Tuning-in to the Beat: Aesthetic Appreciation of Musical Rhythms Correlates with a Premotor Activity Boost

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Abstract: Listening to music can induce us to tune in to its beat. Previous neuroimaging studies have shown that the motor system becomes involved in perceptual rhythm and timing tasks in general, as well as during preference-related responses to music. However, the role of preferred rhythm and, in particular, of preferred beat frequency (tempo) in driving activity in the motor system remains unknown. The goals of the present functional magnetic resonance imaging (fMRI) study were to determine whether the musical rhythms that are subjectively judged as beautiful boost activity in motor-related areas and if so, whether this effect is driven by preferred tempo, the underlying pulse people tune in to. On the basis of the subjects' judgments, individual preferences were determined for the different systematically varied constituents of the musical rhythms. Results demonstrate the involvement of premotor and cerebellar areas during preferred compared to not preferred musical rhythms and indicate that activity in the ventral premotor cortex (PMv) is enhanced by preferred tempo. Our findings support the assumption that the premotor activity increase during preferred tempo is the result of enhanced sensorimotor simulation of the beat frequency. This may serve as a mechanism that facilitates the tuning-in to the beat of appealing music. *Hum Brain Mapp 31:48–64, 2010.*   © 2009 Wiley-Liss, Inc.

Key words: fMRI; ventral premotor cortex; rhythm; motor control; aesthetic judgment

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INTRODUCTION

When listening to music that appeals to us, we often feel an immediate urge to tune in by head nodding, toe tapping, or humming. It has been shown that complex musical stimuli inducing pleasurable responses enhance BOLD activity in a subset of motor-related sites—the supplementary motor area (SMA), the cerebellum, and the Rolandic operculum [Blood and Zatorre, 2001; Koelsch et al., 2006]. However, it remains uncertain whether these preference-associated activations can be induced by preferred rhythm alone, a component of music considered to be most fundamental with respect to linking sound to movement [Cross, 2001; Janata and Grafton, 2003; Thaut et al., 1999].

The motor system has been found to be recruited during attention to auditory and visual rhythm [Bengtsson et al., 2009; Chen et al., 2008; Coull et al., 2004; Grahn and Brett, 2007; Platel et al., 1997; Schubotz et al., 2000; Schubotz et al., 2003; Wolfensteller et al., 2007]. Typically, motor-related areas are engaged by perceptual input in tasks that require attention to events of a subseconds duration such as a musical beat frequency, which corresponds to the time-range of voluntary movements [Lewis and Miall, 2003; Moelants, 2003]. Within this motor network, the lateral premotor component has been specifically attributed to implicit perceptual timing of stimuli with a predictable temporal structure [Coull and Nobre, 2008]. Studies report especially the ventralmost portion of the premotor cortex (PMv) for perceptual rhythm tasks [Schubotz and von Cramon 2001b, 2003], an area that also corresponds to vocal imagery [Kleber et al., 2007; Riecker et al., 2000; Wolfensteller et al., 2007]. This led to the assumption that PMv provides a common platform for attention to rhythmic structure, both perceived and produced [Schubotz, 2007]. To explain the above convergence between motor and perceptual functions, the computational perspective offered the notion of sensorimotor simulation via internal forward models [Grush, 2004; Schubotz, 2007; Wolpert and Flanagan, 2001]. These simulations serve to predict future motor, as well as perceptual states based on established sensorimotor representation of previous event templates such as rhythmical patterns in perceptual rhythm tasks. Although suggested by tuning-in behavior such as head nodding, toe tapping, or humming to the music that appeals to us, it is an open question, whether the aesthetic appreciation of rhythms is positively correlated with such sensorimotor simulation.

In the present fMRI study, we used systematically controlled rhythmic musical patterns to test the hypothesis that activity in the motor system is particularly enhanced when subjects aesthetically appreciate musical rhythms. More specifically, we aimed to clarify whether activity enhancement for preferred musical rhythms can be traced back to preferred beat frequency, i.e., *tempo*. We expected tempo to be the most important time-related property influencing the subjects' preferences (i) due to its prominent role in auditory rhythm perception [Baruch and Drake, 1997; Dalla Bella et al., 2001; Drake et al., 2000; Trainor et al., 2004], and (ii) because it provides the underlying pulse, a beat, people tune in to when listening to music, i.e., it often triggers sensorimotor coupling [Chen et al., 2006; Drake et al., 2000; Fraisse, 1982; Large, 2000; Moelants, 2002; Moelants, 2003; van Noorden and Moelants, 1999]. To this end, we modeled brain data on the basis of individual judgment analyses including all constituents of the musical rhythms as predictors for the subjects' aesthetic judgments. Besides tempo, we varied orthogonally traits such as beat grouping (measure), beat subdivision, non-isochronous repetitive patterns, and instrumental timbre that a musical rhythm typically contains.

In addition, to determine whether the hypothesized activity increase in motor-related areas during preferred tempo can be explained by enhanced sensorimotor simulation essential in a perceptual rhythm task, we employed a tempo judgment condition besides an aesthetic judgment condition. The subjects were asked to decide whether a musical rhythm is fast or not. In line with the notion of sensorimotor-driven forward models and the evidence for the involvement of motor-related areas in perceptual rhythm tasks, we assumed that the tempo judgment task required enhanced sensorimotor simulation. Accordingly, to identify the tempo of an incoming auditory rhythm the subjects had to map an external beat frequency on their audiomotor representation of a template established on the basis of previous rhythms. Thus, the tempo judgment condition served as a control to determine whether the hypothesized activity increase in motor-related areas during preferred tempo can be explained by enhanced sensorimotor simulation. In addition, the tempo judgment condition was used to ensure that the aesthetic judgments engaged the subjects in an evaluative in contrast to a tempo identification task.

MATERIALS AND METHODS

Participants

Eighteen right-handed healthy volunteers (11 female, mean age 25.1 years, range 22–29 years) participated in the study. One additional participant had to be excluded due to inadequate behavioral performance (compare results section). All subjects received regular musical education at school which comprises singing melodies to a piano accompaniment, basic ensemble performance, the acquisition of elementary theoretical knowledge about Western musical harmony and rhythm, as well as about the general principles of musical notation, but no professional musical training. Six subjects received additional instrumental training or attended a choir for 1–13 years (mean: 6.1 years, SD: 5.4 years), but only three reported musical activities of 4–5 h per week at the time of their participation in the experiment. To ensure that the stimulus material elicited appreciation in all participants, we preselected the subjects on the basis of a behavioral test, in which they were exposed to the stimulus material used in the current experiment. When asked how much they enjoyed the test, all 18 participants of the present fMRI-experiment indicated at least 5 on a 7-point rating scale ranging from ''not at all'' to ''very much.'' After being informed about the potential risks and screened by a physician of the institution (Max Planck Institute for Cognitive and Brain Sciences, Leipzig), subjects gave informed consent before participating. The experimental standards were approved by the local ethics committee of the University of Leipzig. Data were handled anonymously.
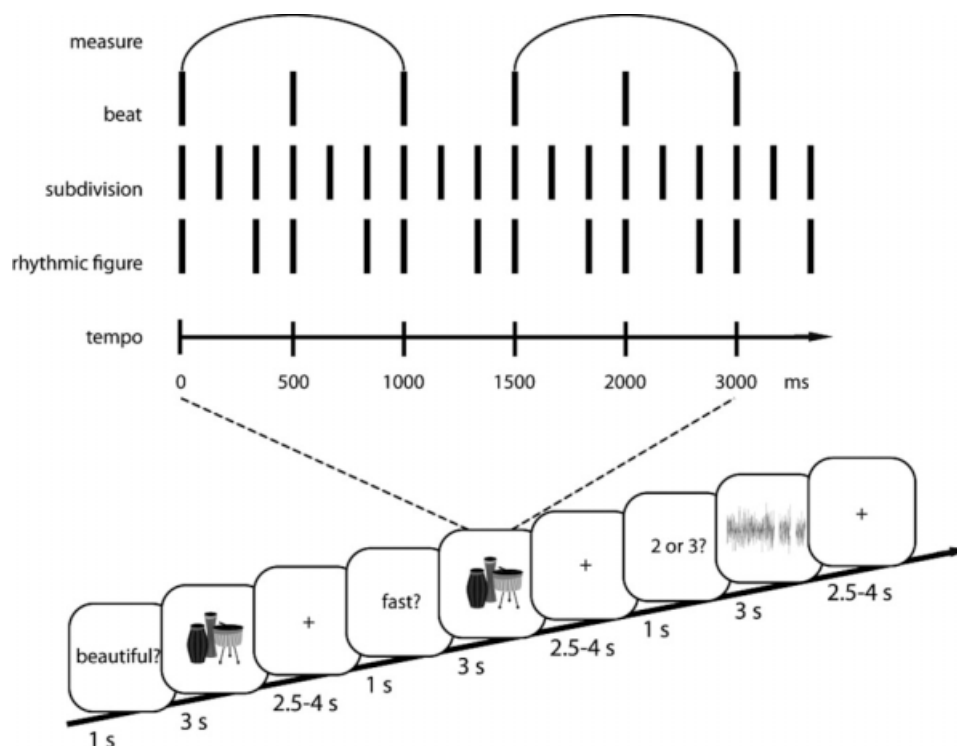
Figure 1.

Structural elements of a musical rhythm and an exemplary trial sequence of both judgment tasks and the control condition. The rhythmical structure of a musical rhythm was determined by tempo (inter-onset-interval of beats), measure (the grouping of beats), beat subdivision (elements per beat), and rhythmic figure. In addition, instrument type was introduced to increase variety in the stimulus material. The depicted rhythm example possesses a middle tempo with three beats per measure, three elements per beat and a repetitive rhythmic figure containing a long, fol-lowed by a short interval. A variable jitter time of 2.5–4 s was followed by a task cue (1 s) and an auditory stimulus presented for 3 s. Participants were asked to press the selected response button when they had decided but still while the sound was presented. They were asked to decide whether or not the presented musical rhythm was beautiful (aesthetic judgment) or fast (tempo judgment); in the control condition, they were asked to press the left button if a white noise was interrupted by two silent gaps and the left button for three silent gaps.

Stimuli and Tasks

Subjects were presented with auditory musical rhythms. The rhythm stimuli were constructed of drum sounds generated with the Microsoft Software Wavetable Synthesizer (GM drum map). The stimuli had five properties, each property varying on two or three levels respectively: tempo (slow, middle, fast; i.e. 600, 500, and 400 ms inter-onset-interval of beats corresponding to the beat frequencies: 1.7, 2, and 2.5 Hz, or 100, 120, and 150 beats per minute (BPM); quarter notes in musical notation), measure or beat grouping (3, 4, 5 beats; 3/4, 4/4, 5/4 meter in musical notation), beat subdivision (3, 4, 5 elements per beat; eighths note triplet, four sixteenth notes and sixteenth note quintuplet in musical notation), rhythmic figure (long interval–short interval, short interval–long interval; dotted note and syncopation in musical notation) and instrument type ("bongo": predominantly wooden drum instruments; "rock": predominantly metal drum instruments; two ver-sions each) (cf. Fig. 1, upper part). The latter property was not time-related and was introduced to increase the variety of the stimulus material. The tempo (beat frequency) varied within the range of the preferred "tempo-octave" of contemporary dance music [Moelants, 2003; van Noorden and Moelants, 1999]. The rhythm stimuli appeared in all 216 possible combinations, e.g. the rhythmic figure "long interval–short interval" occurred in all tempi, measure types, beat subdivisions, instrument types, and instrument versions (cf. Supp. Info; Stimulus examples). Each combination of property levels was presented only once in the experiment, i.e., there were no stimulus repetitions.

Similar to the paradigm introduced by Jacobsen et al. [2006] in the context of aesthetic and symmetry judgments of abstract visual patterns, we used the stimulus material for aesthetic (AJ) and tempo (TJ) judgment conditions (cf. Fig. 1, lower part). In a forced choice paradigm, participants were instructed to attend to the presented stimuli and to decide whether or not the presented stimulus was

beautiful (aesthetic judgment) or fast (tempo judgment). The subjects were asked to judge the stimuli with regard to previous stimuli in the experiment. They were instructed to press the selected response button when they had decided while the rhythm was presented.

In German, the word "beautiful," "schön," also means "nice" and "pleasant." Thus, the judgments "beautiful" and "not beautiful" was chosen to assess each subject's liking of the rhythms. However, to ensure the correspondence between the judgment "beautiful" and liking in the current experiment, the subjects were asked to indicate on a scale between −3 ("do not agree") and +3 ("agree") how strongly they consent to the statements that they (i) like and (ii) do not like musical rhythms which they judge as beautiful in a post-experimental interview. Results support that the judgment "beautiful" was strongly coupled to liking (mean consent rating ($N = 16$): +2.4; 0.2 SE) in contrast to not liking (mean consent rating ($N = 16$): −2.7; 0.2 SE).

The temporal judgment task required dichotomous judgments on nondichotomous features, just as the aesthetic judgment task, yet continuous attention to beat frequency for the identification of tempo. In addition, a more basic control condition (CC) intermixed with the experimental trials was designed to monitor the subject's overall attention, in which they were presented white noise stimuli that were interrupted by two or three silent gaps of 50 ms. They were asked to press the left button for two and the right button for three interruptions. All stimuli were normalized in intensity level using root mean square (RMS).

Each trial (8 s) started with a cue (1 s), indicating whether to perform an aesthetic judgment ("beautiful?"), tempo judgment ("fast?"), or control condition task ("2 or 3?"), followed by the stimulus (3 s) and a fixation phase (2.5–4 s), which length depended on the variable jitter times (0, 500, 1,000, or 1500 ms) that were inserted between the trials to enhance the temporal resolution of the BOLD response. The duration of the stimulus was set to 3 s, i.e. approximately 1 s after the average RT, which we identified by preceding pilot testing. Altogether, 300 trials were presented: 108 in the AJ, 108 in the TJ, 54 in CC, as well as 30 empty trials (resting condition; RC), which were intermixed with the experimental trials. Each judgment condition was assigned 108 of 216 rhythm stimuli, the temporal factors (tempo, measure, beat subdivision and rhythmic figure) counterbalanced across conditions and the two instrument versions of "bongo" and "rock" counterbalanced across subjects. Instrument type "bongo" and "rock" were equally distributed across both judgment tasks. Each judgment task could occur maximally three times in a row. CC trials did not occur in a row. The frequency of all conditions, as well as all tempo types (slow, middle, and fast), were equally distributed across subblocks of 100 trials. Moreover, all trial transitions between the two judgment conditions were counterbalanced across the session. We used 16 different trial randomizations matching the above criteria for 18 subjects.

To ensure the subjects became familiarized with the task and the musical rhythms as a point of reference for their preference and tempo judgments, a training containing 30 example trials (12 trials AJ, 12 trials TJ, 4 trials CC, 2 trials RC), which were randomly chosen from the pool of stimuli for each subject and counterbalanced for tempo type, was presented prior to the experimental session.

MRI Data Acquisition

Imaging was performed at a 3 T scanner (Siemens TRIO, Erlangen, Germany) equipped with a standard birdcage head coil. Participants were placed on the scanner bed in a supine position with their right index and middle fingers positioned on the appropriate response buttons of a response box. To prevent postural adjustments, the participants' arms and hands were carefully stabilized by tape. In addition, form-fitting cushions were utilized to prevent head, arm, and hand movements. Rhythms were presented over SereneSound Digital audio headphones with 30 dB headset gradient noise attenuation. Further attenuation was achieved with insert earplugs rated to attenuate scanner noise by ∼38 dB. Thirty axial slices (192 mm field of view, 64 × 64 pixel matrix, 4 mm thickness; 1 mm spacing, in-plane resolution of 3 mm × 3 mm) positioned parallel to the bicomissural plane (AC-PC) covering the whole brain were acquired using a single-shot gradient echo-planar imaging (EPI) sequence (TE 30 ms, flip angle 90°, TR 2,000 ms, 116 kHz acquisition bandwidth) sensitive to blood oxygenation level-dependent (BOLD) contrast. In total, 1,212 functional images were acquired in a single run. Prior to the functional imaging, 30 two-dimensional anatomical T1-weighted MDEFT images and 30 T1-weighted EPI images with the same spatial orientation as the functional data were acquired. The EPI acquisition was continuous to prevent periodic silent gaps between TRs to disrupt the participants' encoding of the rhythms. We chose a slice acquisition frequency of 15 Hz to ensure the continuous scanner noise to be well above the fastest frequency of elements of the rhythmical stimuli (12.5 Hz) to prevent an auditory interaction between the two sources of rhythmic patterns and ensure that the participants were able to attend to the stimuli. By conducting an auditory test (56 s) with the EPI sequence prior to data acquisition, we adjusted the sound level for each participant in such a way that the stimuli could be easily heard over the scanner noise by each participant at an individually comfortable sound pressure level. When explicitly asked in a post-experimental interview, participants reported no difficulty hearing the stimuli during the whole course of the measurement or performing any of the tasks.

Judgment Analysis

For each individual participant, a linear mathematical model (individual case model) of judgment strategy was computed to examine the influence of stimulus properties on aesthetic judgments [Brehmer and Joyce, 1988; Cooksey,
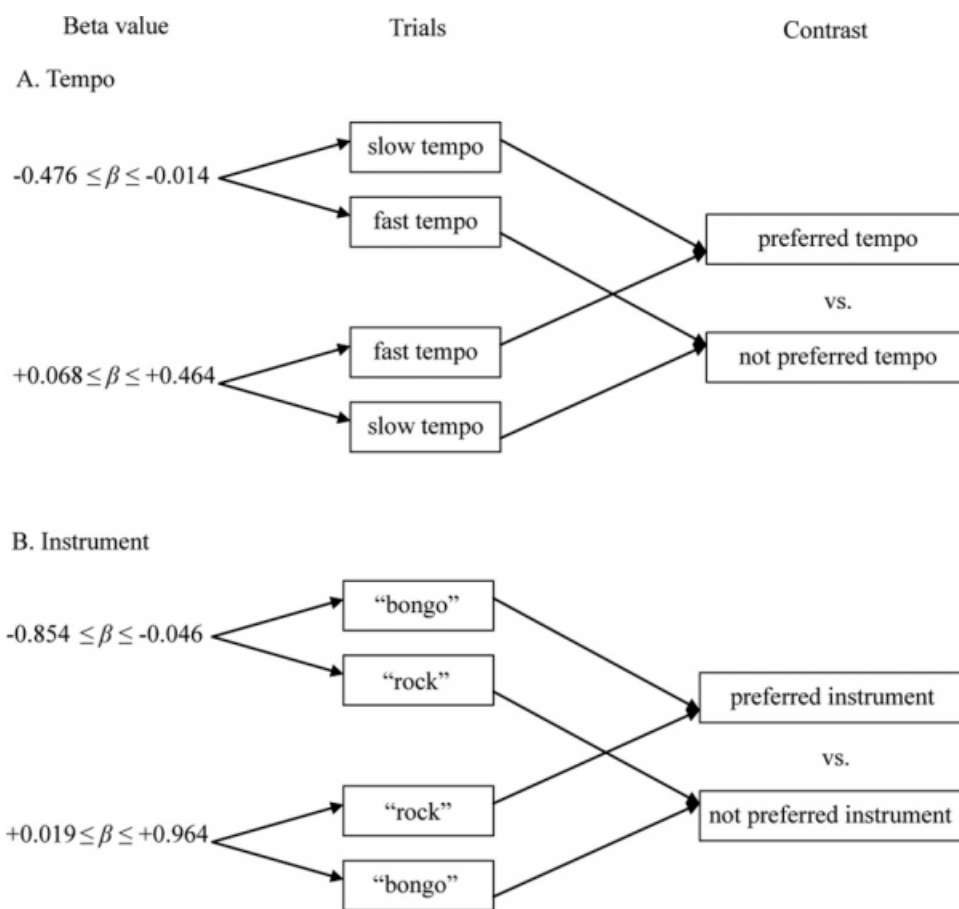
Figure 2.

Grouping of trials for the BOLD-contrasts preferred vs. not preferred tempo and preferred vs. not preferred instrument. The grouping was performed according to Table II, i.e., each subjects' beta weights for tempo and instrument obtained by multiple regression (individual case models), which describe the influence of each stimulus property of the musical rhythm on individual aesthetic judgments. In subjects with negative weights for tempo, slow tempo trials were classified as preferred tempo and fast tempo were classified as not preferred tempo. In sub-jects with positive beta weights for tempo, fast tempo trials were classified as preferred tempo and slow tempo trials were classified as not preferred tempo. Consequently, for instance, slow tempo trials in subjects with a preference for slow tempo and fast tempo trials in subjects with a preference for fast tempo were grouped together under the condition "preferred tempo." The trial grouping according to instrument preference followed the same logic.

1996; Jacobsen, 2004; Jacobsen et al., 2006]. To this end, multiple regressions were computed using the stepwise method, including all properties of the 108 musical rhythms in the aesthetic judgment task as potential predictors of individual performance: tempo (slow = "1," middle = "2," fast = "3"), measure (3 beats = "1," 4 beats = "2," 5 beats = "3"), subdivision (3 elements per beat = "1," 4 elements per beat = "2," 5 elements per beat = "3"), rhythmic figure (long followed by short interval = "1," short followed by long interval = "2") and instrument type ("bongo" = "1," "rock" = "2"). The latter two, being nominal, were assigned "dummy" variables. For example, a musical rhythm with a slow beat frequency, three beats per measure, four elements per beat, a long-short figure, consisting of predominantly metal drum sounds ("rock") was assigned tempo = 1, measure = 1, subdivision = 2, rhythmic figure = 1, and instrument type = 2. In principle, the orthogonality of all stimulus properties as implemented in the experimental design allowed for all predictors to enter the model simultaneously. However, only variables providing incremental explanation of variance (P-value less than or equal to 0.05) entered the model. The beta weights of the predictors which did enter the individual model were taken to reflect the subject's individual preferences [e.g., Cooksey, 1996] (cf. Table II). In an additional step of the analysis, the individual predictor beta weights were used to categorize the subjects for the subsequent BOLD-analysis (cf. Fig. 2). In case the predictors

tempo and instrument, which were the most important ones at the group level, did not enter an individual case model of a subject (P-value higher than 0.05), the enter method of multiple regression was used, which includes all specified predictors in the model irrespective of the significance of their contribution. This way, full models were computed to obtain the respective beta weights, irrespective of their significance. These beta weights provided information on the mere tendency of every subject to prefer rhythms with slow tempo (negative beta weights) or fast tempo (positive beta weights), as well as the instrument type "bongo" (negative beta weights) or "rock" (positive beta weights). Note that this approach of classification according to beta weights is rather conservative, because the effect is not magnified by forming groups of subjects with extreme values.

MRI Data Analysis

Functional data were motion-corrected online with the Siemens motion correction protocol (Siemens, Erlangen, Germany). Further processing of the fMRI data was performed using the software package LIPSIA [Lohmann et al., 2001]. To correct for the temporal offset between the slices acquired in one image, a cubic-spline interpolation was employed. Low-frequency signal changes and baseline drifts were removed using a temporal highpass filter with a cutoff frequency of 1/96 Hz. Spatial smoothing was performed with a Gaussian filter of 5.65 mm FWHM. To align the functional data slices with a 3D stereotactic coordinate reference system, a rigid linear registration with six degrees of freedom (three rotational, three translational) was performed. The rotational and translational parameters were acquired on the basis of the MDEFT [Norris, 2000] and EPI-T1 slices to achieve an optimal match between these slices and the individual 3D reference data set. This 3D reference data set was acquired for each subject during a previous scanning session. The MDEFT volume data set with 160 slices and 1 mm slice thickness was standardized to the Talairach stereotactic space [Talairach and Tournoux, 1988]. The rotational and translational parameters were subsequently transformed by linear scaling to a standard size. The resulting parameters were then used to transform the functional slices using trilinear interpolation, so that the resulting functional slices were aligned with the stereotactic coordinate system, thus generating output data with a spatial resolution of 3 mm × 3 mm × 3 mm (27 mm^3). The statistical evaluation was based on a least-squares estimation using the general linear model for serially autocorrelated observations [Friston, 1994; Friston et al., 1995a; Friston et al., 1995b; Worsley and Friston, 1995]. The design matrix was generated with a synthetic hemodynamic response function [Friston et al., 1998; Josephs et al., 1997] and its first derivative modeled at the onset of the stimuli and at trial onset in the resting condition. The model equation, including the observation data, the design matrix and the error term, was convolved with a Gaussian kernel of dispersion of 4 s FWHM to deal with the temporal autocorrelation [Worsley and Friston, 1995]. In the following, contrast-images, i.e. beta value estimates of the raw-score differences between specified conditions, were generated for each participant. As noted earlier, each individual functional dataset was aligned with the standard stereotactic reference space, so that a group analysis based on the contrast-images could be performed. One-sample t-tests were employed for the group analyses across the contrast images of all subjects, which indicated whether observed differences between conditions were significantly distinct from zero. T values were subsequently transformed to Z scores.

To correct for false-positive results, in a first step, the initial voxelwise z-threshold was set to $Z = 2.576$ ($P = 0.005$, uncorrected) for the main contrast beautiful vs. not beautiful and the contrast tempo judgment (TJ) vs. resting condition (RC) used in a subsequent conjunction analysis, as well as $Z = 2.33$ ($P = 0.01$, uncorrected) for the contrast preferred vs. not preferred tempo and preferred vs. not preferred instrument. In a second step, the results were corrected for multiple comparisons using cluster-size and cluster-value thresholds obtained by Monte-Carlo simulations at a significance level of $P < 0.05$. To determine which of the areas enhanced during aesthetic judgment could be due to preference of tempo and which due to preference of instrument, we masked the contrast preferred tempo vs. not preferred tempo and preferred instrument vs. not preferred instrument by the contrast beautiful vs. not beautiful.

In addition, we analyzed the signal change in several functionally defined regions of interest (ROIs). A ROI was defined as the peak voxel of a premotor (a priori hypothesis), an anterior cingulate and cerebellar area (identified in a post-hoc analysis) that was activated relatively more for musical rhythms judged as beautiful in contrast to not beautiful or for rhythms with a preferred in contrast to a not preferred tempo masked by the contrast beautiful vs. not beautiful. Within each ROI, the percentage signal change was calculated in relation to the mean signal intensity across all time steps. Subsequently, the mean signal change over a 4 s epoch, starting 5 s after stimulus onset, was extracted for each condition and participant. Correlational analyses were performed using standard Pearson correlation coefficient and Pearson correlation significance (two-tailed) on percent signal changes to examine the functional association between activity in premotor and anterior cingulate ROIs. Cases with a Cook's distance index [Cook and Weisberg, 1980] above the value of one, a measure of how much the residuals of all cases would change if a particular case were excluded from the calculation of the regression coefficients, were considered as outliers. A repeated-measure analysis of variance (ANOVA) with the factors TASK (aesthetic judgment/tempo judgment) and PREFERENCE (preferred tempo/not preferred tempo) was computed for the percent signal change in the premotor ROI identified by the contrast preferred versus

**TABLE I. Individual linear mathematical models (individual case models)
of judgment strategy computed to examine the influence of stimulus
properties on aesthetic judgments**

Subject	Tempo	Measure	Subdivision	Rhythm. fig.	Instrument	R
1	**0.271**				−0.259	0.373
2					**−0.796**	0.796
3					**−0.248**	0.248
4						/
5					**−0.443**	0.443
6						/
7	−0.229		−0.229		**−0.460**	0.563
8	**−0.414**					0.414
9	**−0.476**		−0.251		0.389	0.664
10	**0.464**				0.178	0.497
11	−0.204		−0.181		**0.500**	0.570
12						/
13					**−0.778**	0.778
14	0.227		0.204		**−0.482**	0.565
15					**−0.854**	0.854
16					**0.964**	0.964
17	0.253		**−0.282**			0.379
18	**−0.277**		−0.231			0.361

Standardized regression coefficients and multiple regression coefficients (R) as obtained by stepwise multiple regression are shown. Columns show all predictors of preference judgments (tempo, measure, beat subdivision, rhythmic figure and instrument type; the latter two, being nominal, were assigned "dummy" variables.). Each subject's most important predictor for the judgment "beautiful" is in bold font.

not preferred tempo during aesthetic judgment masked by the contrast beautiful vs. not beautiful.

The anatomical locations of the functional activation were assigned by considering both the peak voxel and the position of the respective activation cluster in Talairach stereotaxic space [Talairach and Tournoux, 1988] for cortical and subcortical activations. The MRI atlas of the cerebellum by Schmahmann et al. [2000] was used to locate cerebellar activations. For this purpose, Talairach coordinates of cerebellar activation were converted to MNI305 space by an algorithm implemented in the GingerALE application [Laird et al., 2005; Lancaster et al., 2007].

RESULTS

Behavioral Results

Behavioral performance was assessed by error rates in the control condition (CC), reaction times and frequency of response. 94.0% (1.7 SE) of all responses in the CC were correct. There were 0.1% nonresponses and 5.9% erroneous responses. Aesthetic judgment (AJ) responses showed 0.5% nonresponses and tempo judgment (TJ) 0.1% nonresponses. 47.2% (3.3 SE) of the stimuli under the aesthetic judgment task were judged as beautiful, 52.8% as not beautiful, the difference being not significant ($P = 0.409$, paired t-test). 51.9% (2.4 SE) of the stimuli under the tempo judgment

condition were judged as fast, 48.5% (2.4 SE) as not fast, the difference being not significant ($P = 0.485$, paired t-test). 90.1% (1.7 SE) of the musical rhythms with a fast beat frequency (tempo) were judged as fast, 81.6% (2.4 SE) of the musical rhythms with a slow tempo were judged as not fast. Mean response times and standard errors (in parentheses) were as follows: beautiful (aesthetic judgment "yes") 2042 ms (123 ms); and not beautiful (aesthetic judgment "no") 2036 ms (121 ms); fast (tempo judgment "yes") 1564 ms (127 ms); and slow (tempo judgment "no") 1710 ms (118 ms). A repeated-measures ANOVA over the judgment latencies with the factors TASK (AJ/TJ) and ANSWER (yes/no) revealed a main effect of TASK ($F_{(1,17)} = 4.61$, $P < 0.05$) and an interaction ($F_{(1,17)} = 4.61$, $P < 0.05$). Further investigation of the interaction TASK by ANSWER showed an effect of judgment latencies for ANSWER under the tempo task ($P < 0.03$, Bonferroni corrected), with delayed response for stimuli that were judged as slow. One additional subject (see methods/participants) had to be excluded from analysis because he judged all stimuli as beautiful in the aesthetic judgment condition, although we instructed all participants to judge each rhythm in relation to previous rhythms in the experiment.

For 15 of 18 participants, a substantial individual case model was derived. Standardized regression coefficients (beta weights) and multiple regression coefficients (R) are shown in Table I. The remaining three participants did not

TABLE II. Grouping of subjects according to tempo and instrument preference

	A			B	
Subject	Preferred tempo	Tempo (beta weight)	Subject	Preferred instrument	Instrument (beta weight)
1	Slow tempo	−0.476*	12	"Bongo"	−0.854*
2		−0.414*	9		−0.796*
3		−0.277*	11		−0.778*
4		−0.229*	15		−0.482*
5		−0.204*	4		−0.460*
6		−0.127	7		−0.443*
7		−0.024	17		−0.259*
8		−0.014	6		−0.248*
9		0	8		−0.130
10		0	16		−0.046
11	Fast tempo	0.068	13	"Rock"	0.019
12		0.091	14		0.094
13		0.094	2		0.131
14		0.184	3		0.151
15		0.227*	18		0.178*
16		0.253*	1		0.389*
17		0.271*	5		0.500*
18		0.464*	10		0.964*

Standardised regression coefficients (beta weights) for tempo (A) and instrument type (B), which describe the influence of these predictors on individual aesthetic judgments, were obtained by stepwise (*) and enter multiple regression. Because of the linear mathematical modelling, these beta weights provided information on the tendency of every subject to prefer rhythms with slow tempo (negative beta weights) or fast tempo (positive beta weights), as well as the instrument type "bongo" (negative beta weights) or "rock" (positive beta weights). Subjects are sorted according to the respective absolute value of beta weights for tempo and instrument separately. They were divided according to their tendency to prefer slow (negative beta weights) and fast (positive beta weights) (A), as well as instrument type A (negative beta weights) and B (positive beta weights) (B), respectively. This information was used to determine differences in BOLD-response during trials with preferred compared to not preferred tempo and preferred compared to not preferred instrument type (cf. Fig. 2 for the grouping of trials according to preference).

show a significant linear relationship between any of the stimulus properties and their judgments.

Instrument type was found to be the most important stimulus property determining participants' aesthetic judgments (cf. Table I). As predicted by pilot testing, tempo was the most influential time-related stimulus property determining participants' aesthetic judgments at the group level with beta weights ranging from −0.48 to 0.46. However, for half of the participants tempo was not a significant predictor for aesthetic judgments. To determine whether these subjects tended to prefer slow or fast tempo, even though the preference was not pronounced, we obtained the beta weights for the remaining subjects using the enter method of multiple regression which includes all specified predictors in the model irrespective of the significance of their contribution to the model (cf. Table II). To allow a subsequent analysis of the BOLD response to preference for the most important time-related predictor-tempo, we divided the participants into two groups on the basis of the beta weights for tempo, of which one group

tended to prefer fast (positive beta weights) and the other group slow tempo (negative beta weights). Two of 18 subjects had to be excluded from classification having beta weights of zero, and thus indicating the absence of a linear preference trend towards slow or fast tempo. Thus 16 subjects could be classified with regard to their tendency to prefer slow (eight subjects) or fast tempo (eight subjects), so that attention both to preferred and not preferred tempo during the aesthetic task contained an equal amount of slow and fast tempo trials on the single-subject and the group level, respectively (cf. Table II and Fig. 2). The individual beta weights for tempo ranged from −0.01 to −0.48 in the group that preferred slow and from +0.07 to +0.46 in the group that preferred fast tempo. The same procedure was employed for instrumental preference (cf. Fig. 2). All subjects could be classified with regard to their tendency to prefer "bongo" (10 subjects) or "rock" (eight subjects), so that attention both to preferred and nonpreferred instrument contained an equal number of trials with the instrument types "bongo" and "rock" on single-

subject and approximately the same on group level, respectively. Here the individual beta weights for instrument type ranged from −0.046 to −0.854 in the group that preferred "bongo" and from +0.019 to 0.964 in the group that preferred "rock".

Furthermore, participants for whom a substantial individual case model was obtained revealed differences in linear predictability, i.e., the degree to which individual judgments captured using a linear equation differed between participants. Multiple R's ranged from 0.25 to 0.96, i.e., a range of explained judgmental variance from 6 to 92%. Differences in explained variance are typically interpreted as an index of strategy use [Steward, 1988]. Participants with a higher linear predictability, i.e., stronger linear relationships, used systematic judgment strategies, while linearly unpredictable judges most likely employed highly configural cue combinations, i.e., particular configurations of combinations of stimulus features [Brehmer and Joyce, 1988; Cooksey, 1996].

Finally, because tempo was an important cue for the aesthetic judgment, it was crucial to rule out on the behavioral level that the aesthetic judgment can be explained by explicit tempo judgments (i.e., "fast, therefore beautiful" or "fast, therefore not beautiful" depending on the preferences, respectively). A one-tailed correlation between the beta weights for preferred tempo, which indicated how much there was a tendency to prefer fast (positive value) or slow tempo (negative value), and the percentage of accurate classification of fast and slow tempo, respectively, did not reveal any significant relationship (beta weight for preferred tempo and correct classification of fast tempo: $r = -0.300$; $P = 0.113$; beta weight for preferred tempo and correct classification of slow tempo: $r = 0.136$; $P = 0.295$).

fMRI Results

Beautiful vs. not beautiful judgments

As hypothesized, trials presenting rhythmic stimuli that were judged as beautiful led to significantly stronger bilateral activations within inferior ventral premotor cortex, which extended into the frontal opercular cortex adjacent to the anterior insula, the so-called precentral operculum (PCO/PMv; Brodmann area (BA) 6) [Peters and Jones, 1985], and in the cerebellum (superior semilunar lobule bilaterally, left lobule simplex and left inferior semilunar lobule) (cf. Fig. 3A and Table III). In addition, we found activations in the anterior cingulate cortex (ACC; BA 24), the right superior frontal gyrus (BA 10), and the middle frontal gyrus (BA 9). Importantly, the above activity pattern was preserved when excluding six subjects who received instrumental training or attended a choir at some point in their life in addition to the regular musical education at school, indicating that these results were not driven by musical education (Supp. Info., Fig. 1A).
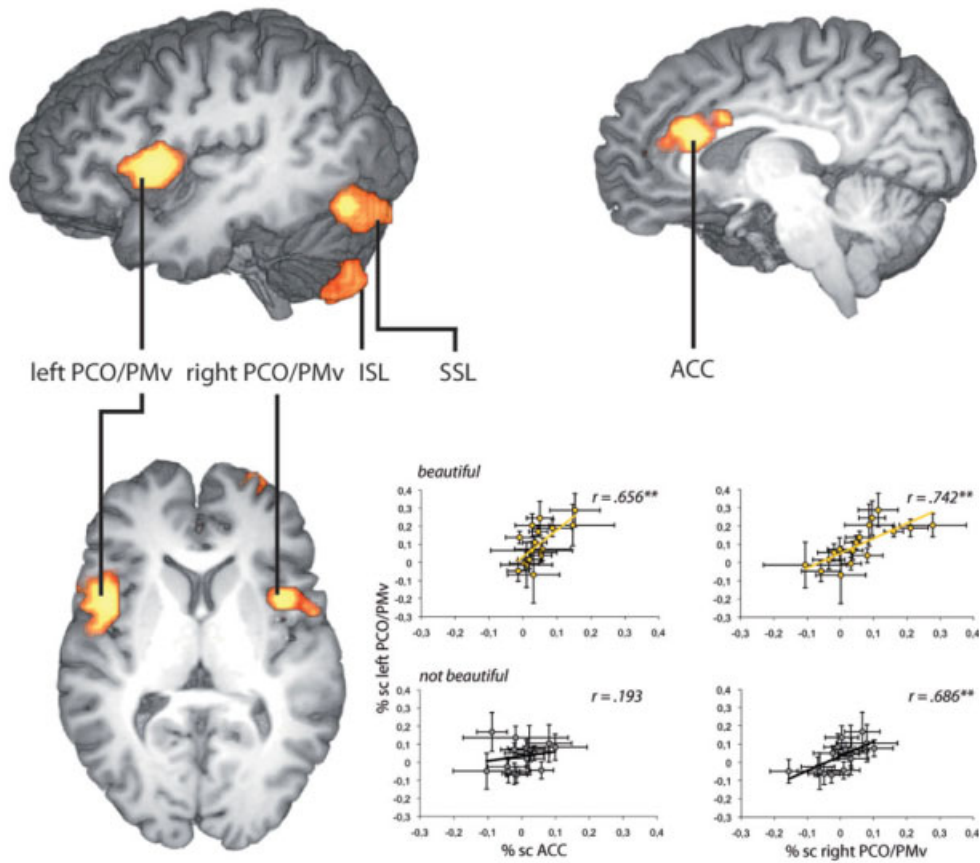
In a subsequent post-hoc analysis, we sought to identify whether there was a response-specific linear relationship between ACC and PCO/PMv, areas that are known to be related to voluntary initiation/suppression of emotional vocal utterances and control of learned vocal patterns, respectively [Jurgens, 2002; Jurgens, 2009; Jurgens and von Cramon, 1982]. To express quantitatively the relationship in activation of these regions as a function of preference, the percentage signal change was extracted from the peak voxel in the respective ROIs that were defined by the contrast beautiful vs. not beautiful in each subject. Pearson correlation coefficients were computed for ACC and left PCO/PMv, ACC and right PCO/PMv, as well as left and right PCO/PMv. ACC and left PCO/PMv correlated in trials judged as beautiful ($r = 0.656$**, $P < 0.005$), but not in trials judged as not beautiful ($r = 0.193$, $P = 0.458$), after excluding an outlier (with outlier: $r = 0.578$*, $P < 0.05$ and $r = 0.253$, $P = 0.311$). There was no correlation in either aesthetic judgment between ACC and the right PCO/PMv (beautiful: $r = 0.382$, $P = 0.131$; not beautiful: $r = 0.373$, $P = 0.141$), whereas a significant correlation between right and left PCO/PMv was preserved during both aesthetic judgments (beautiful: $r = 0.742$**, $P < 0.005$; not beautiful: $r = 0.686$**, $P < 0.005$), pointing to a functionally invariant relationship. The percent signal changes between ventral premotor and cerebellar sites (superior semilunar lobule bilaterally) did not yield any significant correlations in beautiful or in not beautiful judgments.

Preferred tempo vs. not preferred tempo

In addition to a general effect of preference for musical rhythms, we examined which of the above components could be traced back to the preference for the most important time-related property determining whether a musical rhythm was judged as beautiful or not. In accordance with previous studies that demonstrated the importance of tempo in auditory rhythms perception [Baruch and Drake, 1997; Dalla Bella et al., 2001; Drake et al., 2000; Trainor et al., 2004] and sensorimotor coupling [Chen et al., 2006; Drake et al., 2000; Fraisse, 1982; Large, 2000; Moelants, 2002; Moelants, 2003; van Noorden and Moelants, 1999], tempo was the most influential time-related property both in preceding pilot testing (cf. Supp. Info.; Table I) and in the behavioral results of the fMRI experiment (Table I). The preference for slow or fast tempo was identified in every subject by judgment analysis (cf. Methods/Judgment analysis and Results/Behavioral results for classification procedure). The contrast between attention to preferred vs. not preferred tempo during the aesthetic judgment task masked by the contrast beautiful vs. not beautiful yielded a significant activation in the left PCO/PMv only (-50, 4, 12; $Z = 2.72$; 54 mm^3). There was an interaction between TASK (aesthetic judgment/tempo judgment) and PREFERENCE (preferred tempo/not preferred tempo) in the above premotor ROI (repeated measures ANOVA; $F_{(1,15)} = 5.018$; $p < 0.05$) with a pronounced percent signal change difference between preferred and not preferred tempo only
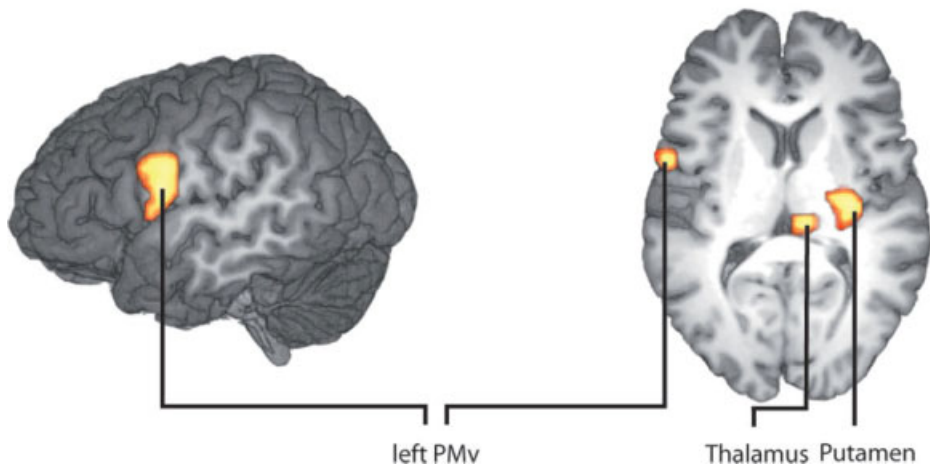
Figure 3.

Effects of rhythmical preference. (**A**) Areas elevated for rhythms judged as beautiful compared to not beautiful (beautiful vs. not beautiful rhythms in AJ; $P < 0.005$, corrected). Scatter diagrams indicate correlations of percentage signal changes in left PCO/ PMv and ACC, as well as left and right PCO/PMv during beautiful and not beautiful judgments, respectively. Each data point represents the mean and standard error of the percent signal change for each subject and location. (**B**) Areas elevated for preferred tempo vs. not preferred tempo ($P < 0.01$, corrected). The overlap between the contrast beautiful vs. not beautiful and preferred tempo vs. not preferred tempo during the aesthetic judgment task revealed a significant activation in the left PCO/ PMv (-50, 4, 12, $Z = 2.72$; 54 mm^3). ACC = anterior cingulate cortex; ISL = inferior semilunar lobule; PCO = precentral operculum; PMv = ventral premotor cortex; SSL = superior semilunar lobule.

TABLE III. Anatomical specification, hemisphere (R, right; L, left), Talairach coordinates (x, y, z), volume (mm^3) and maximal Z scores (Z) of significant activations in the direct contrasts

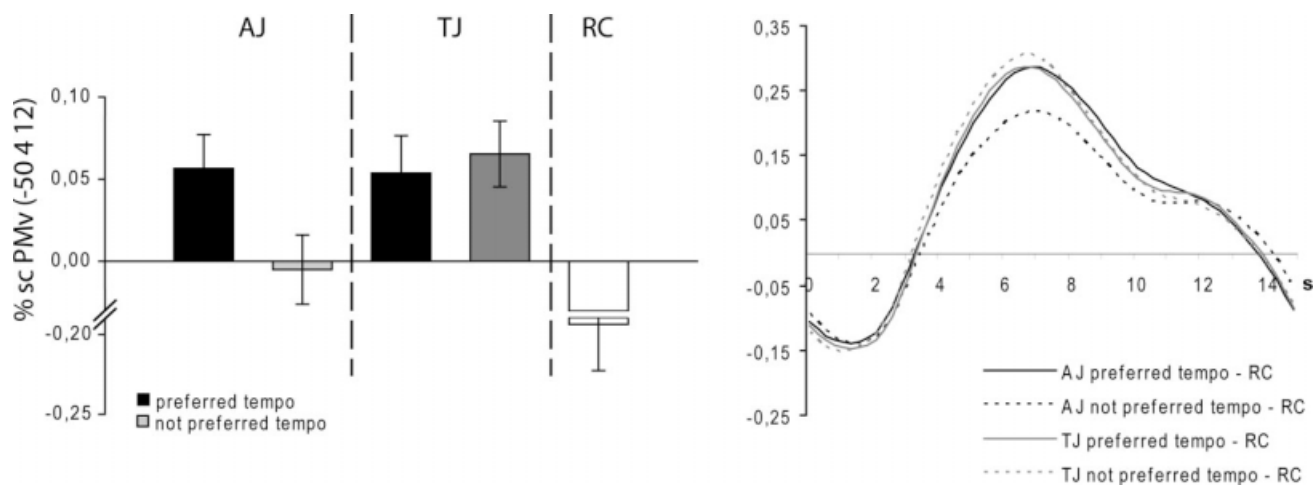| Area	Brodmann area	Hemisphere	Talairach coordinates x	y	z	mm^3	Z
Beautiful vs. not beautiful rhythms							
Predicted areas							
Precentral operculum/inferior ventral premotor cortex (PCO/PMv)	BA 6	L	−41	4	9	4,158	3.82
		R	37	7	12	1,782	3.53
Cerebellum, superior semilunar lobule (Crus I)		L	−29	−80	−12	7,101	4.61
		R	40	−62	−12	4,482	3.65
Cerebellum, lobule simplex (lobule VI)		L	−23	−65	−21	l.m.	3.63
Cerebellum, inferior semilunar lobule (Crus II)		L	−35	−74	−42	1,080	3.61
Not predicted areas							
Anterior cingulate cortex (ACC)	BA 24	R	4	19	21	3,888	4.38
Superior frontal gyrus	BA 10	R	22	58	0	945	3.83
Middle frontal gyrus	BA 9	R	22	37	21	1,026	3.54
Preferred tempo vs. not preferred tempo (AJ)							
Predicted areas:							
Lateral ventral premotor cortex (PMv)	BA 6	L	−53	1	24	1,431	3.82
Putamen		R	28	−17	12	2,943	3.67
Not predicted area:							
Thalamus, pulvinar		R	7	−26	12	l.m.	3.39
Aesthetic judgment (AJ) vs. tempo judgment (TJ)							
Antero-medial frontal gyrus	BA 9	L	−5	55	27	9,639	3.55
	BA 9/32	R	−2	43	21	l.m.	3.51
	BA 10	R	13	52	9	l.m.	3.36
Anterior ventral insula		L	−32	16	−3	4,455	4.19
Inferior frontal gyrus	BA 47		−32	31	−12	l.m.	3.64
Midbrain		L	−14	−23	−12	l.m.	3.42
Pons		R	−2	−32	−21	1,026	3.6

Figure 4.

Effects of tempo preference on premotor activity: Percent signal change (% sc) for musical rhythms with preferred and not preferred tempo during the aesthetic (AJ) and tempo judgment (TJ) conditions, as well as % sc during the resting condition (RC) in the ventral premotor ROI (−50, 4, 12; identified by the overlap between the contrast preferred vs. not preferred tempo during the aesthetic judgment task and the contrast beautiful vs. not beautiful). In the timeline chart, the onset corresponds to the onset of the respective stimulus and the % sc during the AJ and TJ conditions is depicted relative to the % sc of the RC.
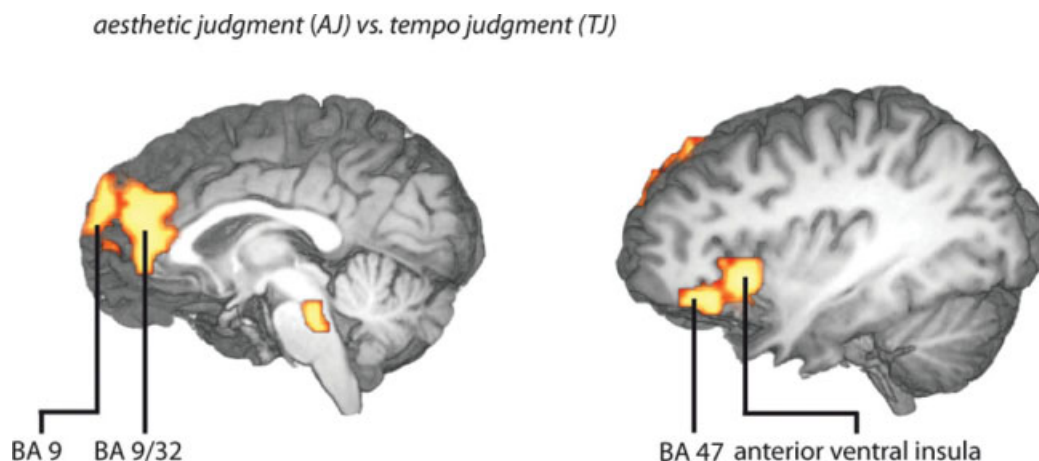
aesthetic judgment (AJ) vs. tempo judgment (TJ)

Figure 5.
Significantly activated areas for aesthetic as opposed to tempo judgments ($P < 0.005$, corrected).

during the aesthetic, but not the tempo judgment task (see Fig. 4]. In line with this finding, a conjunction analysis revealed a common activation of the left PMv ($-53, 2, 15$; $Z = 3.72$; 1,026 mm³) both during the tempo task vs. rest and preferred vs. not preferred tempo in the aesthetic judgment task.

Besides the ventral premotor overlap between the contrasts preferred vs. not preferred tempo during the aesthetic judgment task and beautiful vs. not beautiful, musical rhythms with preferred tempo during the aesthetic judgment task elevated activity in the lateral and superior part of the left ventral premotor cortex (PMv; BA 6), as well as the putamen and the pulvinar nucleus of the thalamus (Fig. 3B and Table III). As in the valence analysis (beautiful vs. not beautiful judgments), the above activity pattern was preserved when excluding five subjects who received instrumental training or attended a choir at some point in their life in addition to the regular musical education at school (Supp. Info.; Fig. 1B). Moreover, individual percent signal change data revealed that in the PMv, the hemodynamic signal increase when listening to musical rhythms with a preferred tempo was not driven by musical training ($r = -0.08$; $P = 0.384$; one-tailed), but rather by how strongly a subject preferred a tempo ($r = 0.626$; $P < 0.01$; one-tailed), as expected from the categorization of preferred and not preferred tempo (Supp. Info. Fig. 2).

Preferred instrument vs. not preferred instrument

To determine whether the activation of the left PCO/PMv was related to tempo preference and not to instrumental preference, we examined whether instrumental preference was accompanied by activity in this area. The preference for instrument type was identified in every subject by judgment analysis (cf. Methods/Judgment analysis and Results/Behavioral results for classification proce-

dure). The contrast between attention to preferred vs. not preferred instrument during the aesthetic judgment task masked by the contrast beautiful vs. not beautiful did not yield significant activation in the left PCO/PMv, but extended cerebellar activations, particularly in the superior semilunar lobule bilaterally ($-32, -77, -9$; $Z = 2.95$; 594 mm³; and $28, -71, -12$; $Z = 3.48$; 1,782 mm³).

Aesthetic judgment vs. tempo judgment

As tempo was the most important time-related cue for aesthetic judgments, one might argue that aesthetic judgments of rhythms simply amount to explicit tempo judgments (i.e., "slow, therefore beautiful" or "slow, therefore not beautiful," respectively), which would mean that subjects bypassed the instruction to deliver an evaluative judgment. Therefore, we computed a direct contrast between preference and tempo judgment tasks. Significant cortical activity differences were observed in the anterior ventral insula, the antero-medial frontal gyrus (BA 9, BA 9/32, and BA 10) and the inferior frontal gyrus (BA 47) (Fig. 5 and Table III). There was no significant activation for the reverse contrast (tempo vs. aesthetic judgment).

DISCUSSION

In this study, we used fMRI to investigate how aesthetic appreciation of musical rhythms modulates activity in motor-related areas. As expected, the results demonstrate that attention to preferred musical rhythms correlated with activity increase in a network of motor-related areas. In particular, musical rhythms judged as beautiful compared to not beautiful enhanced the BOLD response bilaterally in the precentral operculum/ventral premotor cortex (PCO/PMv; BA 6) and in the cerebellum.

Moreover, the results show that preference-associated effects in the motor areas induced by musical stimuli [Blood and Zatorre, 2001; Koelsch et al., 2006] emerge even when musical appraisal is reduced to that of tempo (beat frequency) alone, i.e. to a time-related feature that provides a pulse people tune in to when listening to music [Chen et al., 2006; Drake et al., 2000; Fraisse, 1982; Large, 2000; Moelants, 2002, 2003; van Noorden and Moelants, 1999]. Activity in the PMv increased not only during attention to musical rhythms judged as beautiful, but, more specifically, also during attention to rhythms with a preferred tempo. These findings extend research on auditory and visual timing, showing that the motor system is not only engaged during attention to rhythm in general [Bengtsson et al., 2009; Chen et al., 2008; Coull et al., 2004; Grahn and Brett, 2007; Schubotz et al., 2000, 2003; Wolfensteller et al., 2007], but more specifically, that it is more engaged for preferred rhythm.

Because subjects were asked to deliver an aesthetic (or, more generally, an evaluative) judgment, it was important to examine in more detail how they behaved under this instruction. To this end, we employed two controls: first, we sought to rule out that aesthetic judgments of rhythms simply amount to explicit tempo judgments. In that case, subjects would have bypassed the instruction to deliver an evaluative judgment. However, the absence of significant correlations between tempo preference and performance on the tempo judgment task is in line with the assumption of independent behavioral mechanisms underlying these tasks. Importantly, the significant hemodynamic differences between aesthetic appraisal of rhythm and temporal judgments demonstrated that the subjects engaged in an evaluative in contrast to a tempo identification task: The antero-medial and inferior frontal activations directly replicated the findings of a study on aesthetic judgments of abstract visual patterns [Jacobsen et al., 2006]. Second, a judgment analysis allowed us to examine the strategies underlying these evaluative judgments. We analyzed the systematic influence of the different constituents of the musical rhythms on the subjects' aesthetic judgments on the basis of individual case models [Brehmer and Joyce, 1988; Cooksey, 1996; Jacobsen, 2004; Jacobsen et al., 2006] and determined each subject's preferences for the two most influential constituents ruling individual aesthetic judgments of the musical rhythms—instrument type (either "bongo" or "rock") and tempo (either fast or slow). This enabled us to dissociate the influence of tempo and instrumental preference on activity enhancement in motor-related areas elevated by rhythms judged as beautiful. Hence, we could decompose the network identified for beautiful as compared to not beautiful rhythms, revealing one component related to tempo preference (PCO/PMv) and the other related to instrumental preference (cerebellum).

The PMv activated during preferred rhythms and tempo and its adjacent areas, the inferior frontal gyrus and the Rolandic operculum, have been shown to be involved in voice-related tasks, such as singing [Ozdemir et al., 2006; Perry et al., 1999] and speech [Wildgruber et al., 1996], as well as singing imagery [Kleber et al., 2007; Riecker et al., 2000] and speech imagery [Rauschecker et al., 2008; Shergill et al., 2006]. The premotor activation we found most likely overlaps with the precentral area crucial for the control of learned vocal patterns, e.g. in speech and song. When this region is electrically stimulated, movements of the vocal chords are triggered in human and non-human primates [Jurgens, 2002; Penfield and Rasmussen, 1952]. Furthermore, if it is damaged bilaterally in humans, singing and speaking is no longer possible [Groswasser et al., 1988]. In squirrel monkeys, it has been shown to be a part of the motorcortical pathway, which controls the patterning of learned vocal utterances via the reticular formation [Jurgens, 2009]. The activation of a vocalization-related premotor area supports our hypothesis based on the notion of a correspondence of movement execution or imagery and attention to external events in the premotor cortex [Schubotz and von Cramon, 2003; Wolfensteller et al., 2007]. Following the account of the "Habitual Pragmatic Event Map" [Schubotz, 2007], which proposes a generic framework for the neural overlap of motor and nonmotor cognitive functions, activity in the premotor cortex is structured according to the modes of transformations such as rotation, deformation, or acceleration, which self-induced as well as observed events can undergo. More specifically, the inferior ventral premotor region has been associated with attention to event change affected by ac-/deceleration [Schubotz and von Cramon, 2001a; Schubotz et al., 2003; Thaut, 2003; Wolfensteller et al., 2007] and pitch rising/falling [Brown and Martinez, 2007; Meyer et al., 2004; Schubotz and von Cramon, 2002]. These changes are at the heart of both vocalization and articulation. Similarly, external temporal events such as musical rhythms and especially the tempo of a musical rhythm involve changes defined by ac-/deceleration. Thus, as established for the domain of action performance, imagery, and observation, motor networks may be considered providing forward models that enable attention to change beyond the action domain [Grush, 2004; Wolpert and Flanagan, 2001].

Notably, studies have reported the enhancement of dorsal instead of ventral premotor cortex activity during timing tasks [Chen et al., 2006; Lewis et al., 2004]. However, this discrepancy may be due to differences between experimental paradigms such as the use of finger tapping in the above mentioned studies. A systematic comparison between motor and nonmotor timing paradigms would be valuable to clarify the functional contributions of the network components [Schubotz and von Cramon, 2001b].

How can the boosting effect of rhythmic preference on premotor activity be explained? The comparison of tempo preference effects on PMv activity during the aesthetic and tempo judgment tasks, as well as the premotor activity increase common to both preferred tempo and the tempo judgment task shed light on the cognitive and neural mechanisms underlying this effect. According to the framework of sensorimotor forward models [Grush, 2004;

Schubotz, 2007; Wolpert and Flanagan, 2001], to accomplish a perceptual rhythm task such as the tempo task, i.e. to judge whether a musical rhythm is fast or not, the subjects had to map the incoming external beat frequency of the musical rhythms on their audiomotor representation of a template established on the basis of previous rhythms, no matter whether it was preferred or not. The effect of preferred tempo on the percent signal change in the PMv during the aesthetic judgment task and the tempo judgment control (cf. Fig. 4) provides physiological evidence that attention to preferred tempo recruited neural recourses in the premotor cortex which have been shown to support perceptual rhythm tasks: The data pattern shows that activity during the aesthetic judgment task increased to the level of the tempo judgment task only when subjects were listening to the tempo they preferred. Accordingly, a conjunction analysis revealed that both during preferred (compared to not preferred) tempo and during the tempo judgment task (compared to rest) activity increases in the PMv. These analyses thereby corroborate the assumption that ventral premotor activity during preferred tempo is driven by enhanced sensorimotor simulation of the external beat frequency of the musical rhythms, i.e. by ccomputations also recruited during the tempo task.

Interestingly in this context, the lateral premotor cortex is discussed to compensate the functional impairment of the basal ganglia-SMA loop during voluntary movement in Parkinson's disease (PD) in the presence of *external* visual as well as auditory pacing cues [Hanakawa et al., 1999; McIntosh et al., 1997; Okuma, 2006]. In line with these findings, a study contrasting listening to tones occurring at equal time intervals, thus constituting an external beat, and not equal time intervals has demonstrated an enhanced activity in the pars opercularis of the inferior frontal gyrus, which is adjacent to the PMv [Bengtsson et al., 2009]. All musical rhythms in the present study provided such an external isochronous cue due to the continuous presence of an overt beat. This is different from studies in which the underlying beat has to be inferred from the auditory rhythmic structure (beat induction)—a process that is suggested to be subserved by the SMA and the putamen [Chen et al., 2008; Grahn and Brett, 2007] and that is impaired in patients with PD [Grahn and Brett, 2009]. Because the PMv has been shown to enable expectations of incoming auditory rhythms [Schubotz et al., 2004], we propose that enhanced activity in the PMv during preferred tempo may support accurate synchronization to an external beat and facilitate the tuning-in to the beat of music that we prefer. Thus, our findings point to a possible significance of preference in sensorimotor coupling during auditory rhythms. Future studies should assess, whether the presence of a preferred beat frequency can increase the therapeutic effect of synchronisation to an external beat on gait and speech reported in patients with PD [Baker et al., 2008; McIntosh et al., 1997; Thaut et al., 1999, 2001; van Wegen et al., 2006; Willems et al., 2007].

Can the effects reported in this study be distinguished from motor imagery of a tuning-in behavior such as head nodding, toe tapping or humming? Our findings confirm this interpretation: First, the co-activation of the PCO/PMv signal elevated for rhythms judged as beautiful with a peri-genual aspect of the ACC (BA 24), which was not predicted initially, may point to a suppression of overt tuning-in to an external rhythm during preferred rhythms, but not to a motor imagery of an internally generated rhythm. A post-hoc ROI analysis revealed that while the signal change between the left and right PCO/PMv significantly correlated both during "beautiful" and "not beautiful" judgments, indicating an, in this respect, functionally invariant connection, the signal change in ACC and the PCO/PMv significantly correlated only during musical rhythms judged as beautiful, but not during those judged as not beautiful. The ACC has been shown to control the readiness to phonate, i.e. the voluntary initiation and suppression of vocal utterances via the periaqueductal grey and the reticular formation [Jurgens, 2009; Jurgens and von Cramon, 1982; Paus, 2001]. In the reticular formation, the limbic pathway converges with the motorcortical pathway, and the output projects to phonatory motoneurons [Jurgens, 2009]. Thus, it is conceivable that the reticular formation allows the ACC to inhibit the initiation of learned vocal patterns triggered by the PCO/PMv. That is to say, the more we prefer a musical rhythm, the lower is the motor threshold due to an increase in PCO/PMv activity, and the more inhibition is provided by the ACC to suppress overt vocalization. In our case, we assume that the enhanced ventral premotor activity during preferred musical rhythms facilitates the sensorimotor transformation of the acoustic afference (rhythmic stimuli) to vocal and articulatory representations, whereas ACC performs a vocal gating function. Second, a motor imagery explanation cannot be reconciled with the absence of activation in dorsal premotor regions for neck and foot movements. And thirdly, there was no activity increase in areas characteristic for motor imagery and motor preparation such as the primary motor cortex, primary and secondary somatosensory areas, and especially the SMA/pre-SMA, an area which has been shown to be most reliably involved in *vocal* imagery [Kawashima et al., 2000; Kleber et al., 2007; Rauschecker et al., 2008; Riecker et al., 2000; Thobois et al., 2000]. Thus, it seems more consistent with the data to consider premotor involvement during preferred rhythms and tempo as an audiomotor fraction of vocal and articulatory representations that are exploited during attention to external rhythmic events. Such a fraction misses proprioceptive-motor and other sensorimotor representations that are part of motor imagery, as well as movement.

Although such an audiomotor fraction exploits a circuit that is mainly involved in vocalization, we propose that this activity boost may facilitate effector-independent tuning-in behavior including toe tapping or head nodding. It was found that the localization of attention-related activation in PM varies not as a function of the motor effector

previously assigned to the attended stimulus, but rather of the produced effects [Wolfensteller et al., 2004]. That means, with respect to PMv involvement here, it should make no difference whether a rhythm is produced by finger tapping, head nodding, foot tapping, or humming. Accordingly, Bengtsson et al. [2005] report activity enhancement in the left ventral BA6/BA44 both during rhythmic speech and during rhythmic left and right finger movement. Macaque studies have shown that there is a family of premotor neurons that is not tuned to motor effectors, but to the perceivable effect that a movement brings about. Thus, some grasping neurons are unspecific for limb and grip type, i.e., grasping a target with the right or left hand or the mouth can engage the same neuron [Rizzolatti et al., 1987]. That is, of course, not to say that other premotor neurons are not tuned to motor effectors. We therefore suggest that activity in PMv in our study reflects a facilitation of producing preferred rhythms with an arbitrary motor effector, including fingers [Chen et al., 2008; Lahav et al., 2007; Zatorre, et al., 2007].

Finally, attention to preferred tempo elicited higher activity in the right putamen. Apart from its recognized general function in timing mechanisms [Coull et al., 2004, 2008; Ferrandez et al., 2003; Nenadic et al., 2003; Rao et al., 1997, 2001], putamen activation is enhanced by the presence of a regular compared to an irregular beat. This has been shown both during an auditory rhythm discrimination task [Grahn and Brett, 2007] and during bipedal dance movements to music [Brown et al., 2006]. In music the predominance of, and thus a preference for, a regular beat or repetitive temporal patterns is a cross-cultural universal, presumably because musical rhythms have their origin in the motor rhythms controlling locomotion, breathing and heart rate [Trainor, 2008]. Because all the musical rhythms in this experiment had a regular beat, our results suggest that putamen activation can be modulated not only by beat regularity, but also by the preference for a beat frequency (tempo).

Using fMRI we cannot resolve the issue of causality, i.e. whether activation of the PMv is a function of the extent of the preference for a rhythm that we listen to or whether preference emerges as a function of the extent to which rhythms cause activity in the PMv. This should be addressed by future transcranial magnetic stimulation studies. If rhythmical preference is driven by PMv activity, rhythmical preferences should break down or vanish by inhibitory PMv stimulation; if, however, PMv activity is just an effect of rhythmical preference, rhythmical preferences should be preserved even in the presence of inhibitory PMv stimulation.

CONCLUSION

This study demonstrates that the aesthetic appreciation of musical rhythms is accompanied by activity increase in parts of the motor system and thus lend support to the assumption that the motor-system-based internal simulation of rhythms can be enhanced by preference. Our findings point to a link between activity increase in the ventral premotor cortex during rhythms with a preferred tempo (beat frequency) and the tuning-in to the beat of music that we enjoy.

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