \pm 5.3$  | $-20.8 \pm 4.2$  | $-77.2 \pm 6.4$  | $21.5~\pm~5.4$  |
| Cerebellum                                    |                  | $34.6~\pm~5.9$          | $41.9~\pm~3.2$   | $5.2 \pm 6.5$   | $-38.8 \pm 8.9$  | $45.1~\pm~3.70$  | 8.8 ± 7.6       |
|                                               |                  | <i>x</i> (mm)           |                  | <i>y</i> (mm)   |                  | z (mm)           |                 |
| Middle frontal cortex                         | 10, 32           | $-2.6 \pm 3.1$          |                  | $-76.5 \pm 5.5$ |                  | $24.7 \pm 8.5$   |                 |

The centers of the spherical ROIs were defined separately for each subject in their head-frame coordinate system. The measurements listed are the mean and standard deviation of the central position of the ROIs for all five subjects. The origin of the PPN (preauricular–preauricular–nasion) coordinate system was set at the midpoint of the medial–lateral axis (*x* axis) that is defined by the two preauricular points (positive to the left). The anterior–posterior axis (*y* axis) connects the origin with the nasion (negative to the nasion). Finally, the inferior–superior axis (*z* axis) is defined to be perpendicular to the x-y plane through the origin (positive to the vertex).

performance. Three spherically shaped VOIs were defined in each hemisphere centered at strong activation foci and at well-characterized anatomical positions relative to the cerebral sulci (Fig. 8, upper panels): SM1 (blue) was defined around the lower-lateral part of the omega shaped knob of the central sulcus and precentral gyrus; SMA (green) was defined around the mesial part of Brodmann area 6; PMA (red) encompassed regions of the inferior frontal gyrus (BA 44, 45), within and around Broca's area and its right homologue. The lower lines of Fig. 8 compare the PSDs derived from the regional activations and the audio signal. The comparison shows that distinct PSD peaks in the audio signal have counterpart PSD peaks in the regional brain activations. It thus demonstrates that activations in motor regions generally track the major temporal patterns (periodicities) of the sound envelope.

Fig. 9a shows examples of ACVs from the right SM1 and PMA areas from one subject, corresponding to a temporal window from segment A of the musical motif. The time course of the ACVs shows complex dynamic oscillatory patterns of activity, with elevated transient waves after the onsets of the notes (marked by black arrows in the figure). For SM1, these transient responses are characterized by high amplitudes, which distinguish them from other intervening oscillatory activity. This in turn is reflected in the corresponding scalogram (Fig. 9b, upper line) by high-energy patterns, which extend across a wide range of frequencies. Similar energy profiles are captured in the self-similarity matrix (Fig. 9c), which reveals the regions of high similarity (blue color), as well as their repetition time indicated by their offset from the main diagonal. The PMA activation exhibits also transient waves that are however embedded in a higher oscillatory activity, and thus they are more difficult to identify in the ACV data. While the responses following the first and third note onsets are still observable, the transient response to the second note onset is obscured. The corresponding scalogram (Fig. 9b, lower line) captures accurately these characteristics, showing high-energy patterns for the first and last responses and only a moderate energy increase for the middle response.

The periodicity and relative strength of the rhythmical patterns that are present in the ACVs are finally summarized in their corresponding beat spectra shown in Fig. 9d, which were derived from the first segment A of the musical motif. It should be stressed that rhythmically transient responses that preserve the stimulus periodicities will have similar beat spectra with the musical segment. The beat spectrum derived from the SM1 activation shows clear spectral peaks that closely resemble the spectral peaks of the musical segment A, indicating a phase-locking of the transient responses in respect to the notes onsets. Conversely, the low-energy profiles of the responses to the middle note in each triplet, which characterize the PMA activation, are reflected by a smearing of the first and third peaks in the beat spectrum. The absence of transient responses to (some) note onsets, as well as a non-time-locking behavior of these transient responses, will contribute to a different degree of smearing of the spectral peaks, which ultimately leads to different degrees of dissimilarity with the beat spectrum of the musical motif.

Fig. 10 shows examples of beat spectra from the motor regions (SM1, PMA, and SMA) of different subjects, displayed together with the beat spectra of the music signal for the same segments. We generally observed that the beat spectra exhibit peaks that roughly correspond to the peaks of the music spectrum and this again demonstrated that periodicities are present in the corresponding

ACVs. Some of these peaks show a good temporal coincidence (and therefore match the temporal periodicities of the music), while others show different degrees of temporal shift compared to the peaks from the music signal. Generally, the beat spectra from the SM1 and PMA areas show a higher similarity with the music beat spectrum compared to those from SMA. This similarity is evident in Fig. 10a, which compares the beat spectra from the left hemisphere SM1 and PMA of subject S1, together with the beat spectrum of the music signal. In a subset of subjects, the SMA beat spectrum showed peaks around 200, 400, and 600 ms, generally better seen over the left hemisphere and from music segments B and C (Figs. 10b,c). When such a clear periodicity occurred in the left SMA, a similar periodicity was observed in left PMA. No such strong correlation between periodicities of the two motor areas was evident in the right hemisphere. The right PMA showed in a few cases major peaks at about 300 and 600 ms (Figs. 9d and 10d). These were not associated with similar shapes in either the right SM1 or the right SMA areas.

Fig. 11 shows the mean (across subjects) of the correlation coefficients between the beat spectrum of the music signal and the beat spectrum of each separate motor area. This quantity is computed and displayed separately for segments A, B, and C. The changes in the mean correlation coefficients show a decrease in the performance-rhythm tracking ability of motor-related regions of the left hemisphere for the second segment of the motif. This was particularly evident for the SM1 and PMA areas. Statistical testing revealed a significant decrease in the mean correlation coefficients after the first switch in musical rhythm, from segment A to segment B, for all left motor areas (t = 4, P =0.008 for left SMA; t = 2.28, P = 0.042 for left SM1; and t = 3.45, P = 0.013 for left PMA). Moreover, a significant increase in the mean correlation coefficient was noticed after the second switch (marking the transition from high DRIR on segment B to small DRIR on segment C) in left SM1 (t = 2.13, P = 0.05). The increase for the left PMA approached significance (t = 1.90, P = 0.06), while no difference was found for the same comparison of the left SMA (t = 0.11, P = 0.46). These lateralized findings suggest dynamic changes in rhythm tracking performance, which are hemisphere specific, while listening to the motif. Changes in the correlation between the brain activity and the musical rhythm occurred after each change in DRIR of the performance rhythm. After the first switch, a change is seen in the motif rhythm tracking, which alters the synchronization between the external rhythm and the oscillatory activity in motor-related areas in the left hemisphere. The corresponding areas of the right hemisphere show no significant decrease in synchronization at this time. This phenomenon leads ultimately to a better representation of these temporal patterns in right motor areas. After the second switch (B to C), the performance rhythm is characterized by the smallest DRIR and the activity in the left PMA and SM1 becomes highly synchronized, whereas the activity in the right PMA and SM1 show again no significant change in their degree of synchronization with the motif rhythm.

#### Discussion

# Identification of brain areas

The current density estimates revealed widely distributed neural networks involved in music perception, together with changes in the structure of their rhythmic activity. Many of the changes persisted for several seconds, and changes in rhythmical features within the motif were reflected in brain activations.

Soon after the onset of the stimulus, activations were noticed within and around the primary and secondary auditory cortices, and in posterior parietal areas. These brain structures are domainspecific for language and music processing, and have also been identified in our previous study of echoic memory using sequences of tones (Ioannides et al., 2003). Activations in areas of the supramarginal and postcentral gyri have been reported in a recent study using intracranial recordings of middle-latency responses to simple auditory stimuli (Hughes et al., 2001), suggesting they are involved in processing the fundamental physical properties of sound. Bilateral activation of the precuneus in response to music listening has also been reported by a PET study (Nakamura et al., 1999), while specific activation of the left precuneus has been reported in a pitch discrimination task (Platel et al., 1997) and in the reading of a musical score by musicians (Sergent et al., 1992). It has been proposed (Nakamura et al., 1999) that the premotorparietal network involved in cognitive processes such as visuospatial tasks (Jonides et al., 1993; Haxby et al., 1994) might include the precunei as part of the neuronal substrate for music perception.

Significant activations emerged bilaterally in the anterior part of the middle and superior temporal gyri. The anterior temporal lobe has been found to play a role in sentence-level comprehension, and this role was clearly dissociated from the simple temporal integration of meaningful auditory stimuli (Humphries et al., 2001). The activation of this region appeared fairly selective for sentence-level stimuli: It does not respond robustly to unstructured meaningful speech stimuli such as word lists, or to random sequences of environmental sounds, but it does respond both to meaningful sentences and meaningless pseudoword sentences. The authors of that study pointed out that it is still an open question if the same area will be active during music listening. Our source reconstruction results showed that authentic music with a highly articulated structure activate these regions bilaterally.

Our finding of the activation of PMA and SMA is consistent with previous findings reported in several studies on music perception. Two PET studies used auditory imagery for music and reported that SMA is specifically active in image generation, suggesting that SMA is involved in a "singing to oneself" strategy during auditory imagery tasks (Halpern and Zatorre, 1999; Zatorre et al., 1996). They, however, did not link directly the SMA activity with the rhythmical dimension of music, although studies of patients with SMA lesions clearly show that patients are impaired in the reproduction of rhythms (Halsband et al., 1993). The progressive decrease in the correlation of SMA activity with the performance-rhythm after each switch in DRIR is analogous to the decrease in SMA activity as a motor task is repeated (Dammers and Ioannides, 2000), underscoring the similarity of motor-related activity during motor action and music perception.

Besides its well-established role in semantic, syntactic, and phonological processing, Broca's premotor area was also associated with nonlinguistic processes such as the analysis of pitch and duration of sounds (Griffiths et al., 1999). The activation of the Broca's premotor area and its right hemisphere homologue was noticed in musical expectancy violation paradigms, and it was thought to reflect the processing of musical syntax (Maess et al., 2001). Nevertheless, these areas were associated with processing and integrating information over time, when movements must be synchronized to a sensory input or when subjects are requested to time in anticipation of sensory events (Platel et al., 1997; Schubotz et al., 2000).

Activations evoked by music in SM1 areas are new and particularly interesting. Recent experiments have shown that brain networks activated during internal motor imagery (MI) overlap those involved in the preparation and execution of real movements and include the primary motor cortex (Beisteiner et al., 1995; Lang et al., 1996; Porro et al., 1996). A transcranial magnetic stimulation study (Pascual-Leone et al., 1995) has also shown that the cortical motor output maps targeting finger flexors and extensors enlarged after several days of *mental* practice of a five-finger piano exercise. It has also been suggested that the motor cortex plays a role in the processing of cognitive information related to motor function (Georgopoulos, 2000). In the few studies that showed a specific role for the motor cortex in music, the effect was attributed to plasticity, most easily demonstrated and discussed in trained pianists (Haueisen and Knösche, 2001; Jancke, 2002). Our reconstruction results showing that the SM1 area activates in the absence of overt motor behavior such as finger or foot tapping supports the hypothesis that it is involved in the perception of the temporal patterns embodied in the musical rhythm.

The ventrolateral prefrontal cortex has been suggested to be responsible for maintenance of items in working memory and the active retrieval that is required when stimuli in memory cannot be automatically driven by a strong, stable, and unambiguous stimulus or by context relations (Petrides, 2002). During listening to music, working memory can be directly related to the accumulating representation of the perceptual context that is progressively set up by the continuous acoustic stream. In addition to their wellestablished role in memory and selective attention (Corbetta et al., 1990), frontopolar and orbitofrontal regions have been implicated in emotional processing (Dias et al., 1996; Lane et al., 1997). Positive correlations of activity in orbitofrontal and bilateral frontopolar cortex during listening to consonant and dissonant musical excerpts reported in a recent PET study (Blood et al., 1999) also suggested a functional interaction between these regions within a given type of affective response. The higher activation of the right frontopolar and orbitofrontal regions in this study is consistent with previous findings that circuitry related to emotional processes (including emotional components of music) are mainly localized in the right hemisphere (Blood et al., 1999; Erhan et al., 1998; Lane et al., 1995).

Our results show clear activation of the cerebellum, especially of the ventrolateral part of the dentate, which mainly projects to dorsolateral prefrontal areas. These areas are associated with higher-level cognitive processing (Leiner et al., 1995; Middleton and Strick, 1994), as opposed to purely sensorimotor functions in which the dorsal dentate is mainly involved. Research in patients has shown that the lateral cerebellum is essential in controlling timing (Ivry and Keele, 1989), and this supports its possible role in rhythm perception.

## Significance of methodological innovations

Most of the areas that we identified by distributed source analysis of the 10-s-long MEG signals are broadly the same as the ones previously reported in studies of music perception that used simpler stimuli and relied on comparing changes in activity across different active conditions and/or between active and baseline conditions. The activation of the sensory/motor area is the one area to our knowledge that has not been identified in earlier studies of passive listening to music by naive subjects. The presence of so many interwoven activations in this study highlights the difficulty in identifying the role that each of these brain areas plays in music perception.

The major new innovations of our work are the methodological tools that have been developed to address the similarity between regional brain activations and their timing structure across a range of temporal scales. Automated performance-rhythm tracking in authentic music has remained difficult to achieve, despite its apparent intuitiveness and simplicity compared to other dimensions of music perception. Our methods differ from previous studies, which assumed that the 'rhythm' is induced mainly from the interonset intervals (IOIs) between events (Lee, 1985; Rosenthal, 1992). The rhythmic function, in earlier studies, was represented by a unit impulse function for each beat onset, for example, note or tap (Large and Kolen, 1994; Brown, 1993), which cannot explain subtle perceptual phenomena. Slightly lengthening the IOI (forming an agogic accent) is perceived as increasing the intensity, while intensifying a beat is perceived as having a longer duration. Furthermore, beats falling within a very short temporal window (less than 40 ms) cannot be perceived as separated in time (Handel, 1989; Parncutt, 1994). Studies of chord asynchrony in piano music have shown that asynchronies of 30-50 ms are common (Goebl, 2001; Sundberg, 1991), and too simple a treatment of the note onsets based on unit impulse functions might separate temporally two onsets (as in chords) corresponding to the same beat of the bar.

Our beat spectrum avoids these limitations and provides an automated performance-rhvthm tracking of authentic music that is objective and quantifiable. This technical achievement relies on a novel combination of multiresolution wavelet decomposition of the amplitude envelope of the music signal and self-similarity measures derived from the wavelet coefficients. Computing the beat spectrum via the rhythmogram rather than the raw acoustic signal or its scalogram provides a robust and automatic discrimination of the attack onsets, so avoiding confusion with other transient waveforms that are present in the audio signal. An identical analysis can also be applied to individual brain activations to produce the beat spectrum for regional brain activity. The comparison (e.g., correlation) between the beat spectra derived from the music with the ones derived from brain activations provides a robust and powerful measure of how a given brain area follows the rhythmic structure of the music. This similarity measure inherits the advantages of the beat spectra and it exploits the millisecondby-millisecond resolution of MEG, without relying on a precise alignment or even on a fixed time delay between the unfolding audio time course and regional brain activations.

## Relating regional activations to musical rhythm

Analysis of the temporal characteristics of brain activations identified changes that ranged from the very rapid, in areas processing the fine temporal structures of the stimulus (at a level of resolution of individual notes), to changes with long time constants, which generally grow in strength as the musical surface unfolds. In many of these latter areas, the activation persisted well beyond the end of the motif.

The musical score and the novel analysis methods enabled us to explore rhythm perception mechanisms, by relating the rhythms of regional brain activations in motor areas with the rhythmical properties of the motifs. Many psychophysical studies have proposed the abstract notion of an internal clock of an oscillatory nature that underlies the assessment of temporal intervals by the brain and provides a central concept mediating between neuropsychological and theoretical music findings (Handel and Lawson, 1983; Handel and Oshinsky, 1981; Longuet-Higgins and Lee, 1982; Povel and Essens, 1985). The internal rhythm has been thought of as an active, self-sustained network of oscillators, dynamically entrained by *coupling* with the rhythm of the external stimulus. Such models assume that a perceived beat requires a byproduct of the acoustic input and some internal, dynamic constraints such as anticipation or expectancies that are progressively built upon the history of previous events. Other theories governing coupled oscillations (Schmidt et al., 1991; Treffner and Turvey, 1993) and entrainment of putative brain clocks (Shaffer, 1981) have been used to describe the mechanism of motor coordination in rhythmic hand movements and cascade juggling. Our results are consistent with the existence of two interrelated neural subsystems: a subsystem that mediates the auditory input and an internal rhythm generator subsystem. The latter subsystem is likely to involve the SMA, as this showed the highest dissimilarity of activation periodicities with the external rhythm compared to other motor-related areas. Synchronization between the internal rhythm subsystem and the auditory sensory input subsystem can result in phase-locked (constructive) transient waveforms, reflecting their entrainment and ultimately the brain's rhythm tracking ability.

Studies using paced finger tapping (PFT) paradigms support the existence of an internal rhythm generator subsystem that involves the lateral cerebellum and SMA and is independent of motor implementation or feedback mechanisms (Ivry and Keele, 1989; Rao et al., 1997; Sergent et al., 1993). Patients with SMA lesions are impaired in the reproduction of rhythms in the absence of an auditory cue (Halsband et al., 1993). Moreover, patients with Parkinson's disease are impaired in PFT tasks (O'Boyle et al., 1996), presumably due to the loss of nigral dopaminergic neurons projecting to the dorsal putamen (Brooks et al., 1990), which is further connected with SMA to form the medial premotor loop (Alexander et al., 1986). The subsystem that mediates the auditory sensory input on the other hand is likely to involve the lateral PMA and SM1. The activations of premotor areas during the mental representation of motor acts (motor imagery) have been revealed by early neuroimaging studies using photon emission or positron emission tomography (Fox et al., 1987; Ingvar and Philipson, 1977; Roland et al., 1980). More recent observations suggest that perirolandic regions including the anterior bank and crown of the central sulcus (the presumed site of the primary motor cortex) also play a role in motor imagery, even in the absence of overt motor behavior (Beisteiner et al., 1995; Lang et al., 1996; Porro et al., 1996). All these studies pointed out that activity in these regions was generally less pronounced than that induced by actual motor performance of the tasks. The related issue concerning the possible mechanisms of motor inhibition and the corresponding sites (spinal or cortical) is still under debate (Berthoz, 1996; Jeannerod, 1994; Lang et al., 1996).

Our results demonstrate that when an external rhythm is close to metrical (i.e., for small DRIRs in our examples), phase locking occurs in the activity of motor areas for the left hemisphere, which now functions in a highly entrained mode. Metrical rhythms therefore preferentially drive a coherent mode of oscillatory

activity in the *left* hemisphere. The increased synchronization between the internal and external rhythms could result in a subsequent stability of the rhythm percept and the efficient selfgeneration or retrieval from memory of these rhythms. This matching of internal and external rhythms would lead to good performance in memorization and reproduction of these rhythmical patterns (Essens, 1986; Essens and Povel, 1985; Sakai et al., 1999). The change to high DRIR (which in terms of the interval duration ratios leads to what Sakai et al. called nonmetrical rhythm) affects the left hemisphere performance in rhythm tracking, but not the right hemisphere. Hence, the right hemisphere dominates in the representation of rhythms characterized by high DRIR. A better tracking of nonmetrical rhythms in the right hemisphere is consistent with the study of Roland et al. (1981), showing the right hemisphere dominance in discrimination of rhythmical patterns characterized by complex interval ratios. In summary, our study supports and qualifies earlier claims that processing of rhythm is not confined to only one hemisphere (Peretz, 1990; Sakai et al., 1999).

This study opens new directions for exploring how the core elements of music are perceived by allowing the individuality of each performance and the quality of the experience it imparts to be related to the temporal aspects of brain activations. In this work, we focused on the processing of the rhythmic properties of music and obtained insights about regional activations. We have demonstrated that objective measures can be derived from the rather elusive aspects of music, such as its rhythmic content and its artistic expression, and that these measures can be used to probe how the brain deals with the authentic musical experience. We acknowledge that in doing so we have ignored other important properties, such as melody. These other aspects of music-related brain activations and other applications of the methodology will be the subject of future investigations.

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# Appendix A

The automated rhythm tracking of the audio signal has been achieved by implementing a four-step algorithm. At the first step, the amplitude modulation (AM) component has been extracted from the digitized audio signal using standard techniques (Todd, 1994). A prerequisite of any rhythm-tracking algorithm is to extract accurately the relevant information from the musical signal into a one-dimensional signal that retains the prominent rhythmical features and discards the less-relevant information. The AM of the audio signal has been proposed in Todd (1993) to be the ideal candidate to achieve these tasks. For further processing, the sampling rate of the AM signal has been reduced from 44,100 Hz (the sampling rate of the original audio data) to 625 Hz (the sampling rate of the MEG data). The downsampling has been accomplished by a low pass filtering at a cutoff frequency of 200 Hz (i.e., lower than the Nyquist frequency), a cubic spline interpolation, and a resampling procedure.

At the second step, the AM component was parameterized using a pseudocontinuous wavelet transformation. Generally, the wavelet transform decomposes a one-dimensional signal, s(t), into a two-dimensional time-frequency distribution,  $W_s(t, a)$ , representing frequency-specific changes over time:

$$W_s(t,a) = \frac{1}{\sqrt{a}} \int_{-\infty}^{+\infty} s(\tau) g\left(\frac{\tau-t}{a}\right) \mathrm{d}\tau, a > 0$$

where g(t) is a mother-wavelet or reproducing kernel and a is the scale parameter, controlling the dilation of the wavelet function (Grossmann and Morlet, 1984). The geometric scale gives the wavelet transform a *zooming* ability over a logarithmic frequency range, such that high frequencies (small a) are localized by the window over short time scales, and low frequencies (large a) are dilated over longer time scales (Kronland-Martinet and Grossmann, 1991).

A Morlet wavelet transformation has been employed in this study, which relies on a complex valued Gabor mother wavelet, proposed in Grossmann and Morlet (1984):

$$g(t) = A \cdot e^{-t^2/2\sigma} \cdot e^{i\omega_0 t}$$

where the constant A is introduced for energy normalization and  $\omega_0$  is the angular frequency. The Gaussian window over sine and cosine curves (real and imaginary parts of the wavelet function) ensures a best time-frequency resolution. In the frequency domain, the wavelet has the form:

$$\hat{g}(\omega) = e^{-(\omega - \omega_0)^2/2} - e^{-(\omega + \omega_0)^2/2}$$

Due to the noncausality of the Morlet wavelet, the notes onset is projected simultaneously forward and backward in time forming at each scale an *influence cone* (Holschneider, 1995), whose width depends on the support of the wavelet function.

At the third processing step, similarity measures D between feature vectors (matrices) were subsequently computed from successive temporal windows of the AM scalogram. A scalar (dot) product was used as a distance measure, as shown schematically in Fig. 2d:

$$D(i,j) = \langle v_i, v_j \rangle$$

where  $v_i$  and  $v_j$  are feature vectors in the *K*-dimensional parameter space. The scalar product will be large if the vectors have large values and are similarly oriented. To remove the dependence on magnitude, the scalar product could be normalized as proposed in Foote and Uchihashi (2001). However, this could yield a large similarity measure between vectors with little energy (such as those corresponding to silence segments, or prolonged notes). On the other hand, when the distance values are proportional with the energy of the feature vectors, they maintain the degree of a perceptual intensity, which is highly desirable, as intensity of a sound has proved also to play an important role in rhythm perception. The distance measure was embedded in a twodimensional similarity matrix (called rhythmogram), as shown in Fig. 2d.

The periodicity and relative strength of the musical beats were straightforwardly derived at the last step of the algorithm using the autocorrelation of the rhythmogram matrix, as proposed in Foote and Uchihashi (2001).

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