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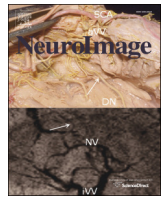


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Getting the beat: Entrainment of brain activity by musical rhythm and pleasantness

Wiebke Trost^{a,b,*}, Sascha Frühholz^{a,b}, Daniele Schön^c, Carolina Labbé^{a,b}, Swann Pichon^{a,d},
Didier Grandjean^{a,b}, Patrik Vuilleumier^{a,e}

^a Swiss Center of Affective Sciences, University of Geneva, Switzerland

^b Neuroscience of emotions and affective dynamics laboratory, University of Geneva, Switzerland

^c Aix-Marseille-University, France

^d Bavelier Lab, University of Geneva, Switzerland

^e Laboratory for Behavioral Neurology and Imaging of Cognition, University of Geneva, Switzerland

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ABSTRACT

Rhythmic entrainment is an important component of emotion induction by music, but brain circuits recruited during spontaneous entrainment of attention by music and the influence of the subjective emotional feelings evoked by music remain still largely unresolved. In this study we used fMRI to test whether the metric structure of music entrains brain activity and how music pleasantness influences such entrainment. Participants listened to piano music while performing a speeded visuomotor detection task in which targets appeared time-locked to either strong or weak beats. Each musical piece was presented in both a consonant/pleasant and dissonant/unpleasant version. Consonant music facilitated target detection and targets presented synchronously with strong beats were detected faster. fMRI showed increased activation of bilateral caudate nucleus when responding on strong beats, whereas consonance enhanced activity in attentional networks. Meter and consonance selectively interacted in the caudate nucleus, with greater meter effects during dissonant than consonant music. These results reveal that the basal ganglia, involved both in emotion and rhythm processing, critically contribute to rhythmic entrainment of subcortical brain circuits by music.

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Introduction

Rhythmic entrainment is a very common phenomenon: Who has not been caught with the foot tapping or the body moving to the music heard in the background? In the present study we directly ask the question how musical rhythm makes our brain act in synchrony with the music, and whether this effect depends on subjective pleasantness or not. To study the nature of rhythmic entrainment and its neural underpinnings, we engaged participants in a functional magnetic resonance imaging (fMRI) paradigm while they performed a visuomotor attentional task in which targets appeared either in or out of synchrony with the music, and manipulated musical pleasantness by using either consonant or dissonant music.

The term entrainment describes a physical principle “whereby two rhythmic processes interact with each other in such a way that they adjust towards and eventually ‘lock in’ to a common phase and/or periodicity” (Clayton et al., 2005, p. 5). The synchronization

of bodily rhythms with music entails entrainment phenomena at different levels of the organism, which can take place at the motor level, the autonomic physiological level, the attentional level, and even the social level (Trost and Vuilleumier, 2013).

In this study we will focus on entrainment operating on attentional processes engaged during a visuomotor target detection task. Previous research on entrainment with EEG recordings showed that neuronal activity may synchronize to an external periodic signal (Nozaradan et al., 2011). Moreover, most music is based on a precise temporal structure, i.e., meter, which creates the perception of a repetitive beat. It has been suggested that the discernment of musical beats emerges from the entrainment of neuronal populations that resonate at the frequency of the musical beats (Jones, 1987; Large and Kolen, 1994; Large, 2008). Entrainment processes also operate on higher order harmonics of the beat frequency and lead to the perception of a distinctive hierarchy between individual beats. This hierarchy is thought to determine the perceived metrical structure of the music. Dynamic attending theory (DAT) further proposes that the perception of meter is an emergent process resulting from the time-locking of attentional cycles onto rhythmic events via music-neural coupling (Jones and Boltz, 1989). Thus, meter perception might reflect an ability to dynamically orient attention in time.

Abbreviations: fMRI, functional magnetic resonance imaging.

* Corresponding author at: Swiss Center of Affective Sciences, Biotech Campus, University of Geneva, 9, chemin des Mines, 1202 Geneva, Switzerland.

E-mail address: Johanna.trost@unige.ch (W. Trost).

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In keeping with this view, it has been shown that temporal expectancies can engender cross-modal integrative effects on attentional resources (Lange and Roder, 2006). This implies that if attention is enhanced at a specific moment in time, stimulus processing can be facilitated for all sensory modalities, independently of the task-relevant modality (Teder-Salejarvi et al., 2002). Accordingly, behavioral findings suggest that entrainment induced by an auditory rhythm can influence visual attention (Escoffier et al., 2010) and that listening to classical music can entrain attentional resources in synchrony with the musical meter (Bolger et al., 2013; Tierney and Kraus, 2013).

In addition, it has been suggested that entrainment may constitute a key source of emotions experienced during music listening (Janata et al., 2012; Witek et al., 2014). According to a recent psychological framework proposed by Juslin and colleagues (Juslin et al., 2010), different bodily rhythms may synchronize to those present in the music, consequently generating emotional feelings via proprioceptive feedback mechanisms. However, this framework does not specify which synchronization level is particularly critical, or whether the same principle applies to different levels of the system, including not only bodily and physiological rhythms but also higher cognitive processes such as attention. Moreover, few studies have investigated the neural mechanisms linking musical rhythms with entrainment and emotion. Recent work using transcranial magnetic stimulation (TMS) reported that corticospinal excitability is increased during metrically strong rhythmical sequences (Cameron et al., 2012) or high-groove music (Stupacher et al., 2013). However, an ideal candidate brain substrate for mediating such links might lie in the basal ganglia, as these structures are implicated in motor control (Jueptner and Weiller, 1998; Turner and Desmurget, 2010), rhythm processing (Grahn and Brett, 2007; Thaut et al., 2008), as well as pleasant emotional experiences (Salimpoor et al., 2011; Trost et al., 2012). The basal ganglia might therefore be well placed for integrating rhythmical information with both cognitive and affective components of musical experience. On the other hand, cross-modal influences on attention and its deployment over time are known to recruit cortical areas in posterior parietal lobule (Coull and Nobre, 1998; Macaluso and Driver, 2001), including for synchronization of motor responses with auditory (non-musical) sequences (Bolger et al., 2014). Therefore, parietal attention systems might also contribute to the effect musical rhythm has on attention and entrainment.

Here, we directly tested how musical meter engenders cross-modal entrainment of visuomotor processes, by obtaining both behavioral and fMRI measures in human volunteers. We also investigated whether entrainment would interact with the affective appreciation of the music, and thus be enhanced by its pleasantness. Based on previous research (Bolger et al., 2013), we expected that an attentional entrainment of visuomotor performance by concomitant music should make response times faster to visual targets appearing simultaneously with strong beats of the musical meter, as compared with targets appearing on weak beats.

In addition, we also tested the *affective entrainment hypothesis*, according to which there is a link between rhythmic entrainment processes and emotion induction via music (Juslin et al., 2010; Trost and Vuilleumier, 2013). Previous research already suggested that entrainment in terms of sensorimotor synchronization may enhance subjective experience of pleasantness even in non-musical conditions (Fairhurst et al., 2012; Janata et al., 2012). Furthermore, motor or attentional entrainment appears directly linked to musical pleasantness, as rhythmical patterns of a certain complexity range are rated as more pleasant and evoke stronger feelings of groove (Witek et al., 2014). Here, however, we aimed at testing the affective entrainment hypothesis in a reverse causal direction, by determining whether (and how) positive affect elicited by pleasant music would enhance the rhythmic entrainment of attentional processes. Specifically, we examined whether the pleasantness of music would produce a stronger entrainment of visuomotor performance, by comparing such effects during consonant (pleasant) and dissonant (unpleasant) music (Koelsch et al., 2006). On the one hand, due to greater enjoyment of the

music, consonant harmony might be expected to increase entrainment and thus interact with the perception of the metrical structure. On the other hand, in presence of consonant music with intact harmony, rhythm processing might focus at a different time scale, such that temporal expectations induced by pleasant consonant music would produce different or additive effects on entrainment. At the brain level, given their dual role in emotion processing and rhythm perception, we hypothesized that subcortical mechanisms in the basal ganglia might be involved in entrainment to music beat, but also responsible for any interaction between rhythm and pleasantness. On the contrary, parietal and interconnected cortical areas should be implicated if these effects depend on temporal cross-modal attention processes.

Materials and methods

Subjects

One group of 20 volunteers (13 females, mean age 25.8 years, $SD \pm 7.5$) was tested only behaviorally in a first study. Subsequently, another group of 18 volunteers (11 females, mean age 24.1 years, $SD \pm 4.4$) took part in the fMRI experiment, none of whom participated in the behavioral study. Participants self-reported normal hearing, stated to enjoy classical music, and had a minimum of 5 years of practical musical training. None of the participants were professional musicians. None had a history of neurological or psychiatric disease. Participants in the fMRI experiment were all right-handed, while 4 of those in the behavioral experiment were left-handed. They gave informed consent in accord with the regulation of the local ethics committee.

Stimuli

Ten pieces of piano music with a binary metrical structure (i.e. with an even number of beats per measure, here either 2/4 or 4/4 time signatures) were chosen from the music literature, taking into account their potential entraining power, rhythmic stability, and continuous polyphony (see stimulus list in Table S1). The pieces were played by a professional pianist on an electric MIDI piano (Yamaha, Clavinova) and recorded using GarageBand on a MacBookPro. The recordings were edited in LogicPro. After quantizing the MIDI files, a dissonant version was created for all ten pieces. To create a dissonant version, the pitch of the highest voice was shifted one semitone up and the pitch of the lowest voice was shifted one semitone down. Both the consonant and the dissonant versions were then exported as wav-files (mono, 16 bits, 44100Hz) using a built-in acoustic piano sound (Yamaha room) from LogicPro. The wav files were cut to the length of 90 s and normalized to scale the intensity level of all stimuli to 70 dB.

Attentional task

While listening to the musical epochs (each 90 s long), participants had to perform a visual speeded manual response task. The task required detecting a visual target (a circle) which appeared from time to time around the fixation cross in the middle of the screen (see Fig. 1A). The circle was displayed for 100 ms and participants had to indicate as rapidly as possible the appearance of the target by pressing a button with the index finger of the right hand. The visual targets were presented simultaneously with the music. Critically, however, our manipulated independent variable was the metrical position of the visual target presentation relative to the music heard in the background. Targets could appear at two different temporal positions: on the first beat of the metrical unit or on the second beat. According to DAT (Jones and Boltz, 1989), the first beat of the metrical unit represents a *strong beat* with high attentional level, whereas the second beat of a four beat measure is a *weak beat* with relatively low attentional level. To take into account differences in attentional levels which are naturally

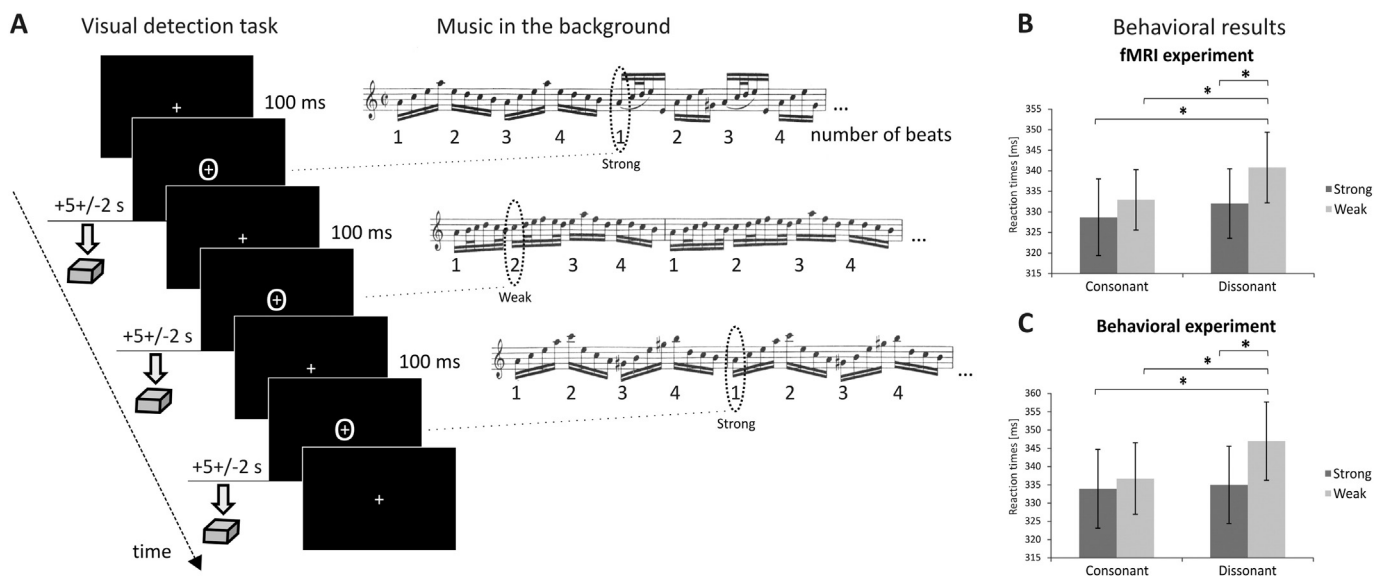


Fig. 1. A) Experimental design. Participants have to detect visual targets which are presented time-locked to the meter of the music played in the background, either on the first or the second beat. B) Behavioral reaction time results for participants in the fMRI experiment ($n = 18$). C) Behavioral reaction time results for participants in the behavioral experiment ($n = 20$). * indicates significant post-hoc tests (Tukey) between the conditions. Error bars indicate standard error.

200 created by temporal expectancies of the visual stimuli themselves, we
 201 generated a distribution of inter-trial-intervals (ITI; i.e. time between
 202 two consecutive visual targets) with a few long and many short intervals
 203 (max 7 s, min 3; non-aging distribution). Thus, on average, a visual
 204 target was presented every 5.02 s. The presentation of the first target
 205 during a musical piece occurred always 3 s after the music onset (and
 206 was always discarded from subsequent analyses), while the following
 207 ITIs were calculated with this first target as a starting point. In each musical
 208 epoch, 17 visual targets were presented in total (8 for each meter
 209 condition, plus the first discarded). The distribution of ITIs was
 210 counterbalanced between the two meter conditions. For the consonant
 211 and the dissonant versions, the same visual target distribution was
 212 always used for one participant. For each visual target distribution, we
 213 checked that there was no significant difference in sound intensity
 214 (root-mean-square, RMS) between the two meter conditions (i.e., at
 215 the time of the strong vs weak beats). The MIDIttoolbox (Errola and
 216 Toiviainen, 2004) was used to identify the timing of the first and second
 217 beats in the MIDI files, while the MIRtoolbox (Lartillot and Toiviainen,
 218 2007) was used to extract the RMS from the wav-files at the corresponding
 219 positions. Consequently a Wilcoxon rank sum test was performed to
 220 determine, for a given piece, if the RMS in a time window from 100 ms
 221 before to 200 ms after the beat onset would be different between the
 222 two meter conditions. A given temporal distribution of visual targets
 223 was only accepted and used in the experiment if the RMS values did not
 224 significantly differ during the strong and weak beats (Wilcoxon rank sum
 225 test, p -value > 0.5). Five different target onset distributions were
 226 thus obtained and alternated between subjects.

227 Experimental design

228 We first performed a behavioral study in order to validate our exper-
 229 imental design, and to ensure that similar results would be obtained in
 230 the fMRI setting as compared with more comfortable listening condi-
 231 tions. The same protocol was then given to a second group during fMRI.

232 Before the experiment, participants were instructed and familiarized
 233 with the task. The instructions emphasized that they should listen
 234 attentively to the music, while performing the speeded response task as fast
 235 and accurately as possible. The fMRI experiment included 2 scanning
 236 runs which were interleaved with the acquisition of the structural MRI
 237 scan. Each run contained 10 pseudo-randomized musical epochs. Before
 238 each trial, participants were reminded by written instructions to listen

239 attentively to the music, to fixate the fixation cross, and to press a button
 240 with the index finger as fast as possible when a circle appeared around
 241 the fixation cross. Immediately after the musical piece ended, six ques-
 242 tions were presented (one after the other) on a different screen back-
 243 ground and probed for the participants' subjective evaluation of the
 244 preceding piece. These questions were evaluations of the subjectively
 245 felt emotions (level of arousal and valence), the subjective impression of
 246 felt entrainment (formulated as the urge to move or dance to the
 247 music), and familiarity with the musical stimulus. The evaluations were
 248 designed as statements to which the participants could agree or disagree
 249 to different degree. The answers were indicated by using a sliding cursor
 250 that could be moved (by right or left key presses) on a horizontal scale
 251 from -3 to $+3$ ($-3 =$ (I agree) not at all, $+3 =$ (I agree) absolutely).
 252 The order of questions was constant for all participants. Subjects were
 253 instructed to answer spontaneously, but there was no time limit for res-
 254 sponses. The last response to the questionnaire automatically triggered
 255 the next musical stimulus presentation. Therefore, the overall scanning
 256 time of a session varied slightly between subjects (average 573 scans
 257 per run, standard deviation 27 scans). However, only the scans during
 258 the musical epochs were included in the analyses, which comprised the
 259 same amount of scans across subjects.

260 In the fMRI experiment, auditory stimuli were presented binaurally
 261 with an audio system and MRI compatible headphones (CONFON
 262 DAP-center mkII and CONFON HP-Pi-US, MR confon GmbH, Germany).
 263 The loudness of the music was adjusted for each participant individually,
 264 prior to fMRI scanning. Visual instructions were seen on a screen back-
 265 projected on a headcoil-mounted mirror. Responses were recorded with
 266 a response button box (HH-1 \times 4-CR, Current Designs Inc., USA). The be-
 267 havioral study was conducted exactly in the same manner, using the
 268 same task and musical stimuli as in the fMRI experiment, but took place
 269 in a quiet, dimly lit room.

270 Data acquisition and analysis

271 For the analysis of behavioral performance, reaction times (RTs) 271
 272 were averaged for each of the experimental conditions, after excluding
 273 trials where the RT was more than twice the standard deviation away
 274 from the mean of each participant. Repeated-measure ANOVAs were
 275 performed on the reaction times with the two factors meter (strong ver-
 276 sus weak beat) and *consonance* (consonant versus dissonant version).
 277 The answers of the questionnaire were analyzed with two-sample 277

dependent t-tests, comparing the two levels of consonance for every question individually. Statistical analyses of the behavioral data were performed using Statistica, version 12 (Statistica, StatSoft).

MRI images were acquired using a 3 T whole body MRI scanner (Trio TIM, Siemens, Germany) with the product 12 channel head coil. A high-resolution T1-weighted structural image ($0.9 \times 0.9 \times 0.9 \text{ mm}^3$) was obtained using a magnetization-prepared rapid acquisition gradient echo sequence (time repetition [TR] = 1.9 s, time echo [TE] = 2.32 ms, time to inversion [TI] = 900 ms). Functional images were obtained using a continuous-sound echo planar imaging (EPI) sequence (Seifritz et al., 2006) with the following parameters: 36 slices, slice thickness 3.2 mm, TR = 1.98 s, TE = 27.31 ms, field of view = $220 \times 220 \text{ mm}^2$, 128×128 matrix, flip angle: 80° . fMRI data were analyzed using Statistical Parametric Mapping (SPM8; Wellcome Trust Center for Imaging, London, UK; <http://www.fil.ion.ucl.ac.uk/spm>). Data processing included realignment, unwarping, slice timing, normalization to the Montreal Neurological Institute space using an EPI template (resampling voxel size: $2 \times 2 \times 2 \text{ mm}$), spatial smoothing (8 mm full-width at half-maximum Gaussian Filter), and high-pass filtering (1/128 Hz cutoff frequency).

A standard statistical analysis was performed using the general linear model implemented in SPM8. Consonant and dissonant musical epochs were modeled by two separate boxcar regressors, in addition to four event regressors modeling the onsets of visual targets in the four experimental conditions. To account for movement-related variance, we entered realignment parameters into the same model as 6 additional covariates of no interest. For the event-related analyses, we computed (at the first-level) the parameter estimates corresponding to the event-related regressors for the four target onset conditions in a design matrix that also modeled the overall state differences associated with consonant and dissonant music epochs, allowing us to covary out these sustained changes from the modulation of phasic responses to targets. The parameter estimates for each target conditions were subsequently entered for the second-level group analysis (random-effects) using a factorial design ANOVA with the factors *meter* and *consonance* and 2 levels each. For all results, we report clusters with a voxel-wise threshold of $p < 0.001$ (uncorrected) and cluster-size > 3 .

Results

Behavioral results

A 2×2 repeated-measures ANOVA with the factors meter and consonance on reaction times of participants from the behavioral experiment revealed significant main effects for the two factors, meter ($F(1,19) = 10.37$, $p < 0.005$) and consonance ($F(1,19) = 7.33$, $p < 0.014$). RTs to visual targets were faster when presented on a strong (1st) relative to a weak (2nd) beat, and faster during consonant than dissonant music, a pattern compatible with an influence of both meter and pleasantness on visuomotor processing. The interaction between the two factors was also significant ($p < 0.024$). The same analysis on the reaction times from participants in the fMRI experiment also showed significant main effects for both meter ($F(1,17) = 11.50$, $p < 0.004$) and consonance ($F(1,17) = 11.31$, $p = 0.015$), with a similar facilitation pattern in RTs. The interaction between the two factors was not significant ($F(1,17) = 1.65$, $p = 0.216$). However, a similar ANOVA on data from all participants, combining the behavioral and fMRI experiments together, with the additional categorical variable *group*, did not only confirm the main effects of meter ($F(1,36) = 21.08$, $p < 0.0001$) and consonance ($F(1,36) = 17.24$, $p < 0.0002$), but also revealed a significant interaction between these two factors ($F(1,36) = 7.07$, $p < 0.012$; Figs. 1B and C). There were no interactions of meter or consonance with the factor *group*, indicating that both groups showed a very similar pattern of reaction times despite the lack of significant meter \times consonance in the behavioral experiment. These results therefore accord with our predictions, namely, that response facilitation by rhythmic entrainment should occur on strong beats (relative to the weak beat) regardless of

consonance, and that consonance may however modulate the perception of meter. Furthermore, as predicted, the strongest entrainment occurred for visual targets synchronized with a strong beat during pleasant music, whereas the least entrainment occurred for visual targets synchronized with a weak beat during unpleasant music (see Figs. 1B and C).

The analyses of answers to the questionnaire showed that consonant pieces were evaluated as more pleasant, more arousing, more entraining, more familiar, or more natural than the dissonant versions (see Table 1).

fMRI results

Effect of consonant music

We first compared the general effect of consonant and dissonant music epochs (t-test contrast), reflecting sustained modulation of brain activity during the whole duration of musical pieces. To this aim, we compared activations modeled by the boxcar regressors for consonant and for dissonant music pieces in the first-level analysis, in which the transient changes due to target processing were covaried out by separate event-related regressors. Consonant relative to dissonant music produced higher activations not only in the right ventral caudate nucleus, a region of basal ganglia at the interface of affective and cognitive processes, but also in somatosensory and primary motor cortices (Table 2, Fig. 2). The opposite contrast did not show any significant voxels above threshold. However, our main analysis and predictions concerned event-related responses to visual targets appearing in different music conditions, as detailed below.

Effect of consonance on visual detection

Using an ANOVA for the event-related analyses of responses to visual targets, we first performed a whole-brain SPM contrast to identify any differential activation evoked during consonant versus dissonant music (regardless of synchronization with strong or weak beats). Significant increases were observed in premotor cortex, superior parietal lobule, and anterior cingulate cortex (see Table 2, Fig. S1). This suggests that consonant music modulated the brain response to visual targets by enhancing cortical networks associated with attention and motor preparation. The opposite contrast comparing visual targets presented during dissonant versus consonant music showed significant voxels in bilateral superior occipital gyri (Table 2), suggesting that visual perceptual processes were more solicited when music was dissonant.

Main effect of meter on visual detection

The next, most crucial comparison concerned visual targets presented during strong versus weak beats in the music (regardless of consonance). This contrast revealed significant activations in bilateral caudate nuclei and the right precuneus (Table 3, Fig. 3A), converging with our predictions that parts of the basal ganglia should be critically involved in rhythmic entrainment. The opposite contrasts of weak versus strong beats did not reveal any significant clusters. When further

Table 1
Behavioral evaluations of the consonant and dissonant versions of the musical pieces.

Question	Consonance		Dissonance		p
	Mean (SD)	Mean (SD)	t(37)	p	
Valence	5.29 (0.12)	3.39 (0.16)	9.80	<.0001	t1.5
Listen again	4.91 (0.14)	3.17 (0.17)	8.42	<.0001	t1.6
Arousal	4.22 (0.14)	3.52 (0.12)	4.63	<.0001	t1.7
Entrainment	4.12 (0.16)	2.87 (0.14)	9.01	<.0001	t1.8
Familiarity	4.91 (0.15)	3.97 (0.15)	6.45	<.0001	t1.9
Naturalness	5.28 (0.15)	3.58 (0.18)	8.18	<.0001	t1.10

t2.1 **Table 2**
t2.2 Effects of consonance.

t2.3	Region	Lateralization	BA	Cluster size	z-Value	Coordinates
t2.4	<i>Consonant vs. dissonant music epochs</i>					
t2.5	Ventral caudate nucleus	R	13	13	3.37	8 8 4
t2.6	Postcentral gyrus (somatosensory cortex)	L	2	19	4.48	−6 −40 76
t2.7		L	*	22	3.4	−28 −34 70
t2.8		L	*	10	3.36	−26 −24 70
t2.9	Precentral gyrus (motor cortex)	L	4	6	3.44	−8 −20 62
t2.10		L	*	13	3.4	−22 −16 56
t2.11		L	*	15	3.37	−10 −12 60
t2.12	<i>Visual cues during consonant vs. dissonant music</i>					
t2.13	Precentral sulcus (Premotor cortex)	L	6	9	3.44	−40 −4 32
t2.14	Superior parietal lobule	R	19	8	3.34	38 −58 46
t2.15	Collateral sulcus	R	38	26	3.68	28 −2 −32
t2.16	<i>Visual cues during dissonant vs. consonant music</i>					
t2.17	Sup occipital gyrus	R	18	17	3.35	−28 −86 20
t2.18		L	18	8	3.22	42 −74 18

t2.24 Abbreviations:

t2.25 Inf: inferior, Sup: superior.

388 analyzing the effect of meter in the two consonance conditions sepa-
389 rately, we found that targets presented with strong versus weak beats
390 in consonant music produced significant increases only in the right
391 precuneus and superior temporal sulcus (Table 3, Fig. 3C). This effect
392 of meter (strong vs weak beat) did not reach statistical threshold for
393 this condition in the basal ganglia (right putamen: $p = 0.009$, right cau-
394 date: $p < 0.05$). Conversely, in dissonant music, the contrast of strong
395 versus weak beats revealed significant and symmetric activations in bi-
396 lateral caudate nuclei, plus left superior temporal sulcus and superior
397 temporal gyrus (Table 3, Fig. 3B). These results indicate that the effect
398 of meter in the caudate is predominating during dissonant music,
399 whereas the effect of meter in the precuneus seems to be primarily driv-
400 en by consonant music.

401 Interactions of consonance and meter in visual detection

402 The interaction between the two experimental factors was finally
403 verified by directly contrasting the strong versus weak beats in disso-
404 nant music against the corresponding beat effect in consonant music.
405 Significant effects were found in bilateral caudate nuclei and right an-
406 terior insula (Table 3, Fig. 4). In other words, the caudate was especially

Table 3
Effects of meter and interaction with consonance.

t3.3	Region	Lateralization	BA	Cluster size	z-value	Coordinates	t3.3	
t3.4	<i>Visual cues during strong versus weak beats</i>							
t3.5	Caudate nucleus	L		89	3.30	−10 16 6	t3.5	
t3.6		R			3.27	14 16 6	t3.6	
t3.7	Precuneus	R	31	37	3.7	12 −56 26	t3.7	
t3.8	<i>Visual cues during strong versus weak beats in consonant music</i>							
t3.9	Precuneus	R	31	51	3.8	12 −56 26	t3.9	
t3.10	Sup temporal sulcus	R	21	23	3.49	56 −18 −12	t3.10	
t3.11	<i>Visual cues during weak versus strong beats in consonant music</i>							
t3.12	Inf frontal gyrus	R	44	8	3.3	46 20 20	t3.12	
t3.13	Inf frontal sulcus	L	44	5	3.15	−38 20 24	t3.13	
t3.14	<i>Visual cues during strong versus weak beats in dissonant music</i>							
t3.15	Caudate nucleus	L	177		4.25	−12 16 4	t3.15	
t3.16		R	141		4.17	14 16 8	t3.16	
t3.17	Sup temporal sulcus	L	21	8	3.69	−46 −28 −4	t3.17	
t3.18	Lateral sulcus	L	22	4	3.23	−42 −22 −2	t3.18	
t3.19	<i>Visual cues during weak versus strong beats in dissonant music</i>							
t3.20	No significant voxels							t3.20
t3.21	<i>Interaction</i>							t3.21
t3.22	Caudate nucleus	L		27	3.35	−14 16 6	t3.22	
t3.23		R		4	3.23	16 16 8	t3.23	
t3.24	Insula	R	13	25	3.32	34 28 6	t3.24	
t3.25		R	13	*	3.13	38 18 8	t3.25	
t3.26	Sup temporal sulcus	L	37	11	3.52	−46 −30 −4	t3.26	
t3.27		L	52	7	3.28	−14 −16 −4	t3.27	
t3.28	Supramarginal gyrus	L	40	6	3.19	−52 −24 18	t3.28	
t3.29	Parieto-occipital sulcus	R	19	16	3.54	18 −68 42	t3.29	

t3.30 Abbreviations:

t3.31 Inf: inferior, Sup: superior.

407 responsive to the difference between strong and weak beats in disso-
408 nant music. No region passed our statistical threshold in the inverse in-
409 teraction testing for stronger meter effects in consonant relative to
410 dissonant music (precuneus: $p < 0.05$). Parameters estimates of activity
411 corresponding to these regions are illustrated for each experimental
412 condition in Fig. 4.

413 Discussion

414 We used a novel cross-modal paradigm to study the effect of en-
415 trainment by musical rhythm on visuomotor performance and its mod-
416 ulation by affective appreciation. Based on the DAT (Jones, 1987), which
417 proposes that attentional orienting may become synchronized to strong

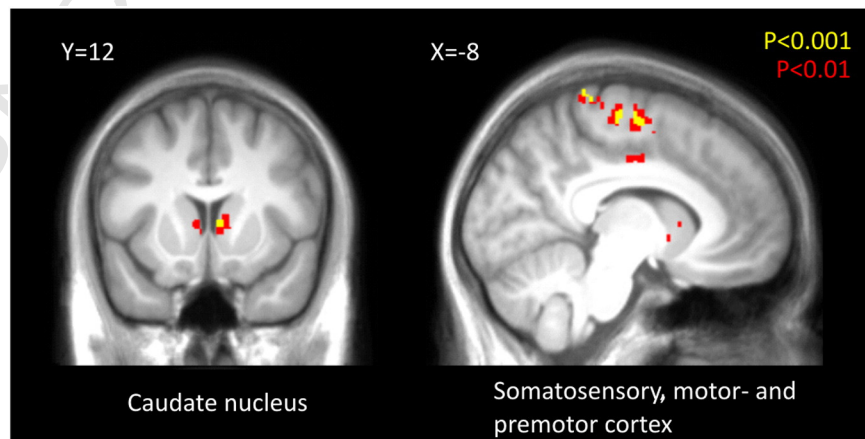


Fig. 2. Main effect of consonant music. Contrast between the blocks of consonant and dissonant music. Effects significant at $p < 0.001$ (uncorrected) are shown in yellow, and effects significant at $p < 0.01$ (uncorrected) are shown in red for illustrative reasons. Coordinates are according to the MNI space (in millimeter resolution). The left panel shows a coronal slice at the level of $y = 12$, whereas the right panel shows a sagittal slice at the level of $x = -8$.

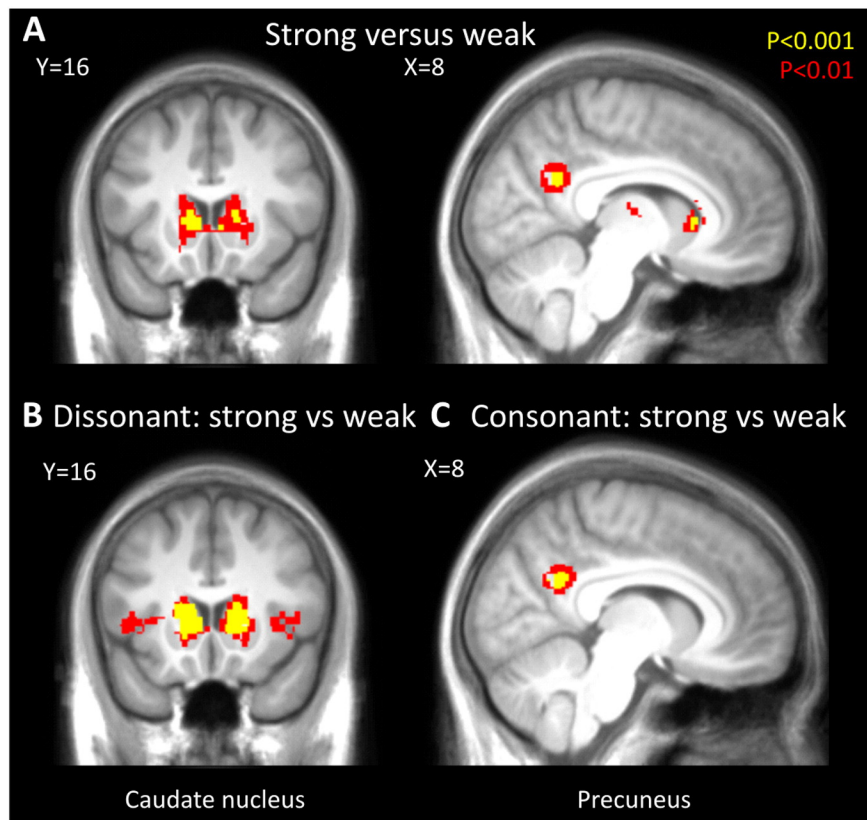


Fig. 3. Main effect of meter. Event-related analysis of the visual targets appearing simultaneously with a strong versus a weak beat of the music.

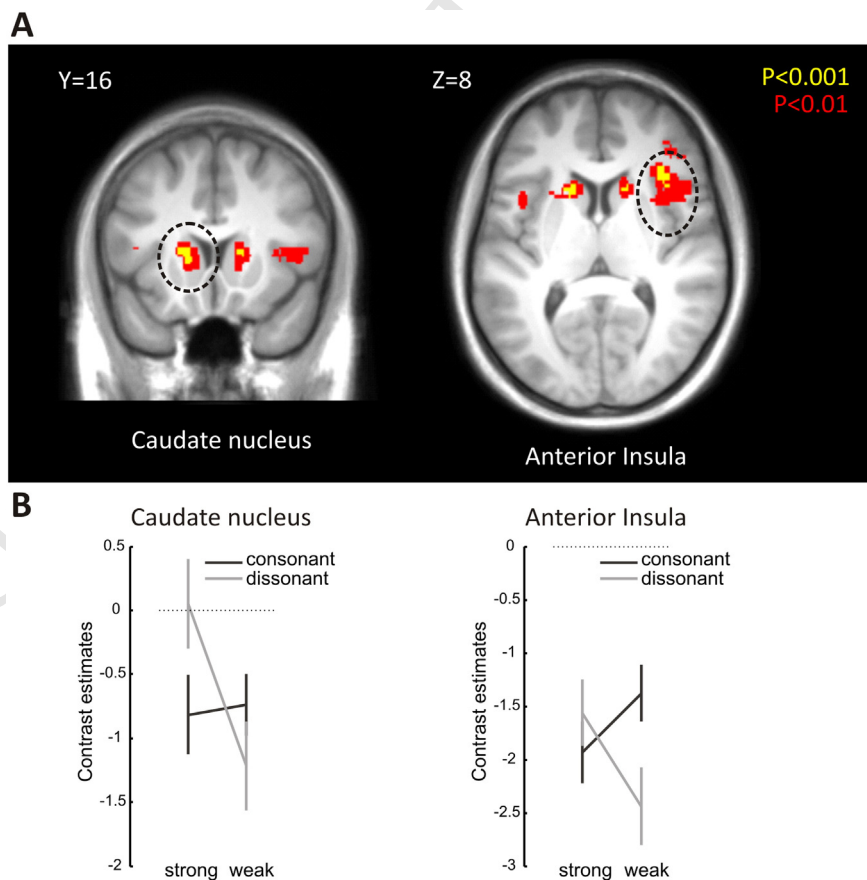


Fig. 4. A) Interaction of the factors consonance and meter. B) Beta estimates from 4 mm-spheres around main peaks of activations in the left caudate ($xyz = -14, 16, 6$) and the right anterior insula ($xyz = 34, 28, 6$).

418 beats in music, we examined how musical meter influenced visual 482
 419 detection in a concomitant visual task and tested the affective entrainment 483
 420 hypothesis (Juslin et al., 2010) according to which pleasant affect asso- 484
 421 ciated with music should elicit stronger entrainment. 485

422 *Cross-modal attention effects entrained by musical meter*

423 The behavioral results of our paradigm show that cross-modally in- 488
 424 duced entrainment leads to significant differences in response times for 489
 425 visual targets appearing at different positions in the metrical hierarchy, 490
 426 a result providing direct support for the DAT (Jones, 1987; Large and 491
 427 Kolen, 1994; Large, 2008). Thus, responses were faster when visual tar- 492
 428 gets appeared on a strong beat (1st) relative to when they appeared on 493
 429 a weak beat (2nd). This indicates that entrainment is implicitly sensitive 494
 430 to the musical meter, even though the latter is totally irrelevant to task 495
 431 goals. In addition, these entrainment effects occurred cross-modally, 496
 432 meaning that the detection of visual events was facilitated by the tempo- 497
 433 ral structure of an auditory rhythm presented in the background, in 498
 434 accord with the view that their onset corresponded to moments with 499
 435 higher attentional engagement that can benefit different sensory mo- 500
 436 dalities. Importantly, our procedure ensured that the two meter condi- 501
 437 tions did not differ in terms of music loudness at the time of strong 502
 438 and weak beats (see methods). These entrainment effects by musical 503
 439 meter extend previous evidence for a beneficial cross-modal integration 504
 440 of sensory processing when attentional resources are directed to specifi- 505
 441 c points in space or time (Lange and Roder, 2006; Escoffier et al., 2010; 506
 442 Bolger et al., 2013; Miller et al., 2013).

443 Moreover, our behavioral results show that reaction times to the visu- 507
 444 al targets were not only influenced by meter but also by consonance (and 508
 445 hence perceived pleasantness) of the music. In the ANOVA, this effect was 509
 446 significant regardless of meter condition, suggesting a general facilitation 510
 447 on attention and motor responses for pleasant compared to unpleasant 511
 448 music. However, of particular interest was the interaction of the two ex- 512
 449 perimental factors. In fact, during pleasant music, reaction times in the 513
 450 two metrical conditions did not differ significantly when compared 514
 451 pairwise, whereas the difference for targets on strong versus weak beats 515
 452 was significant for dissonant music (Figs. 1B and C). One possibility is 516
 453 that this asymmetry in RT benefits reflected a floor effect, canceling the 517
 454 subtle meter effect due to more general speeding produced by conso- 518
 455 nance. Moreover, given the significant main effect of meter in the 519
 456 ANOVA, is that consonant music induced an entrainment of attentional 520
 457 resources on a finer grained temporal level, which facilitated target detec- 521
 458 tion even on a weak beat. Dissonant music, on the contrary, might syn- 522
 459 chronize attentional resources on a coarser temporal level, i.e., at the 523
 460 level of the metrical unit, resulting in larger differences in RTs between 524
 461 the two metrical conditions. This effect might result from the fact that 525
 462 in consonant music multiple cues are available to generate predictions 526
 463 about what is going to happen next in the music, including melodic struc- 527
 464 ture, harmony, and rhythm; whereas in dissonant music the harmonic 528
 465 structure is partly lost due to our manipulation and therefore the metric 529
 466 structure becomes more important for generating temporal expectancies. 530
 467 Thus, when the music is consonant and pleasant, attention might syn- 531
 468 chronize even to small periodicities (i.e. the crotchet), whereas when 532
 469 the music is dissonant and unpleasant, attentional resources might syn- 533
 470 chronize only to slower periodicities of the musical rhythms.

471 In addition to these behavioral findings, our neuroimaging results 534
 472 highlight for the first time the neural substrates implicated in the cross- 535
 473 modal rhythmic entrainment by music. When contrasting neural res- 536
 474 sponses to visual targets presented at strong versus weak beats, we ob- 537
 475 served a highly significant activation in the basal ganglia, particularly in 538
 476 the caudate nucleus, plus a region in the inferior precuneus. The same 539
 477 comparison for epochs with consonant music revealed an effect restricted 540
 478 to the precuneus, whereas activation in the caudate prevailed during 541
 479 epochs with dissonant music. These findings provide evidence that our 542
 480 consonance manipulation did indeed influence attentional entrainment 543
 481 processes, as distinct brain circuits were preferentially engaged by

rhythmic entrainment in the presence of consonant versus dissonant 482
 music. Although the neural modulation may at first sight appear opposite 483
 to the expectation that pleasantness should boost the entrainment of at- 484
 tention by meter, this activation pattern actually converges with our be- 485
 havioral data to suggest that meter and consonance produced distinct 486
 influences on the synchronization of attentional processes to music. 487

The role of the basal ganglia in rhythmic entrainment

 488

In keeping with the notion that the basal ganglia are involved in the 489
 coordination of motor actions and in the perception of rhythmic struc- 490
 tures, our novel results point to the caudate nucleus as a key structure 491
 that encodes musical meter. In previous imaging studies of rhythm on 492
 meter processing, participants had to subsequently reproduce, compare 493
 or categorize short rhythmical sequences, requiring explicit attention 494
 and top-down internal generation of the rhythm (Grahn and Rowe, 495
 2009; Iversen et al., 2009; Chapin et al., 2010). In contrast, in our para- 496
 digm, entrainment to the meter occurred unintentionally and without 497
 voluntary effort, in a stimulus-driven manner solely determined by 498
 task-irrelevant music played in the background. This is probably also 499
 the reason why we did not observe a differential involvement of other 500
 brain structures such as the cerebellum or premotor cortex, which are 501
 often reported in studies on explicit rhythm perception and production 502
 (Molinari et al., 2003; Grahn and Brett, 2007; Chen et al., 2008; 503
 Merchant et al., 2013).

The caudate is classically related not only to motor planning, but also 505
 to error prediction and reward (Bayer and Glimcher, 2005; Asaad and 506
 Eskandar, 2011), and thus constitutes the most “cognitive” portion of 507
 the basal ganglia (Grahn et al., 2008). The caudate has previously been 508
 reported to be involved in rhythm processing (Bengtsson and Ullen, 509
 2006; Grahn and Brett, 2007) and seems especially engaged when a 510
 clear beat is perceived in rhythmical patterns (Chapin et al., 2010) or 511
 when sensorimotor synchronization to a beat is easy (Kokal et al., 512
 2011). In neuroimaging studies on music, caudate activity was reported 513
 to be sensitive to emotional arousal (Trost et al., 2012), correlate with 514
 the anticipation of chills (Salimpoor et al., 2011), and even vary accord- 515
 ing to musical syntax (Koelsch et al., 2008). Based on these results, we 516
 hypothesized that pleasant music would modulate activity particularly 517
 in the ventral striatum. Because this portion of the basal ganglia is 518
 known to play an important role in reward processing and pleasure 519
 (Salimpoor et al., 2011; Trost et al., 2012), we expected stronger en- 520
 trainment effects in ventral striatum during consonant pleasant music. 521
 However, we did not find this pattern of response; instead we found 522
 that event-related activation to targets in the caudate head was most in- 523
 fluenced by meter during dissonant music. Nonetheless, a sustained ac- 524
 tivation in the ventral part of the right caudate was significant in our 525
 contrast of consonant versus dissonant music epochs (Fig. 2 and 526
 Table 2). Taken together, this suggests that consonant music produced 527
 globally higher activation levels in the ventral caudate, over and above 528
 the event-related response associated with visual target detection. 529
 This result accords with the fact that the consonant pieces were evalu- 530
 ated as more pleasant, in line with other findings that positive emotions 531
 recruit ventral striatal regions (Katsyri et al., 2012; Koelsch and Skouras, 532
 2013). This sustained right caudate activity together with concomitant 533
 increases in motor and somatosensory cortical areas (Table 3) could re- 534
 flect the subjective apprehension of more pleasant consonant music 535
 epochs as being more arousing and more entraining (Table 1). Indeed, 536
 caudate activity correlates with felt arousal induced by music as well 537
 as its valence (Trost et al., 2012) and rewarding value (Salimpoor 538
 et al., 2013), being typically more active during pleasant or joyful than 539
 during unpleasant or sad music (Koelsch and Skouras, 2013). Moreover, 540
 it has also been shown that caudate activity is associated with joint 541
 drumming in synchrony and subsequent prosocial behavior (Kokal 542
 et al., 2011).

Interestingly, a recent study (Bolger et al., 2014) with a cross-modal 544
 design similar to our study used isochronic metrical sequences instead 545

of musical stimuli and did not find any involvement of the basal ganglia, unlike what we found in our study. This difference in results suggests that musical stimuli with their associated emotional valence might have a particular impact on entrainment and thus promote a recruitment of the basal ganglia that is modulated by the metrical structure of the music, whereas simple acoustical beats do not produce such effects. The reason for this difference might be due to the more complex rhythmic structure of musical stimuli and might be further enhanced by its emotional impact, which is known to affect activity in the basal ganglia (Salimpoor et al., 2011; Trost et al., 2012). As the basal ganglia are implicated in both motor and limbic loops (Haber and Knutson, 2010), rhythmic information combined with affective content of natural music is likely to account for the robust and bilateral activation in caudate observed in our study – unlike in Bolger et al. (2014) where more abstract metronomic tones were used. Further, in Bolger et al. (2014), targets could appear in either the visual or auditory modality, adding an extra demand of attention disengagement and re-orienting across modalities when attention was entrained by strong beats in the auditory channel (Corbetta and Shulman, 2002; Mayer et al., 2006; Corbetta et al., 2008). A predominance of explicit temporal expectations due to metronomic background and cross-modal attentional shifts in Bolger et al. (2014), as opposed to more implicit effects of natural musical background and additional recruitment of affective processes in our study might account for the different findings.

570 *The influence of consonant music*

571 Here we used a manipulation of dissonance to modulate the level of
572 pleasantness, similar to other studies (Peretz et al., 2001; Koelsch et al.,
573 2006). We chose the option to shift only single notes in every chord, in
574 order to keep the temporal structure and all other acoustic variables
575 constant. Although this consonance manipulation did not make music
576 unbearable, all dissonant pieces were evaluated as significantly less
577 pleasant than their consonant counterparts (Table 1). Behaviorally, in
578 both experiments, the fastest detection times were consistently associ-
579 ated with strong beats in consonant music, while the slowest were asso-
580 ciated with weak beats in dissonant music. Moreover, in the fMRI study
581 and when regrouping participants from the behavioral and the fMRI ex-
582 periment together, we obtained a significant interaction, which
583 highlighted that during dissonant music the metrical level had a strong
584 influence on RT, whereas the RT difference between meter conditions
585 was not significant during consonant music.

586 In accordance with this pattern, our fMRI contrast between the two
587 meter conditions in consonant music showed a selective activation
588 in the inferior right precuneus (Fig. 3C and Table 3), but no signifi-
589 cant effect in basal ganglia (only at lower threshold). The precuneus
590 is involved in a wide range of cognitive functions including self-
591 referential processing, episodic memory, and attention (for review
592 see Cavanna and Trimble, 2006). Some studies reported a selective
593 involvement of the precuneus in shifting and reorienting attention
594 (Nagahama et al., 1999; Shomstein and Yantis, 2004). Accordingly,
595 one interpretation for our finding could be that unpredictable visual
596 targets appearing on the screen required attention to be shifted from
597 the auditory to the visual modality. Such attentional shifts might be
598 enhanced when the target coincides with a strong beat through a
599 modulation of the precuneus by pleasant/consonant music that pro-
600 motes rhythmic entrainment to meter. This enhancement seems
601 however to occur without generating significantly larger RT differ-
602 ences between meter conditions, suggesting that such effect may
603 not manifest at the level of motor facilitation, but only at the level
604 of attentional processing. Another possibility is that the pleasant/
605 consonant harmony might engender a greater absorption of the lis-
606 tener into music due to its more natural and familiar character, ac-
607 companied by greater recruitment of the precuneus as observed in
608 certain meditative or hypnotic states (Lou et al., 2005; Cojan et al.,
609 2009). Moreover, precuneus activity has been proposed to be

modulated by dopaminergic inputs from striatum (Lou et al., 610
2005). Interestingly, a study by Fairhurst et al. (2012) found that 611
precuneus activation was also associated with high synchronicity, 612
when participants performed a tapping task in synchrony with a vir- 613
tual partner. Interpersonal synchrony in sensorimotor tasks is 614
known to represent a pleasant state that increases the feelings of af- 615
filiation and prosocial behavior (Hove and Risen, 2009; Valdesolo 616
and Desteno, 2011; Launay et al., 2013). Being in synchrony with a 617
partner also means however that there are no conflicting or unex- 618
pected events that disturb performance. Pleasant consonant music 619
might thus enhance the facilitation of attention to visual targets by 620
increasing concentration on music and reducing interference by 621
distracting events or thoughts. 622

In support of such an attention effect, we found that consonance pro- 623
duced a general speeding of RTs in the visual detection task (Fig. 2). Sev- 624
eral studies have shown that visual attention can be influenced by the 625
affective state of a person (Ashby et al., 1999; Olivers and Nieuwenhuis, 626
2006). There is even evidence that visual neglect after parietal lobule 627
stroke is reduced when patients are listening to their preferred versus 628
non-preferred music (Soto et al., 2009). The “broaden-and-built” theory 629
formulated by Fredrickson (2001) proposes that positive emotions have 630
a beneficial effect on various cognitive functions, including in particular a 631
broadening of attentional resources. The global behavioral benefit of con- 632
sonance in our study could be interpreted in this framework, as an effect 633
of broadened attention induced by pleasant music could have a more 634
global facilitating impact on visuomotor performance and attentional 635
orienting. This could enhance target detection even when these appear 636
in less attended moments in the music (i.e., weak beats). Likewise, re- 637
search on visual attention has shown that positive affect primes can in- 638
crease perceptual flexibility and allows switching more rapidly from a 639
local to a global focus in detection tasks (e.g., Tan et al., 2009). In the au- 640
ditory domain, Olivers and Nieuwenhuis (2005) reported that listening 641
to natural music can abolish the attentional blink effect. In keeping 642
with these data, our results for the pleasant music condition corroborate 643
the notion that listening to music may particularly affect the temporal as- 644
pects of attentional processing. Our fMRI results for the effect of conso- 645
nance on event-related response to visual targets (across meter 646
conditions) accord with this interpretation as we found differential acti- 647
vations in a set of cortical areas encompassing superior parietal lobule, 648
dorsal ACC, and dorsolateral PFC that partly overlapped with the atten- 649
tional network (Behrmann et al., 2004). 650

The affective entrainment hypothesis

651 What support does our study bring to the DAT and the affective en- 652
trainment hypothesis (Juslin et al., 2010; Trost and Vuilleumier, 2013)? 653
On the one hand, we show evidence for time-locking of visuomotor 654
performance with musical meter, associated with highly selective 655
engagement of the bilateral caudate – consistent with rhythmic en- 656
trainment. On the other hand, our results reveal that the metrical hi- 657
erarchy of the music does not become more salient or effective with 658
consonant music, in terms of the facilitation of RTs between metrical 659
conditions. Rather, we find that targets presented with weak beats 660
are equally fast detected as targets presented with strong beats 661
when music is more pleasant. According to DAT, all kinds of metrical 662
music should entrain attentional processes, and therefore strong and 663
weak beats should also produce different attentional levels during 664
pleasant music. However, our results might not necessarily contra- 665
dict this notion. Our study specifically aims at testing whether the 666
emotional valence of music modulate the entraining effect of 667
meter, a factor which was not explicitly predicted or addressed by 668
DAT. In addition, the facilitation induced by pleasantness might pro- 669
duce ceiling effects in the present paradigm and prevent detection of 670
entrainment in that condition. Further, for design simplicity, here we 671
only compared weak and strong beats but it remains possible that 672
differential entrainment by meter would be better evidenced during 673

pleasant music when comparing several on-beat vs off-beat conditions (Bolger et al., 2013). We therefore surmise that the obtained pattern of similar RT for targets on strong and weak beats in consonant music is likely to result from more general modulation of attention that enhanced the processing of weaker beats in the metrical hierarchy (e.g. crotchet level) due to the affective factor. As noted above, this attentional boosting by pleasant music might reflect enhanced shifting ability or greater absorption. In ethno-musicology, rhythmic entrainment is often associated to rhythmically-induced altered states of consciousness similar to trance or flow (Csikszentmihalyi, 1990; Clayton et al., 2005; Merker et al., 2009), which may also be experienced in sensorimotor synchronization with a virtual partner (Fairhurst et al., 2012). On the contrary, dissonant music may not favor absorption or flow-like attention states, making the temporal structure of music meter more salient. This interaction between meter and consonance was not only demonstrated for RTs (when grouping participants from the behavioral and fMRI experiment together), showing a larger difference between the two meter conditions during dissonant music, but also supported by a formal interaction contrast in our fMRI results. The caudate was not only bilaterally and symmetrically activated for the main effect of meter (Fig. 3A), but further enhanced when directly comparing this effect in the dissonant relative to the consonant condition (Fig. 4). This confirms that encoding of musical meter in the caudate was significantly stronger during dissonant music. Thus, our behavioral and fMRI data converge to indicate that, during dissonant music, temporal expectations created by the musical meter and encoded in the caudate are predominant; whereas during consonant music, attention may be modulated at a different temporal scale, with more general effects on visual detection and benefits even when targets appear on the weak beats. This pattern is consistent with the more sustained activity observed in the right caudate during consonant music epochs, presumably leading to smaller transient increases to visual targets presented in the consonant condition.

Conclusions

This is the first neuroimaging study that provides evidence for cross-modal attentional effects induced by entrainment to the meter of natural music and demonstrates specific neural substrates for such effects in both subcortical (basal ganglia) and cortical (parietal networks). Our results furthermore illuminate the neural basis of the DAT. We show that the caudate nucleus is sensitive to the metrical structure of music, even without explicit orienting of attention to the music. In addition, a region in the right inferior precuneus was also found to be selectively sensitive to musical meter, but only during pleasant/consonant music, which could mediate affective influences on cross-modal attentional shifts or absorption.

Taken together, our data suggest that rhythmic entrainment in basal ganglia circuits represents a powerful and automatic process, which is engendered even by dissonant/unpleasant music, and more broadly deployed when music is perceived as pleasant. We propose that consonant music may establish a sustained pleasant emotional state, in which attention is globally broadened and readiness to react is heightened, whereas dissonant music makes attention more focused on rhythmic musical features. More research is needed to characterize the link between rhythmic entrainment and affective processes with other task paradigms, in particular to understand how entrainment of cognitive and bodily rhythms by music can lead to complex and intense emotional feelings.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2014.09.009>.

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