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

Johanna Wiebke Trost, Sascha Frühholz, Daniele Schön, Carolina Labbé, Swann Pichon, Didier Grandjean, Patrik Vuilleumier

HAL Id: hal-02446627
https://hal.science/hal-02446627

Submitted on 3 Nov 2022

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

ARTICLE INFO

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.

© 2014 Published by Elsevier Inc.

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.

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 ± 7.5) was tested only behaviorally in a first study. Subsequently, another group of 18 volunteers (11 females, mean age 24.1 years, SD ± 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
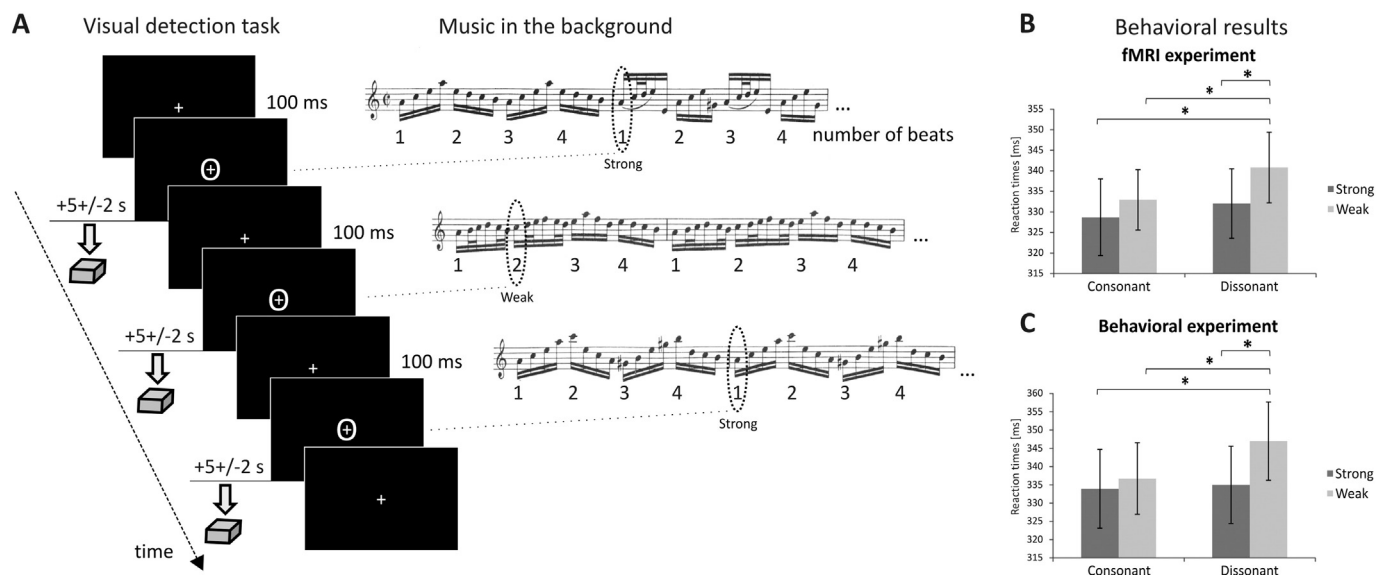
Fig. 1. A) Experimental design. Participants have to detect visual targets which are presented time-locked to the meter of the music played in the background, either on the first or the second beat. B) Behavioral reaction time results for participants in the fMRI experiment (n = 18). C) Behavioral reaction time results for participants in the behavioral experiment (n = 20). * indicates significant post-hoc tests (Tukey) between the conditions. Error bars indicate standard error.

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

Experimental design

We first performed a behavioral study in order to validate our experimental design, and to ensure that similar results would be obtained in the fMRI setting as compared with more comfortable listening conditions. The same protocol was then given to a second group during fMRI.

Before the experiment, participants were instructed and familiarized with the task. The instructions emphasized that they should listen attentively to the music, while performing the speeded response task as fast and accurately as possible. The fMRI experiment included 2 scanning runs which were interleaved with the acquisition of the structural MRI scan. Each run contained 10 pseudo-randomized musical epochs. Before each trial, participants were reminded by written instructions to listen attentively to the music, to fixate the fixation cross, and to press a button with the index finger as fast as possible when a circle appeared around the fixation cross. Immediately after the musical piece ended, six questions were presented (one after the other) on a different screen background and probed for the participants' subjective evaluation of the preceding piece. These questions were evaluations of the subjectively felt emotions (level of arousal and valence), the subjective impression of felt entrainment (formulated as the urge to move or dance to the music), and familiarity with the musical stimulus. The evaluations were designed as statements to which the participants could agree or disagree to different degree. The answers were indicated by using a sliding cursor that could be moved (by right or left key presses) on a horizontal scale from −3 to +3 (−3 = (I agree) not at all, +3 = (I agree) absolutely). The order of questions was constant for all participants. Subjects were instructed to answer spontaneously, but there was no time limit for responses. The last response to the questionnaire automatically triggered the next musical stimulus presentation. Therefore, the overall scanning time of a session varied slightly between subjects (average 573 scans per run, standard deviation 27 scans). However, only the scans during the musical epochs were included in the analyses, which comprised the same amount of scans across subjects.

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

Data acquisition and analysis

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

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 ($0.9 \times 0.9 \times 0.9$ mm³) 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 = 220×220 mm², 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: $2 \times 2 \times 2$ 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 ($(1,36) = 7.07$, $p < 0.012$; 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 x 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 Mean (SD)	Dissonance Mean (SD)	t(37)	p
Valence	5.29 (0.12)	3.39 (0.16)	9.80	<.0001
Listen again	4.91 (0.14)	3.17 (0.17)	8.42	<.0001
Arousal	4.22 (0.14)	3.52 (0.12)	4.63	<.0001
Entrainment	4.12 (0.16)	2.87 (0.14)	9.01	<.0001
Familiarity	4.91 (0.15)	3.97 (0.15)	6.45	<.0001
Naturalness	5.28 (0.15)	3.58 (0.18)	8.18	<.0001

t2.1	**Table 2**

Effects of consonance.

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

Abbreviations:
Inf: inferior, Sup: superior.

t3.1	**Table 3**	**Q1**

Effects of meter and interaction with consonance.

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

Abbreviations:
Inf: inferior, Sup: superior.

analyzing the effect of meter in the two consonance conditions separately, we found that targets presented with strong versus weak beats in consonant music produced significant increases only in the right precuneus and superior temporal sulcus (Table 3, Fig. 3C). This effect of meter (strong vs weak beat) did not reach statistical threshold for this condition in the basal ganglia (right putamen: p = 0.009, right caudate: p < 0.05). Conversely, in dissonant music, the contrast of strong versus weak beats revealed significant and symmetric activations in bilateral caudate nuclei, plus left superior temporal sulcus and superior temporal gyrus (Table 3, Fig. 3B). These results indicate that the effect of meter in the caudate is predominating during dissonant music, whereas the effect of meter in the precuneus seems to be primarily driven by consonant music.

Interactions of consonance and meter in visual detection

The interaction between the two experimental factors was finally verified by directly contrasting the strong versus weak beats in dissonant music against the corresponding beat effect in consonant music. Significant effects were found in bilateral caudate nuclei and right anterior insula (Table 3, Fig. 4). In other words, the caudate was especially responsive to the difference between strong and weak beats in dissonant music. No region passed our statistical threshold in the inverse interaction testing for stronger meter effects in consonant relative to dissonant music (precuneus: p < 0.05). Parameters estimates of activity corresponding to these regions are illustrated for each experimental condition in Fig. 4.

Discussion

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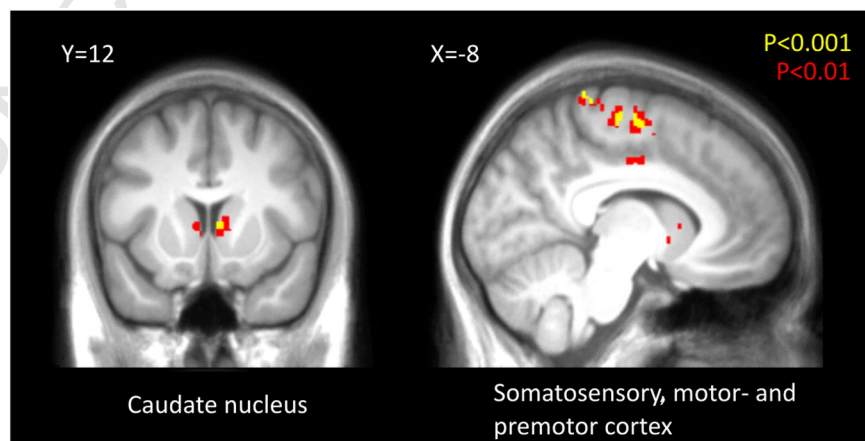

Fig. 2. Main effect of consonant music. Contrast between the blocks of consonant and dissonant music. Effects significant at p < 0.001 (uncorrected) are shown in yellow, and effects significant at p < 0.01 (uncorrected) are shown in red for illustrative reasons. Coordinates are according to the MNI space (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.
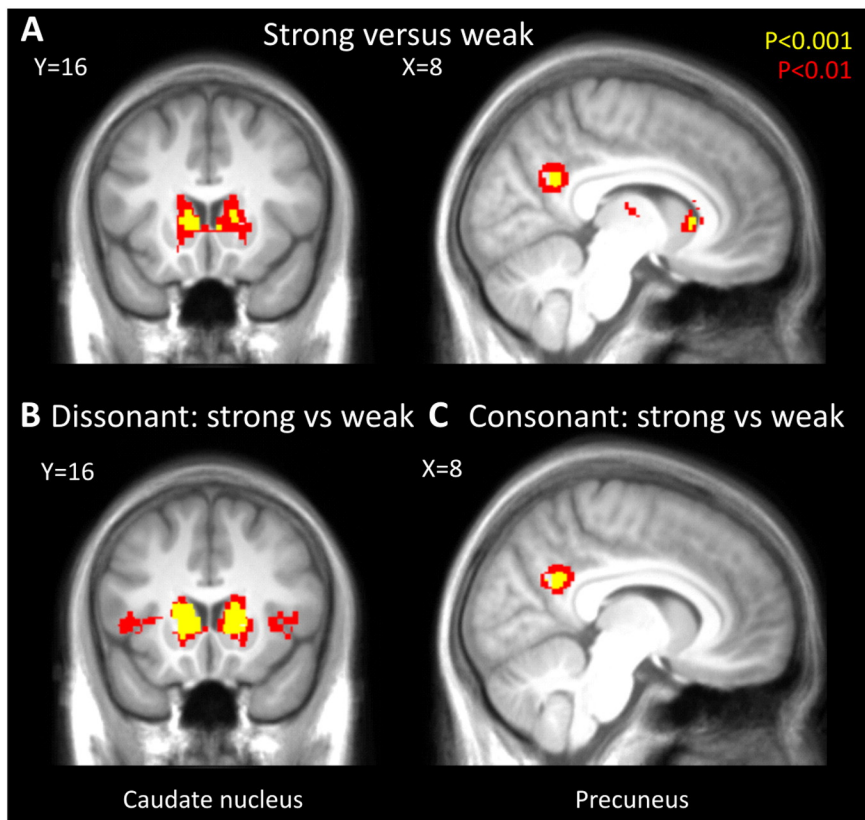
Fig. 3. Main effect of meter. Event-related analysis of the visual targets appearing simultaneously with a strong versus a weak beat of the music.
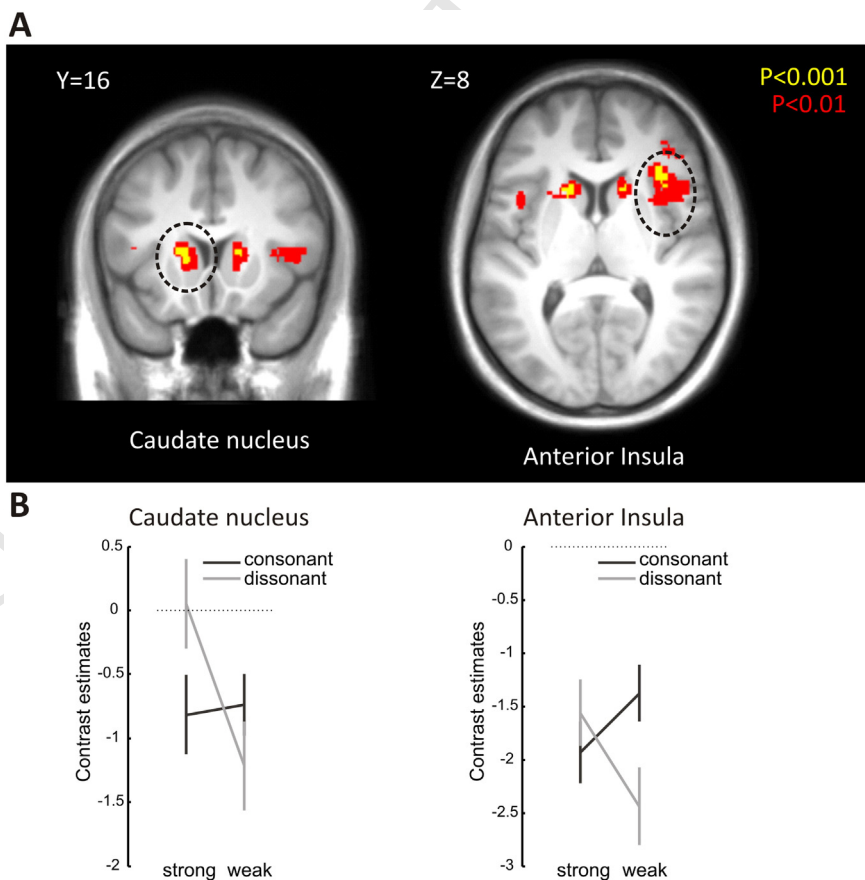

Fig. 4. A) Interaction of the factors consonance and meter. B) Beta estimates from 4 mm-spheres around main peaks of activations in the left caudate (xyz = −14, 16, 6) and the right anterior insula (xyz = 34, 28, 6).

beats in music, we examined how musical meter influenced visual detection in a concomitant visual task and tested the affective entrainment hypothesis (Juslin et al., 2010) according to which pleasant affect associated with music should elicit stronger entrainment.

Cross-modal attention effects entrained by musical meter

The behavioral results of our paradigm show that cross-modally induced entrainment leads to significant differences in response times for visual targets appearing at different positions in the metrical hierarchy, a result providing direct support for the DAT (Jones, 1987; Large and Kolen, 1994; Large, 2008). Thus, responses were faster when visual targets appeared on a strong beat (1st) relative to when they appeared on a weak beat (2nd). This indicates that entrainment is implicitly sensitive to the musical meter, even though the latter is totally irrelevant to task goals. In addition, these entrainment effects occurred cross-modally, meaning that the detection of visual events was facilitated by the temporal structure of an auditory rhythm presented in the background, in accord with the view that their onset corresponded to moments with higher attentional engagement that can benefit different sensory modalities. Importantly, our procedure ensured that the two meter conditions did not differ in terms of music loudness at the time of strong and weak beats (see methods). These entrainment effects by musical meter extend previous evidence for a beneficial cross-modal integration of sensory processing when attentional resources are directed to specific points in space or time (Lange and Roder, 2006; Escoffier et al., 2010; Bolger et al., 2013; Miller et al., 2013).

Moreover, our behavioral results show that reaction times to the visual targets were not only influenced by meter but also by consonance (and hence perceived pleasantness) of the music. In the ANOVA, this effect was significant regardless of meter condition, suggesting a general facilitation on attention and motor responses for pleasant compared to unpleasant music. However, of particular interest was the interaction of the two experimental factors. In fact, during pleasant music, reaction times in the two metrical conditions did not differ significantly when compared pairwise, whereas the difference for targets on strong versus weak beats was significant for dissonant music (Figs. 1B and C). One possibility is that this asymmetry in RT benefits reflected a floor effect, canceling the subtle meter effect due to more general speeding produced by consonance. Moreover, given the significant main effect of meter in the ANOVA, is that consonant music induced an entrainment of attentional resources on a finer grained temporal level, which facilitated target detection even on a weak beat. Dissonant music, on the contrary, might synchronize attentional resources on a coarser temporal level, i.e., at the level of the metrical unit, resulting in larger differences in RTs between the two metrical conditions. This effect might result from the fact that in consonant music multiple cues are available to generate predictions about what is going to happen next in the music, including melodic structure, harmony, and rhythm; whereas in dissonant music the harmonic structure is partly lost due to our manipulation and therefore the metric structure becomes more important for generating temporal expectancies. Thus, when the music is consonant and pleasant, attention might synchronize even to small periodicities (i.e. the crotchet), whereas when the music is dissonant and unpleasant, attentional resources might synchronize only to slower periodicities of the musical rhythms.

In addition to these behavioral findings, our neuroimaging results highlight for the first time the neural substrates implicated in the cross-modal rhythmic entrainment by music. When contrasting neural responses to visual targets presented at strong versus weak beats, we observed a highly significant activation in the basal ganglia, particularly in the caudate nucleus, plus a region in the inferior precuneus. The same comparison for epochs with consonant music revealed an effect restricted to the precuneus, whereas activation in the caudate prevailed during epochs with dissonant music. These findings provide evidence that our consonance manipulation did indeed influence attentional entrainment processes, as distinct brain circuits were preferentially engaged by

rhythmic entrainment in the presence of consonant versus dissonant music. Although the neural modulation may at first sight appear opposite to the expectation that pleasantness should boost the entrainment of attention by meter, this activation pattern actually converges with our behavioral data to suggest that meter and consonance produced distinct influences on the synchronization of attentional processes to music.

The role of the basal ganglia in rhythmic entrainment

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

The caudate is classically related not only to motor planning, but also to error prediction and reward (Bayer and Glimcher, 2005; Asaad and Eskandar, 2011), and thus constitutes the most "cognitive" portion of the basal ganglia (Grahn et al., 2008). The caudate has previously been reported to be involved in rhythm processing (Bengtsson and Ullen, 2006; Grahn and Brett, 2007) and seems especially engaged when a clear beat is perceived in rhythmical patterns (Chapin et al., 2010) or when sensorimotor synchronization to a beat is easy (Kokal et al., 2011). In neuroimaging studies on music, caudate activity was reported to be sensitive to emotional arousal (Trost et al., 2012), correlate with the anticipation of chills (Salimpoor et al., 2011), and even vary according to musical syntax (Koelsch et al., 2008). Based on these results, we hypothesized that pleasant music would modulate activity particularly in the ventral striatum. Because this portion of the basal ganglia is known to play an important role in reward processing and pleasure (Salimpoor et al., 2011; Trost et al., 2012), we expected stronger entrainment effects in ventral striatum during consonant pleasant music. However, we did not find this pattern of response; instead we found that event-related activation to targets in the caudate head was most influenced by meter during dissonant music. Nonetheless, a sustained activation in the ventral part of the right caudate was significant in our contrast of consonant versus dissonant music epochs (Fig. 2 and Table 2). Taken together, this suggests that consonant music produced globally higher activation levels in the ventral caudate, over and above the event-related response associated with visual target detection. This result accords with the fact that the consonant pieces were evaluated as more pleasant, in line with other findings that positive emotions recruit ventral striatal regions (Katsyri et al., 2012; Koelsch and Skouras, 2013). This sustained right caudate activity together with concomitant increases in motor and somatosensory cortical areas (Table 3) could reflect the subjective apprehension of more pleasant consonant music epochs as being more arousing and more entraining (Table 1). Indeed, caudate activity correlates with felt arousal induced by music as well as its valence (Trost et al., 2012) and rewarding value (Salimpoor et al., 2013), being typically more active during pleasant or joyful than during unpleasant or sad music (Koelsch and Skouras, 2013). Moreover, it has also been shown that caudate activity is associated with joint drumming in synchrony and subsequent prosocial behavior (Kokal et al., 2011).

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

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 rhythmical 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.

The influence of consonant music

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

In accordance with this pattern, our fMRI contrast between the two meter conditions in consonant music showed a selective activation in the inferior right precuneus (Fig. 3C and Table 3), but no significant effect in basal ganglia (only at lower threshold). The precuneus is involved in a wide range of cognitive functions including self-referential processing, episodic memory, and attention (for review see Cavanna and Trimble, 2006). Some studies reported a selective involvement of the precuneus in shifting and reorienting attention (Nagahama et al., 1999; Shomstein and Yantis, 2004). Accordingly, one interpretation for our finding could be that unpredictable visual targets appearing on the screen required attention to be shifted from the auditory to the visual modality. Such attentional shifts might be enhanced when the target coincides with a strong beat through a modulation of the precuneus by pleasant/consonant music that promotes rhythmic entrainment to meter. This enhancement seems however to occur without generating significantly larger RT differences between meter conditions, suggesting that such effect may not manifest at the level of motor facilitation, but only at the level of attentional processing. Another possibility is that the pleasant/consonant harmony might engender a greater absorption of the listener into music due to its more natural and familiar character, accompanied by greater recruitment of the precuneus as observed in certain meditative or hypnotic states (Lou et al., 2005; Cojan et al., 2009). Moreover, precuneus activity has been proposed to be modulated by dopaminergic inputs from striatum (Lou et al., 2005). Interestingly, a study by Fairhurst et al. (2012) found that precuneus activation was also associated with high synchronicity, when participants performed a tapping task in synchrony with a virtual partner. Interpersonal synchrony in sensorimotor tasks is known to represent a pleasant state that increases the feelings of affiliation and prosocial behavior (Hove and Risen, 2009; Valdesolo and Desteno, 2011; Launay et al., 2013). Being in synchrony with a partner also means however that there are no conflicting or unexpected events that disturb performance. Pleasant consonant music might thus enhance the facilitation of attention to visual targets by increasing concentration on music and reducing interference by distracting events or thoughts.

In support of such an attention effect, we found that consonance produced a general speeding of RTs in the visual detection task (Fig. 2). Several studies have shown that visual attention can be influenced by the affective state of a person (Ashby et al., 1999; Olivers and Nieuwenhuis, 2006). There is even evidence that visual neglect after parietal lobule stroke is reduced when patients are listening to their preferred versus non-preferred music (Soto et al., 2009). The "broaden-and-built" theory formulated by Fredrickson (2001) proposes that positive emotions have a beneficial effect on various cognitive functions, including in particular a broadening of attentional resources. The global behavioral benefit of consonance in our study could be interpreted in this framework, as an effect of broadened attention induced by pleasant music could have a more global facilitating impact on visuomotor performance and attentional orienting. This could enhance target detection even when these appear in less attended moments in the music (i.e., weak beats). Likewise, research on visual attention has shown that positive affect primes can increase perceptual flexibility and allows switching more rapidly from a local to a global focus in detection tasks (e.g., Tan et al., 2009). In the auditory domain, Olivers and Nieuwenhuis (2005) reported that listening to natural music can abolish the attentional blink effect. In keeping with these data, our results for the pleasant music condition corroborate the notion that listening to music may particularly affect the temporal aspects of attentional processing. Our fMRI results for the effect of consonance on event-related response to visual targets (across meter conditions) accord with this interpretation as we found differential activations in a set of cortical areas encompassing superior parietal lobule, dorsal ACC, and dorsolateral PFC that partly overlapped with the attentional network (Behrmann et al., 2004).

The affective entrainment hypothesis

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

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.

References

Asaad, W.F., Eskandar, E.N., 2011. Encoding of both positive and negative reward prediction errors by neurons of the primate lateral prefrontal cortex and caudate nucleus. J. Neurosci. 31, 17772–17787.

Ashby, F.G., Isen, A.M., Turken, A.U., 1999. A neuropsychological theory of positive affect and its influence on cognition. Psychol. Rev. 106, 529–550.

Bayer, H.M., Glimcher, P.W., 2005. Midbrain dopamine neurons encode a quantitative reward prediction error signal. Neuron 47, 129–141.

Behrmann, M., Geng, J.J., Shomstein, S., 2004. Parietal cortex and attention. Curr. Opin. Neurobiol. 14, 212–217.

Bengtsson, S.L., Ullen, F., 2006. Dissociation between melodic and rhythmic processing during piano performance from musical scores. NeuroImage 30, 272–284.

Bolger, D., Trost, W., Schon, D., 2013. Rhythm implicitly affects temporal orienting of attention across modalities. Acta Psychol. (Amst.) 142, 238–244.

Bolger, D., Coull, J.T., Schon, D., 2014. Metrical rhythm implicitly orients attention in time as indexed by improved target detection and left inferior parietal activation. J. Cogn. Neurosci. 26, 593–605.

Cameron, D.J., Stewart, L., Pearce, M.T., Grube, M., Muggleton, N.G., 2012. Modulation of motor excitability by metricality of tone sequences. Psychomusicology Music, Mind, Brain 22.

Cavanna, A.E., Trimble, M.R., 2006. The precuneus: a review of its functional anatomy and behavioural correlates. Brain 129, 564–583.

Chapin, H.L., Zanto, T., Jantzen, K.J., Kelso, S.J., Steinberg, F., Large, E.W., 2010. Neural responses to complex auditory rhythms: the role of attending. Front. Psychol. 1, 224.

Chen, J.L., Penhune, V.B., Zatorre, R.J., 2008. Listening to musical rhythms recruits motor regions of the brain. Cereb. Cortex 18, 2844–2854.

Clayton, M., Sager, R., Will, U., 2005. In time with the music: the concept of entrainment and its significance for ethnomusicology. Eur. Meet. Ethnomusicol. 11, 3–142.

Cojan, Y., Waber, L., Schwartz, S., Rossier, L., Forster, A., Vuilleumier, P., 2009. The brain under self-control: modulation of inhibitory and monitoring cortical networks during hypnotic paralysis. Neuron 62, 862–875.

Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. 3, 201–215.

Corbetta, M., Patel, G., Shulman, G.L., 2008. The reorienting system of the human brain: from environment to theory of mind. Neuron 58, 306–324.

Coull, J.T., Nobre, A.C., 1998. Where and when to pay attention: the neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. J. Neurosci. 18, 7426–7435.

Csikszentmihalyi, M., 1990. Flow: The Psychology of Optimal Experience. Harper & Row, New York, NY.

Eerola, T., Toiviainen, P., 2004. MIDI Toolbox: MATLAB Tools for Music Research.

Escoffier, N., Darren, Y.J.S., Schirmer, A., 2010. Unattended musical beats enhance visual processing. Acta Psychol. 136, 12–16.

Fairhurst, M.T., Janata, P., Keller, P.E., 2012. Being and feeling in sync with an adaptive virtual partner: brain mechanisms underlying dynamic cooperativity. Cereb. Cortex 23, 2592–2600.

Fredrickson, B.L., 2001. The role of positive emotions in positive psychology. The broaden-and-build theory of positive emotions. Am. Psychol. 56, 218–226.

Grahn, J.A., Brett, M., 2007. Rhythm and beat perception in motor areas of the brain. J. Cogn. Neurosci. 19, 893–906.

Grahn, J.A., Rowe, J.B., 2009. Feeling the beat: premotor and striatal interactions in musicians and nonmusicians during beat perception. J. Neurosci. 29, 7540–7548.

Grahn, J.A., Parkinson, J.A., Owen, A.M., 2008. The cognitive functions of the caudate nucleus. Prog. Neurobiol. 86, 141–155.

Haber, S.N., Knutson, B., 2010. The reward circuit: linking primate anatomy and human imaging. Neuropsychopharmacology 35, 4–26.

Hove, M.J., Risen, J.L., 2009. It's all in the timing: interpersonal synchrony increases affiliation. Soc. Cogn. 27, 949–960.

Iversen, J.R., Repp, B.H., Patel, A.D., 2009. Top-down control of rhythm perception modulates early auditory responses. Ann. N. Y. Acad. Sci. 1169, 58–73.

Janata, P., Tomic, S.T., Haberman, J.M., 2012. Sensorimotor coupling in music and the psychology of the groove. J. Exp. Psychol. Gen. 141, 54–75.

Jones, M.R., 1987. Dynamic pattern structure in music: recent theory and research. Percept. Psychophys. 41, 621–634.

Jones, M.R., Boltz, M., 1989. Dynamic attending and responses to time. Psychol. Rev. 96, 459–491.

Jueptner, M., Weiller, C., 1998. A review of differences between basal ganglia and cerebellar control of movements as revealed by functional imaging studies. Brain 121 (Pt 8), 1437–1449.

Juslin, P.N., Liljeström, S., Västfjäll, D., Lundqvist, L.-O., 2010. How does music evoke emotions? Exploring the underlying mechanisms. In: Juslin, P.N., Sloboda, J. (Eds.), Handbook of Music and Emotion: Theory, Research, Applications. Oxford University Press, Oxford, pp. 605–642.

Katsyri, J., Hari, R., Ravaja, N., Nummenmaa, L., 2012. The opponent matters: elevated fmri reward responses to winning against a human versus a computer opponent during interactive video game playing. Cereb. Cortex.

Koelsch, S., Skouras, S., 2013. Functional centrality of amygdala, striatum and hypothalamus in a "Small-World" network underlying joy: an fMRI study with music. Hum. Brain Mapp.

Koelsch, S., Fritz, T., Cramon, V., Muller, K., Friederici, A.D., 2006. Investigating emotion with music: an fMRI study. Hum. Brain Mapp. 27, 239–250.

Koelsch, S., Fritz, T., Schlaug, G., 2008. Amygdala activity can be modulated by unexpected chord functions during music listening. Neuroreport 19, 1815–1819.

Kokal, I., Engel, A., Kirschner, S., Keysers, C., 2011. Synchronized drumming enhances activity in the caudate and facilitates prosocial commitment—if the rhythm comes easily. PLoS One 6, e27272.

Lange, K., Roder, B., 2006. Orienting attention to points in time improves stimulus processing both within and across modalities. J. Cogn. Neurosci. 18, 715–729.

Large, E.W., 2008. Resonating to musical rhythm: theory and experiment. In: Grondin, S. (Ed.), Psychology of Time. Emerald Group Publishing Limited, Bingley U.K., pp. 189–231.

Large, E.W., Kolen, J.F., 1994. Resonance and the perception of musical meter. Connect. Sci. 6, 177–208.

Lartillot, O., Toiviainen, P., 2007. A Matlab toolbox for musical feature extraction from audio. International Conference on Digital Audio Effects (DAFx-07) Bordeaux, France.

Launay, J., Dean, R.T., Bailes, F., 2013. Synchronization can influence trust following virtual interaction. Exp. Psychol. 60, 53–63.

Lou, H.C., Nowak, M., Kjaer, T.W., 2005. The mental self. Bound. Conscious. Neurobiol. Neuropathol. 150, 197–204.

Macaluso, E., Driver, J., 2001. Spatial attention and crossmodal interactions between vision and touch. Neuropsychologia 39, 1304–1316.

Mayer, A.R., Harrington, D., Adair, J.C., Lee, R., 2006. The neural networks underlying endogenous auditory covert orienting and reorienting. NeuroImage 30, 938–949.

Merchant, H., Perez, O., Zarco, W., Gamez, J., 2013. Interval tuning in the primate medial premotor cortex as a general timing mechanism. J. Neurosci. 33, 9082–9096.

Merker, B.H., Madison, G.S., Eckerdal, P., 2009. On the role and origin of isochrony in human rhythmic entrainment. Cortex 45, 4–17.

Miller, J.E., Carlson, L.A., McAuley, J.D., 2013. When what you hear influences when you see: listening to an auditory rhythm influences the temporal allocation of visual attention. Psychol. Sci. 24, 11–18.

Molinari, M., Leggio, M.G., De Martin, M., Cerasa, A., Thaut, M., 2003. Neurobiology of rhythmic motor entrainment. Ann. N. Y. Acad. Sci. 999, 313–321.

Nagahama, Y., Okada, T., Katsumi, Y., Hayashi, T., Yamauchi, H., Sawamoto, N., Toma, K., Nakamura, K., Hanakawa, T., Konishi, J., Fukuyama, H., Shibasaki, H., 1999. Transient neural activity in the medial superior frontal gyrus and precuneus time locked with attention shift between object features. NeuroImage 10, 193–199.

Nozaradan, S., Peretz, I., Missal, M., Mouraux, A., 2011. Tagging the neuronal entrainment to beat and meter. J. Neurosci. 31, 10234–10240.

Olivers, C.N.L., Nieuwenhuis, S., 2005. The beneficial effect of concurrent task-irrelevant mental activity on temporal attention. Psychol. Sci. 16, 265–269.

Olivers, C.N., Nieuwenhuis, S., 2006. The beneficial effects of additional task load, positive affect, and instruction on the attentional blink. J. Exp. Psychol. Hum. Percept. Perform. 32, 364–379.

Peretz, I., Blood, A.J., Penhune, V., Zatorre, R., 2001. Cortical deafness to dissonance. Brain 124, 928–940.

Salimpoor, V.N., Benovoy, M., Larcher, K., Dagher, A., Zatorre, R.J., 2011. Anatomically distinct dopamine release during anticipation and experience of peak emotion to music. Nat. Neurosci. 14, 257–262.

Salimpoor, V.N., van den Bosch, I., Kovacevic, N., McIntosh, A.R., Dagher, A., Zatorre, R.J., 2013. Interactions between the nucleus accumbens and auditory cortices predict music reward value. Science 340, 216–219.

Seifritz, E., Di Salle, F., Esposito, F., Herdener, M., Neuhoff, J.G., Scheffler, K., 2006. Enhancing BOLD response in the auditory system by neurophysiologically tuned fMRI sequence. NeuroImage 29, 1013–1022.

Shomstein, S., Yantis, S., 2004. Control of attention shifts between vision and audition in human cortex. J. Neurosci. 24, 10702–10706.

Soto, D., Funes, M.J., Guzman-Garcia, A., Warbrick, T., Rotshtein, P., Humphreys, G.W., 2009. Pleasant music overcomes the loss of awareness in patients with visual neglect. Proc. Natl. Acad. Sci. U. S. A. 106, 6011–6016.

Stupacher, J., Hove, M.J., Novembre, G., Schutz-Bosbach, S., 2013. Musical groove modulates motor cortex excitability: a TMS investigation. Brain Cogn. 82, 127–136.

Teder-Salejarvi, W.A., McDonald, J.J., Di Russo, F., Hillyard, S.A., 2002. An analysis of audio–visual crossmodal integration by means of event-related potential (ERP) recordings. Brain Res. Cogn. Brain Res. 14, 106–114.

Thaut, M.H., Demartin, M., Sanes, J.N., 2008. Brain networks for integrative rhythm formation. PLoS One 3.

Tierney, A., Kraus, N., 2013. Neural responses to sounds presented on and off the beat of ecologically valid music. Front. Syst. Neurosci. 7, 14.

Trost, W., Vuilleumier, P., 2013. 'Rhythmic entrainment' as a mechanism for emotion induction by music: a neurophysiological perspective. In: Cochrane, T., et al. (Eds.), The Emotional Power of Music. Oxford University Press, pp. 213–225.

Trost, W., Ethofer, T., Zentner, M., Vuilleumier, P., 2012. Mapping aesthetic musical emotions in the brain. Cereb. Cortex 22, 2769–2783.

Turner, R.S., Desmurget, M., 2010. Basal ganglia contributions to motor control: a vigorous tutor. Curr. Opin. Neurobiol. 20, 704–716.

Valdesolo, P., Desteno, D., 2011. Synchrony and the social tuning of compassion. Emotion 11, 262–266.

Witek, M.A., Clarke, E.F., Wallentin, M., Kringelbach, M.L., Vuust, P., 2014. Syncopation, body-movement and pleasure in groove music. PLoS One 9, e94446.