NeuroImage 103 (2014) 55–64

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

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

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ARTICLE INFO

Article history:
Accepted 4 September 2014
Available online 16 September 2014

Keywords:
Rhythmic entrainment
Consonance
Basal ganglia
Caudate nucleus
Musical emotions

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.

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.

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http://dx.doi.org/10.1016/j.neuroimage.2014.09.009
1053-8119/

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