Early neural responses underlie advantages for consonance over dissonance

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ABSTRACT

Consonant musical intervals tend to be more readily processed than dissonant intervals. In the present study, we explore the neural basis for this difference by registering how the brain responds after changes in consonance and dissonance, and how formal musical training modulates these responses. Event-related brain potentials (ERPs) were registered while participants were presented with sequences of consonant intervals interrupted by a dissonant interval, or sequences of dissonant intervals interrupted by a consonant interval. Participants were musicians and non-musicians. Our results show that brain responses triggered by changes in a consonant context differ from those triggered in a dissonant context. Changes in a sequence of consonant intervals are rapidly processed independently of musical expertise, as revealed by a change-related mismatch negativity (MMN, a component of the ERPs triggered by an odd stimulus in a sequence of stimuli) elicited in both musicians and non-musicians. In contrast, changes in a sequence of dissonant intervals elicited a late MMN only in participants with prolonged musical training. These different neural responses might form the basis for the processing advantages observed for consonance over dissonance and provide information about how formal musical training modulates them.

1. Introduction

In music theory, the relationship between two tones played simultaneously (i.e. harmonic intervals) can be described as consonant or dissonant. Perceptually, consonant pitch relationships are associated with stability as opposed to dissonant pitch relationships that are associated with instability. In line with these aesthetic perceptual differences, electrophysiological studies have shown a strong correlation between the listener's perceived degree of stability of tone combinations and brain activity (Bidelman and Krishnan, 2009), demonstrating processing differences for consonant and dissonant pitch relationships at the neural level. Even more, behavioral studies suggest that such differences translate in a processing advantage for consonance over dissonance (Schellenberg and Trehub, 1994, 1996; Komeilipoor et al., 2015; Crespo-Bojorque and Toro, 2016). In the present study we explore the neural correlates underlying such processing benefits for consonance and show how they might be modulated by experience.

The degree of consonance-dissonance of an interval has been linked to the simplicity of the frequency ratios between two tones. The simpler the ratio between the tones the more consonant is the sound (e.g., the ratio in a perfect fourth is 5:4). Conversely, the more complex the ratio between two tones the more dissonant the sound (e.g., the ratio in a minor second is 15:16) (Rossing et al., 2002). Prevailing theories ascribe the perception of dissonance to a sensation of roughness that comes from rapid amplitude fluctuations (called "beats") that are produced by the combination of tones with complex frequency ratios. The more beats contained within a sound, the rougher will be the sound, which leads to an increased perception of dissonance (Helmholtz, 1954; Krumhansl, 1990; Plomp and Levelt, 1965). Importantly, differences between consonance and dissonance are continuous, a gradation from the most consonant to the most dissonant sound, rather than clearly defined categories (Kameoka and Kuriyagawa, 1969). Even more, the consonance-dissonance continuum varies with time and culture, its processing is modulated by the musical context (Rossing et al., 2002; Terhardt, 1984), and is one of the bases for Western tonal music (Virtala and Tervaniemi, 2017) where the use of consonant intervals is more prevalent than dissonant ones (North and Hargreaves, 2000; Martindale and Moore, 1989). In Western populations the rank order of consonance is tightly correlated with the simplicity of frequency ratios between two complex tones (Krumhansl, 1990).

Current neurophysiological studies have identified neural correlates of consonant and dissonant pitch relationships at the cortical level in humans. It has been shown that the cerebral blood flow (Blood et al., 1999) and the event-related brain potentials (Itoh et al., 2003, 2010; Regnault et al., 2001) (ERP) change depending on the perceived consonance and dissonance of the auditory stimuli. Consonant chords elicit

a larger N1component than dissonant chords, while dissonant chords elicit a larger P2 component than consonant chords (Regnault et al., 2001). Similarly, intracranial studies with neurosurgical patients have demonstrated differential processing of consonance and dissonance in different brain areas. Recordings of auditory evoked potentials (AEPs) with depth electrodes in response to consonant and dissonant stimuli have shown that dissonant chords trigger a greater phase-locked activity in the Heschl's gyrus (Fishman et al., 2001) as well as a greater power in the theta and alpha frequency bands in the orbitofrontal cortex (Omigie et al., 2014) than consonant chords. Electrocorticographic (ECoG) recordings directly from the superior temporal gyrus (STG) on the right and left hemispheres revealed that only the right hemisphere displayed a robust and organized sensitivity towards dissonance (Foo et al., 2016). Studies using non-invasive methods have also observed different responses to consonant and dissonant intervals at the brainstem. When frequency-following responses (FFRs, an evoked potential which follows the individual cycles of the stimulus) elicited by musical intervals that vary in their degree of consonance are recorded in non-musicians, the amplitude of brainstem responses to consonant intervals is higher than the amplitude of the responses to dissonant intervals (Bidelman and Krishnan, 2009). Interestingly, changes in these subcortical responses match the ordering of consonance for tone combinations as it is often listed in Western music theory (Krumhansl, 1990). Thus, findings from modern neuroimaging and electrophysiological studies provide evidence that the ranking of consonant intervals has clear correlates in how our brain responds to musical chords. However, most of the studies so far have tested Western listeners. There is thus the possibility that differences in brain responses to consonance and dissonance emerge as a result of long-term enculturation (Bidelman, 2013) and not only reflect physical differences in the stimuli. In fact, electrophysiological recordings have shown that neural correlates for consonant and dissonant pitch relationships are modulated by musical expertise (Itoh et al., 2010; Foss et al., 2007; Lee et al., 2009; Minati et al., 2009). Different latencies of ERP components suggest that musicians differentiate consonant and dissonant chords earlier (100–200 ms) than non-musicians (200–300 ms) (Schön et al., 2005). Furthermore, stronger amplitudes of ERP components for musicians when compared to non-musicians indicate that musical training triggers a finer and more tuned neural representation of pitch intervals (Proverbio et al., 2016). Likewise, fMRI data have shown that the areas of activation for consonant chords are right lateralized for non-musicians and are less asymmetric for musicians (Minati et al., 2009). Thus, evidence from neurophysiological studies highlights formal musical training as an important factor underlying consonance and dissonance processing. Still, the question of whether differences between consonance and dissonance emerge only after exposure to a certain musical system remains open, as consonance-dissonance discrimination has been observed at the neural and behavioral level in newborn infants (Virtala et al., 2013; Perani et al., 2010) and other species (Toro and Crespo-Bojorque, 2017).

Different studies have observed a processing benefit for consonance over dissonance. It has been shown that adults (Schellenberg and Trehub, 1994) and infants (Schellenberg and Trehub, 1996) find it easier to identify changes over consonant than over dissonant chords. Similarly, it has been demonstrated that performance in a movement synchronization task is more precise after the presentation of consonant stimuli than after the presentation of dissonant stimuli (Komeilipoor et al., 2015). A recent study showed that humans benefit from consonance as to facilitate the detection of abstract patterns in a rule-learning task (Crespo-Bojorque and Toro, 2016). Participants learned an abstract rule more easily if it was implemented over consonant intervals than if it was implemented over dissonant ones. Interestingly, when non-human animals were presented with the same set of acoustic sequences, they performed equally well in the rule-learning task independently of whether the stimuli contained consonant or dissonant intervals. Likely, human participants' extensive experience with

harmonic music allowed them to benefit from differences between consonance and dissonance as to improve learning over the former when compared to the latter.

The present study explores the neural correlates underlying the processing advantages of consonance over dissonance, and whether formal musical training modulates such advantages. For this, we recorded brain responses triggered when a dissonant interval was presented in a consonant context and when a consonant interval was presented in a dissonant context. To explore how formal musical training might modulate these responses, both musicians and non-musicians were tested. Therefore, the aim of the present study is twofold. First, to study the neural correlates of the processing advantages for consonance over dissonance. Second, to explore how experience, in the form of formal musical training, alters the brain's responses to changes in consonant and dissonant stimuli. Previous studies have investigated the neural correlates of consonance-dissonance discrimination for triad chords in Western adult participants (Virtala et al., 2011), musicians (Brattico et al., 2008) and newborn infants (Virtala et al., 2013). Results have shown that a change-related mismatch negativity (MMN) is elicited when dissonant chords are inserted in a context of major chords that served as examples of highly consonant chords. However, we are still lacking a direct comparison of the neural responses triggered by changes in both consonant and dissonant sequences. If we compare brain responses to changes in dissonance and consonance, we can start to describe the neural correlates of the processing advantage for consonance that has been reported in behavioral studies. Thus, in the present study, event-related brain potentials (ERPs) were recorded by means of electroencephalography (EEG) while stimuli were presented using an oddball paradigm. The oddball paradigm consists on the presentation of sequences of repetitive auditory stimuli (standards) that are occasionally interrupted by infrequent stimuli (deviants). Deviant stimuli often trigger a mismatch negativity (MMN), an ERP component related to the detection of changes in a pattern or a sequence (Näätänen et al., 2005).

The MMN response emerges at a pre-attentive processing level, even when subject's attention is not directed to the auditory stimuli (Näätänen et al., 2001). In fact, to avoid overlap with other ERP components, studies suggest that a good condition to observe the MMN is to direct the subject's attention away from the auditory stimuli (Näätänen, 2000). This automatic brain response reflects thus an incongruity between the features of a deviant stimulus and the neural representation (memory trace) formed by the standard (repetitive) stimuli (Näätänen et al., 2001). The MMN peaks around 100–250 ms after the onset of a change and is distributed over fronto-central scalp locations (Garrido et al., 2009). The MMN is considered an objective marker of auditory sensory accuracy (Näätänen, 2000) and its study has allowed for important insights regarding auditory perception (Denham and Winkler, 2006). Thus, in the field of music cognition the use of MMN experiments has become a useful tool to explore the neural mechanisms underlying music processing (Tervaniemi and Huotilainen, 2003).

There were two conditions in our study, the Consonance Condition and the Dissonance Condition. In the Consonance condition, sequences of highly frequent consonant intervals were occasionally interrupted by infrequent dissonant intervals. In the Dissonance condition, sequences of highly frequent dissonant intervals were occasionally interrupted by infrequent consonant intervals (see Fig. 1). We compared electroencephalographic responses triggered by changes in consonant and dissonant sequences in both musicians and non-musicians participants. Our hypothesis is that familiarity and formal musical training might constrain the processing advantages of consonance over dissonance. As mentioned before, Western tonal music makes a predominant use of consonant pitch relationships. Thus, our participants, who live in a Western culture, are highly familiar with consonance due to cultural exposure. We thus should observe an early neural response (a MMN component) for violations in sequences of consonant intervals (Consonant condition) in both musicians and non-musicians. On the
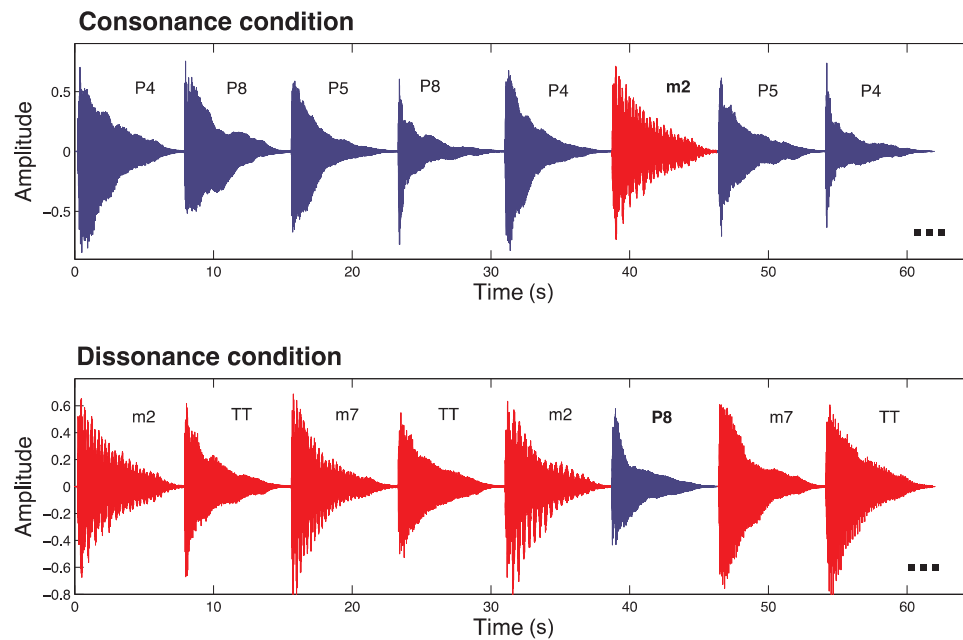
Consonance condition

Dissonance condition

Fig. 1. Graphical depiction of interval sequences used in the present study (see Table 1 for abbreviations). In both the Consonance condition and the Dissonance condition, sequences of standard, frequent, stimuli are interrupted by deviant, infrequent, stimuli.

Table 1
Consonant and dissonant harmonic intervals used in the present study. A lower (the key) and an upper note compose each interval. Each interval used in our experiment was implemented in four different keys: C, E, G and A. The corresponding upper notes are specified for each interval.

	Stimuli		Key			
	Interval	Ratio	C_4	E_4	G_4	A_4
Consonant	P8	2:1	C-C'	E-E'	G-G'	A-A'
	P5	3:2	C-G	E-B	G-D	A-E
	P4	4:3	C-F	E-A	G-C	A-D
	M3	5:4	C-E	E-G#	G-B	A-C#
	m3	6:5	C-D#	E-G	G-A#	A-C
	M6	5:3	C-A	E-C#	G-E	A-F#
	m6	8:5	C-G#	E-C	G-D#	A-F
Dissonant	TT	45:32	C-F#	E-A#	G-C#	A-D#
	m2	16:15	C-C#	E-F	G-G#	A-A#
	M2	9:8	C-D	E-F#	G-A	A-B
	m7	16:9	C-A#	E-D	G-F	A-G
	M7	15:8	C-B	E-D#	G-F#	A-G#
	m9	15:32	C-C'#	E-F'	G-G'#	A-A'#
	M9	9:4	C-D'	E-F'#	G-A'	A-B'

contrary, such an early response might not be elicited for violations in sequences of dissonant intervals (Dissonance condition) with which the participants have not been massively exposed. Even more, formal musical training might modulate the brain responses to consonant and dissonant categories. Musical professional activity causes structural changes in the auditory cortex (Schalug et al., 1995; Aydin et al., 2005), giving rise to a general enhancement of acoustic information processing (Van Zuijen et al., 2005; Drake et al., 2000). In fact, ERPs studies on the processing of simultaneous tones have demonstrated a modulation in brain responses as a function of musical expertise, suggesting a more accurately stimulus categorization in terms of consonance and dissonance for musicians than naïve controls (Minati et al., 2009; Proverbio et al., 2016; Kuriki et al., 2006; Kung et al., 2014). Thus, a MMN could be observed in the Dissonance condition for participants with formal musical training on the present study.

2. Methods

2.1. Participants

Thirty-two volunteers participated in the experiment. Half of the participants ($N = 16$) were experienced musicians (9 females, mean age 19.8 ± 2.3), with several years of formal musical training (10.9 ± 1.8) in Western tonal music. All of them played at a professional orchestra at the time of the experiment. The other half of the participants were non-musicians (8 females, mean age 21.1 ± 1.8) that have never enrolled in formal musical training. All participants were right-handed, reported normal hearing, signed a written informed consent and received a monetary compensation for their participation in the study.

2.2. Stimuli

Stimuli consisted of 7 consonant and 7 dissonant harmonic intervals (two-note chords). Consonant intervals were: octave (P8), minor and major sixths (m6 and M6), fifth (P5), fourth (P4), and minor and major thirds (m3 and M3). Dissonant intervals were: minor and major ninths (m9 and M9), minor and major sevenths (m7 and M7), tritone (TT), and minor and major seconds (m2 and M2). Each interval was implemented in four different keys (C, E, G and A; see Table 1). The stimuli were created using the grand piano setting of GarageBand software for Mac OS X. All the stimuli were played over the frequency range of 261.626–587.330 Hz (C_4 to $D\#_5$). Each stimulus was 800 ms long.

2.3. Procedure

Participants were tested individually in a soundproof room. During the experiment participants were comfortably seated and watched a silent movie while the auditory stimuli were presented through two loudspeakers. Participants were explicitly instructed to pay attention only to the movie and let the auditory stimuli be perceived as background noise.

Each participant was presented with sequences of harmonic intervals following an oddball paradigm with standard (frequent) and deviant (infrequent) stimuli. There were two conditions, the Consonance

Condition and the Dissonance Condition. In the Consonance Condition, the standard stimuli were three of the most consonant intervals (P8, P5 and P4) and the deviant stimuli were the seven dissonant intervals (m2, M2, TT, m7, M7, m9, M9). In the Dissonance Condition, the standard stimuli were the three most dissonant intervals (m2, TT and m7), while the deviant stimuli were the seven different consonant intervals (P8, P5, P4, m3, M3, m6, M6). All the participants were presented with both conditions, and the order of presentation of the conditions was counterbalanced across participants. There was a break of 4 min between conditions. In each condition there were 4 blocks (3.5 min/block). The total duration of the experiment was around 32 min. Each block consisted on the presentation of 231 stimuli in total, 203 standards (88%) and 28 deviants (12%). The stimuli were presented using an oddball paradigm. In this paradigm, sequences of frequent stimuli (standard) are interrupted from time to time by an infrequent stimulus (deviant; see Fig. 1). The stimuli presentation was randomized within each block and across blocks, with the only restriction that there were between 5 and 9 standard stimuli before each presentation of a deviant stimulus. The sound sequences following the oddball paradigm were generated with MATLAB algorithms. The stimulus onset asynchrony (SOA) was set to 1000 ms. All experimental procedures were approved by the ethical committee of the Universitat Pompeu Fabra and the European Research Council and they were carried out in accordance with Spanish and European guidelines.

The main interest of the present study was to compare neural responses to the violation of an abstract "consonance" category versus the abstract "dissonance" category. For this, it was important to use as standard stimuli intervals that could be clearly assigned to the target category. The consonance-dissonance phenomenon is a continuum that runs from the most consonant to the most dissonant sound rather than clearly defined categories. Thus, in order to create a clear context of consonance or dissonance we chose to use as standards the three intervals considered the most consonant or the three intervals considered the most dissonant (depending on the condition) according to literature (Kameoka and Kuriyagawa, 1969). Using the entire set of seven intervals as standard stimuli could have led to difficulties in the creating of the target category as some of those intervals are not good exemplars of it. In this way, we aimed to create a clear abstract representation of consonance and dissonance to be used as standard context in each condition.

2.4. ERP recording

The EEG was recorded using an elastic cap of 32 channels (actiCAP) with the Modified Combinatorial Nomenclature (MNC) system. As a result, 28 electrodes were recorded from the scalp (Fp1, 2; F3, 4, 7, 8; Fz, FC1, 2, 5, 6; T7, 8; C3, 4; Cz; CP1, 2, 5, 6; TP9, 10; P3, 4, 7, 8; Pz; Oz). Two more electrodes were placed to the left and right mastoid (M1 and M2) and to monitor the ocular movements and blinking, two different electrodes were placed on the outer side (HEOG) and below (VEOG) the right eye. In addition, an electrode placed on the tip of the nose was used as an online reference. The signals were sampled at a rate of 500 Hz. The electrode impedances were maintained under 10 kΩ and EEG was recorded during the familiarization phase of the experiment.

2.5. Analyses

ERP data were offline band-pass filtered from 0.1 to 30 Hz (12 dB) and re-referenced to the average of the linked mastoids. An ocular correction was applied and epochs with an amplitude > 10 0 µV at EOG channels and with an amplitude > 100 µV at EEG channels were rejected. For both conditions, epochs of 900 ms were extracted with a baseline from − 100–0 ms relative to the stimulus onset. The permutation test described in Maris and Oostenveld (Maris and Oostenveld, 2007) was separately applied to each condition (consonance and dissonance) and group of participants (musicians and non-musicians).

First, the mean difference between standards and deviants for each data point was calculated. Then, data from standard and deviant stimuli were mixed. This mixed data was randomly divided into two parts, and a stimulus label (standard or deviant) was assigned to each part. For each permutation test, 1000 reassignments were run and a p value was obtained. This value reflected the probability of obtaining similar differences just by chance. During passive listening of a repetitive series of sounds, a mismatch negativity (MMN) could be elicited when an infrequent change in the series of sounds occurs. Because we used an oddball paradigm, we expected to observe a mismatch negativity (MMN) component elicited in the frontal electrodes. Thus, the analyses were performed in the Fz electrode. Data from standard stimuli was compared to the data from deviant stimuli across both conditions (consonant and dissonant) and groups (musicians and non-musicians). Complementary permutation tests analyses were conducted over the ERPs responses to stimuli as a function of the interval type. We thus compared responses after consonant intervals and dissonant intervals when they were presented as standard and when they were presented as deviant stimuli. We also compared responses after standard stimuli and after deviant stimuli when they were implemented by consonant intervals and by dissonant intervals. All the comparisons were performed for both non-musicians and musicians.

In order to compare the peak voltages and latencies between groups and conditions, we conducted repeated measures ANOVAs with the within-subject factors Region (2 levels; frontal and central), Position (3 levels; left, midline and right) and Condition (2 levels; consonant and dissonant) and also Region × Position × Condition repeated measures ANOVAs with the between-subjects factor Group (2 levels; musicians and non-musicians). The electrodes included in these analyses were F3, Fz, F4, C3, Cz, C4, P3, Pz and P4. The results were corrected with the Greenhouse-Geisser adjustment when the sphericity was violated. The Bonferroni correction was applied on multiple comparisons.

3. Results

3.1. Consonance condition

In non-musicians, a significant positive response from 96 to 150 ms (cluster mass permutation test, $p = 0.036$; see Fig. 2; for the mean amplitude after consonant and dissonant intervals see Table 2, and Supplementary Fig. S1 online) was observed after a dissonant interval was presented within a sequence of consonant intervals. This positivity is consistent with the P1 component, which has been associated to an increased level of arousal after the presentation of a deviant auditory stimulus (Kuriki et al., 2006; Nikjeh et al., 2009). This positivity was followed by a negative component from 172 to 250 ms (cluster mass permutation test, $p = 0.007$; see Fig. 2, Table 2, and Supplementary Fig. S2 online).

In the group of musicians, a significant negative response from 152 to 258 ms (cluster mass permutation test, $p = 0.001$; see Fig. 3, Table 2, and Supplementary Fig. S3 online) was also observed. Timing of this negativity in both musicians and non-musicians is consistent with a MMN and suggests that changes in consonance are readily detected independently of musical training. Musician participants also exhibited a significant negative response from 502 to 582 ms (cluster mass permutation test, $p = 0.02$; see Fig. 3, Table 2 and Supplementary Fig. S3 online). This late negativity is consistent with the N5 component. Previous studies have found that elicitation of this negativity is related to violations of harmonic expectations (Koelsch et al., 2000; Koelsch and Siebel, 2005) and, similarly to the MMN, it has been suggested that it could be elicited under incidental conditions (Koelsch et al., 2002).

3.2. Dissonance condition

No significant differences between standard and deviant stimuli were observed for non-musicians (see Fig. 2, Table 2, and
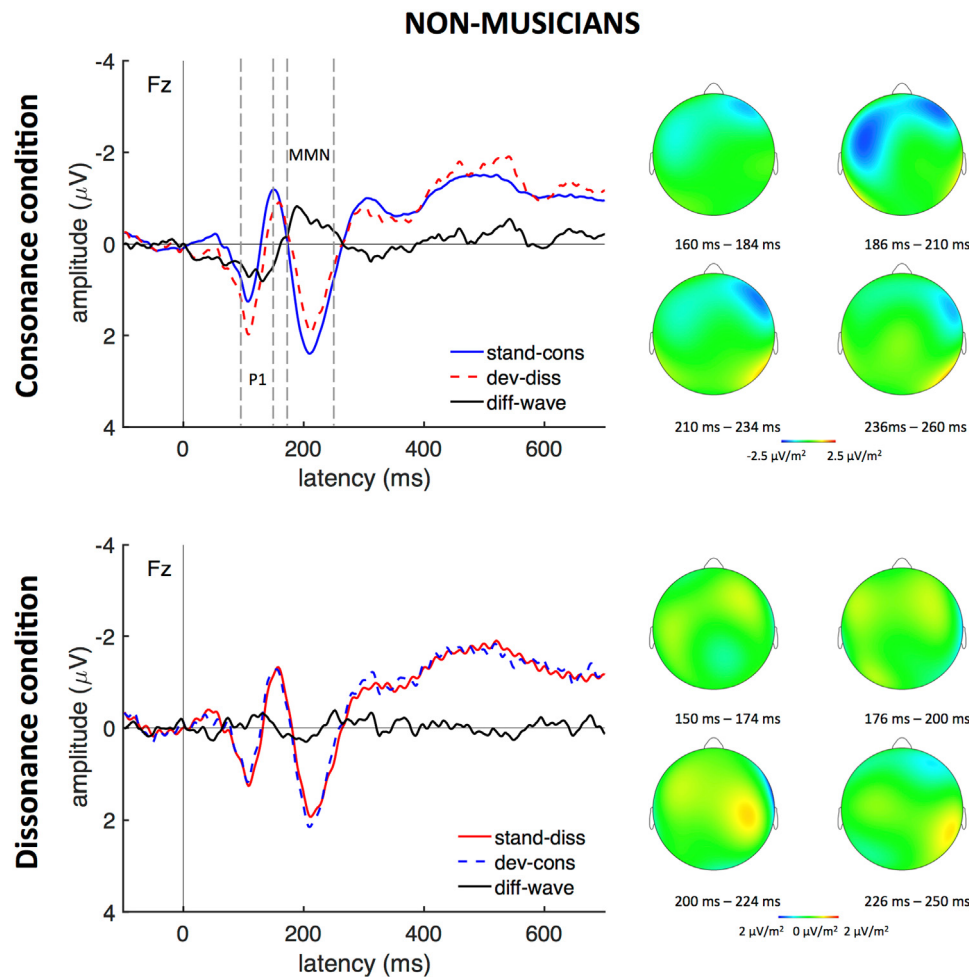
NON-MUSICIANS

Fig. 2. ERPs and scalp topographies elicited for changes in consonant and dissonant sequences for non-musicians. Difference waves (black line) are the result of substracting the averaged response to standard stimuli (continuous line) from the averaged response to deviant stimuli (dashed line) in the Fz electrode. In the consonance condition two significant components were observed, an early positivity (P1) and a later negativity (MMN). For the dissonance condition no significant components were found. Scalp topographies reflect the activity for all the participants during the timing consistent with a MMN component.

Table 2
Amplitude means (in µV) for the MMN and the P1 time windows. All the data refers to the Fz electrode. Time windows were directly taken from the Permutation test. For the analysis of the Dissonance condition in the Non-musicians group we selected the same time window as in the Dissonance condition of the musicians group.

	Time window	Standard amplitude (SD)	Deviant amplitude (SD)
Musicians			
Consonance condition	P1MMN	0.76 (0.83)	1.17 (1.05)
		2.26 (0.98)	1.38 (1.39)
Dissonance condition	P1MMN (late)	0.74 (0.74)	0.98 (1.08)
		1.69 (0.77)	1.23 (1.07)
Non-musicians			
Consonance condition	P1MMN	0.40 (1.10)	1.05 (1.35)
		1.91 (0.97)	1.39 (1.15)
Dissonance condition	P1MMN (late)	0.51 (0.87)	0.32 (1.19)
		1.47 (1.02)	1.56 (0.94)

Supplementary Fig. S2 online). The change from dissonance (standards) to consonance (deviants) did not produce any distinct neural activation in these participants.

However, in the group of musicians, a negative component from 232 to 314 ms (cluster mass permutation test, $p = 0.021$) was observed (see Fig. 3, Table 2, and Supplementary Fig. S3 online). Timing of this

negative response is consistent with a late MMN component that has been previously observed in the context of especially difficult tasks (Goydke et al., 2004).

3.3. Complementary analyses

A comparison of the responses to consonant intervals when they were presented as standards (Consonance condition) and when they were presented as deviants (Dissonance condition) showed no significant differences between them in either musicians or non-musicians (see Fig. 4, left panel). Comparisons of the responses to dissonant intervals when they were presented as standards (Dissonance condition) and when they were presented as deviants (Consonance condition) revealed significant differences in musicians from 192 to 258 ms (cluster mass permutation test, $p = 0.028$) and from 516 to 628 ms (cluster mass permutation test, $p = 0.001$; see Fig. 4, right panel). No differences were observed for non-musicians.

Analyses comparing the responses to standard stimuli depending on whether they are implemented by consonant intervals (Consonance condition) or by dissonant intervals (Dissonance condition) revealed significant differences in both non-musicians (from 162 to 224 ms; cluster mass permutation, $p = 0.015$) and musicians (from 150 to 230 ms; cluster mass permutation, $p = 0.010$; see Fig. 5, left panel) showing larger ERPs amplitudes for consonant intervals. Analyses comparing the responses to deviant stimuli depending on whether they
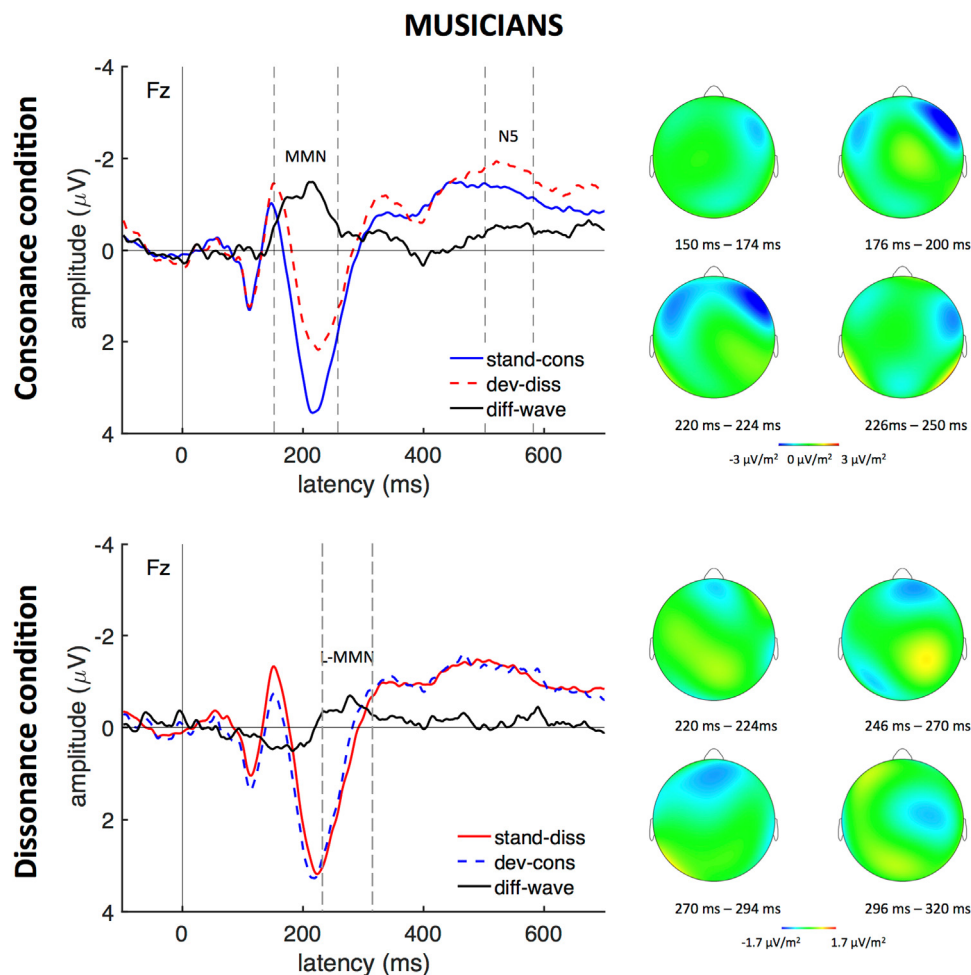
MUSICIANS

Fig. 3. ERPs and scalp topographies elicited for changes in consonant and dissonant sequences for musicians. Difference waves (black line) are the result of substracting the averaged response to standard stimuli (continuous line) from the averaged response to deviant stimuli (dashed line) in the Fz electrode. In the Consonance condition two significant components were elicited, a MMN and a later negativity (N5). In the dissonance condition a MMN component was also elicited. Scalp topographies reflect the activity for all the participants during the timing consistent with a MMN component.

are implemented over consonant intervals (Dissonant condition) or dissonant intervals (Consonant condition) revealed a significant difference only in the group of musicians (from 136 to 240 ms; cluster mass permutation, $p = 0.009$; see Fig. 5, right panel).

3.4. Exploring differences across groups and conditions

In musicians, a significant frontal negativity was observed in both the Consonance and the Dissonance conditions. We thus explored possible differences across conditions in this response for this group of participants. First, the peak voltages of the difference waves (Deviant stimuli minus Standard stimuli) were compared in the respective time-windows (see Table 2). A Region x Position x Condition ANOVA showed a Condition main effect ($F(1,15) = 4.95$, $p < 0.05$) indicating that the negative peak was greater in the Consonance condition. A significant Position x Condition interaction ($F(1,24) = 4.54$, $p < 0.05$) was also observed. Pairwise comparisons showed that in the right position the negative peak was greater for the Consonance condition ($p = 0.017$). So, in listeners with extensive musical experience, a similar distribution of the negative response independently whether the deviant stimulus was consonant or dissonant was observed. However, a greater response was elicited when deviant stimuli were dissonant. Next, the latencies of the difference waves were compared. A Region x Position x Condition ANOVA demonstrated a difference across conditions ($F(1,15) = 155.03$, $p < .001$; see Supplementary table S4 online), with the

negativity appearing much later when a consonant interval was presented within a sequence of dissonant intervals (Dissonance condition) than when a dissonant interval was presented within a sequence of consonant intervals (Consonance condition).

In the group of participants with no formal musical training a MMN was observed in Consonance condition, but not in the Dissonance condition. To confirm that the responses differed across conditions we ran a Region x Position x Condition ANOVA on the difference wave's peak voltage in the MMN time window. We observed a significant Region × Condition interaction ($F(1571) = 11.57$, $p = 0.001$). The pairwise comparisons showed that the MMN only appeared in the Consonance condition in the frontal region ($p = 0.044$). Analysis over the latency of the MMN response did not show any significant main effect or interactions.

A P1 component was also observed in non-musicians in the Consonance condition (but not in the Dissonance condition). A Region × Position × Condition ANOVA on the difference wave's peak voltage in the P1 time window showed a Region × Condition interaction ($F(1359) = 5.62$, $p = 0.02$; see Supplementary Table S5 online). Pairwise comparisons showed that P1 appeared in the frontal region only in the Consonance condition ($p = 0.012$). Thus, in non-musicians, the comparisons across the Consonance and Dissonance conditions confirm that deviant stimuli trigger different neural responses (a P1 and a MMN) only in the former, but not in the latter condition.

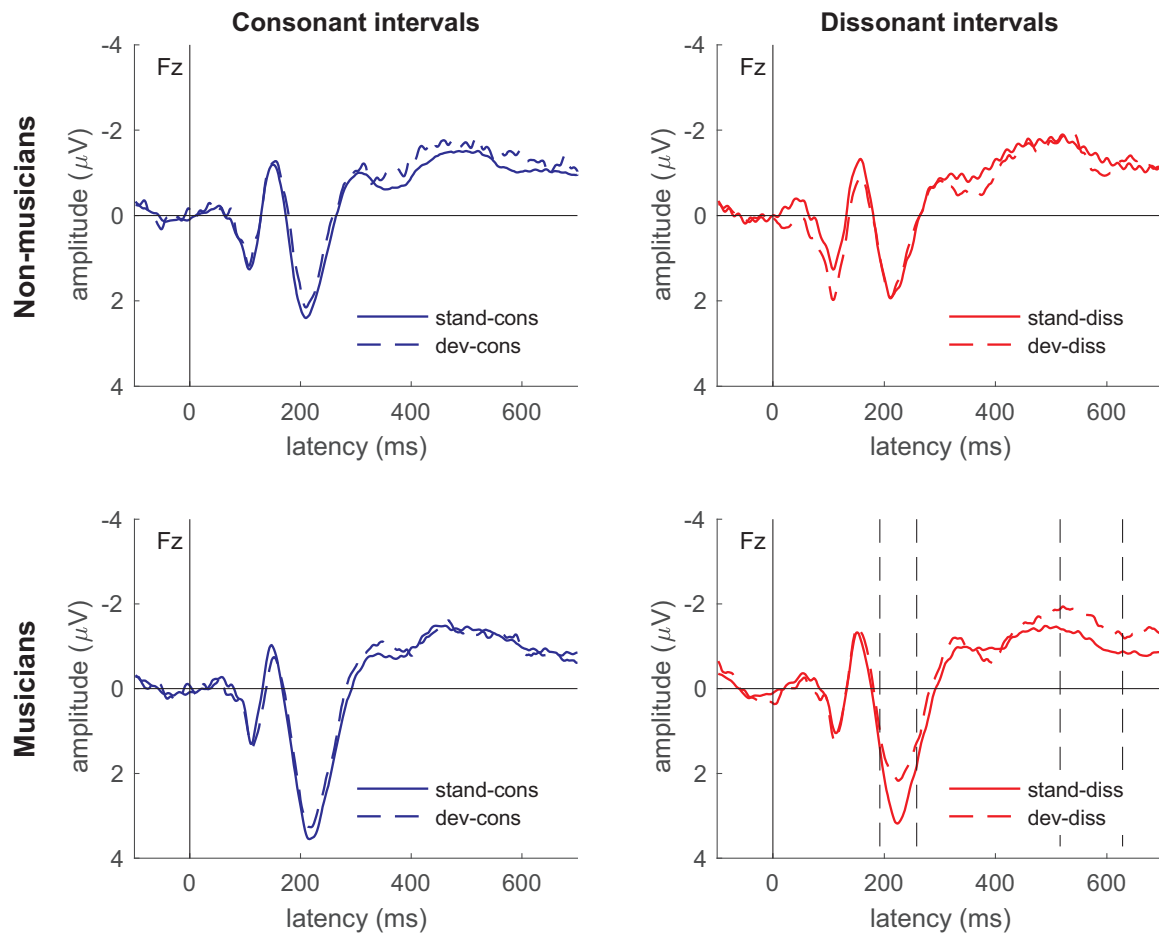Next we wanted to explore possible differences across conditions

Fig. 4. ERPs for consonant intervals (left panel) and dissonant intervals (right panel) in the Fz electrode depending on whether they are presented as standard or as deviant stimuli.

and groups in the frontal negativity observed in musicians and non-musicians. Thus, comparisons of the difference wave's peak voltage of the MMN time window in the two conditions and the two groups were performed. A Region x Position × Condition repeated measures ANOVA was conducted with the between-subjects factor Group. We observed a main effect of Region ($F(1,44) = 6.12$, $p = 0.009$) showing that the negative response was greater in the central region than in the parietal region ($p = 0.015$) and a main effect of Condition ($F(1,30) = 4.94$, $p = 0.03$) showing that the negative response was greater during the consonance condition. Additionally, a Region × Condition interaction ($F(1,53) = 11.246$, $p < 0.001$) was found. Pairwise comparisons showed that in the frontal ($p = 00.1$) and in the central ($p = 0.029$) regions the negativity was greater in the Consonance condition than in the Dissonance condition. Also, a Group × Position × Condition interaction was observed ($F(1,53) = 3.325$, $p < 0.05$). Pairwise comparisons showed that during the Consonance condition, both in the midline position ($p = 0.008$) and in the right position ($p = 0.004$), the negative response was greater for the participants with musical training. Also, likely because for the participants with no musical training the MMN was only observed in the Consonance but not in the Dissonance condition, we observed a marginal difference in the midline position during the Dissonance condition ($p = 0.07$).

The analysis conducted over the latencies of the MMN showed a main effect of Condition ($F(1,30) = 83.91$, $p < 0.001$) suggesting that the MMN appeared earlier in the consonance condition. Also, a significant Group × Condition interaction ($F(1,30) = 54.54$, $p < 0.001$) was observed. The pairwise comparisons showed that in both the Consonance ($p = .038$) and the Dissonance condition ($p < 0.001$) the

latencies differed for musicians and non-musicians. In the Consonance condition, the MMN response was observed earlier in musicians than in non-musicians. In the Dissonance condition, the latency of the negative peak was observed earlier in non-musicians. Importantly, the MMN response was only observed in musicians (see Fig. 6).

The visual analysis of the Grand-average data suggested that musicians and non-musicians might be responding differently to the highly frequent standard stimuli across conditions. To explore this possible difference across groups, a Position × Condition repeated measures ANOVA was conducted with the between-subjects factor Group on the standard stimuli's peak voltage in the MMN time windows. No effects for the factor Group were observed. So there were no significant differences across groups in how listeners responded to standard stimuli.

4. General discussion

Consonance is one of the most salient features in music, to the point that it has been considered as one of its universal parameters (Fritz et al., 2009). Understanding the processes leading to its prevalence is one of the outstanding issues in music cognition. In the present study we used an oddball paradigm to record ERP responses when a dissonant interval is presented in a consonant context and compare them when a consonant interval is presented in a dissonant context, for both musicians and non-musicians. Our results show that brain responses elicited for the transition from consonance to dissonance differ from brain responses to the transition from dissonance to consonance. While changes in consonant sequences elicited a MMN component in all participants (musicians and non-musicians), changes in dissonant sequences elicited a late MMN only in musicians. These different neural responses might
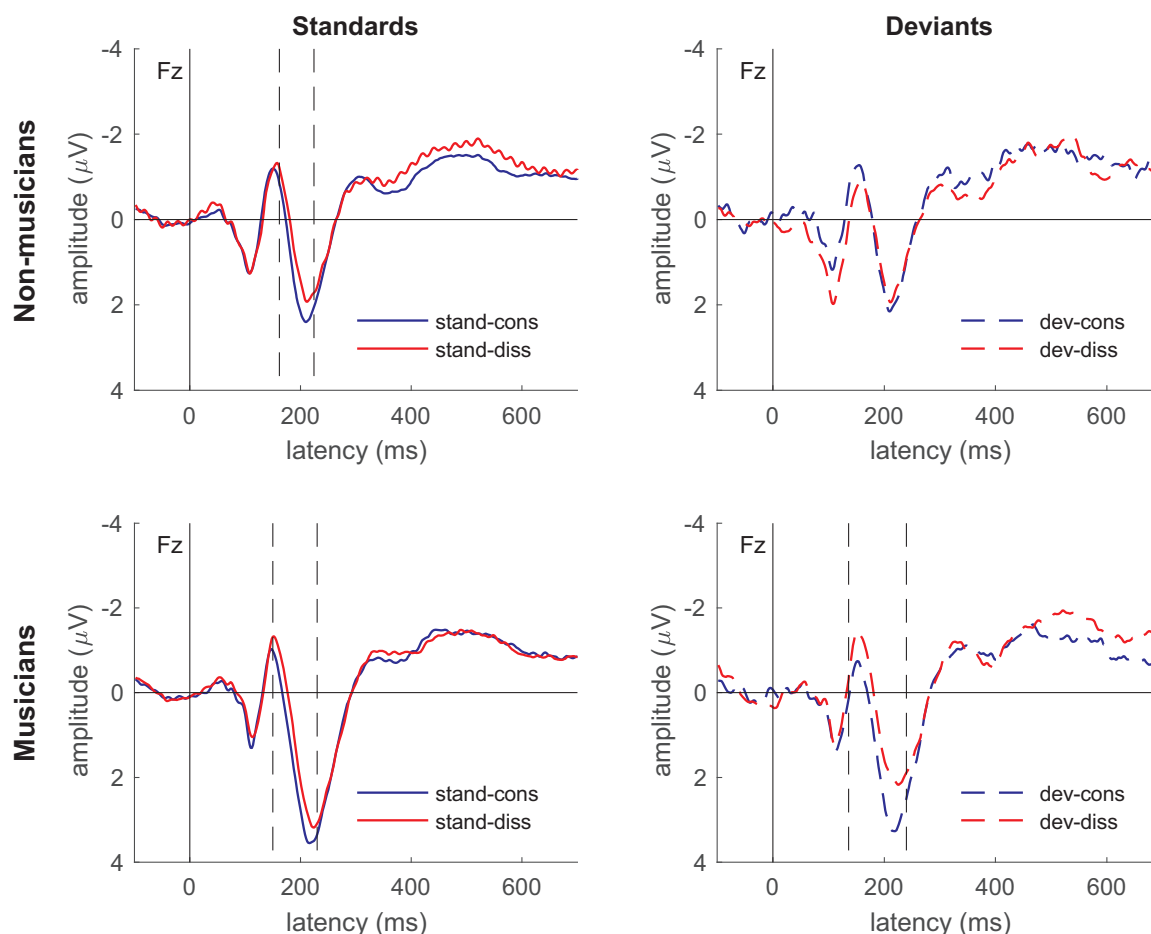
Fig. 5. ERPs for standard (left panel) and deviant (right panel) stimuli in the Fz electrode depending on whether they are implemented over consonant or dissonant intervals.

underlie the processing advantages for consonance that has been reported in behavioral studies and provide information about how formal musical training modulates them.

Previous studies have advanced our knowledge of how the brain differentially responds to consonant and dissonant musical chords.

These studies have demonstrated that the amplitude of brain waveforms (Bidelman and Krishnan, 2009), the cerebral blood flow (Blood et al., 1999) and event-related brain potentials (Itoh et al., 2003, 2010; Regnault et al., 2001) change depending on the perceived consonance and dissonance of the auditory stimuli and on musical expertise. The
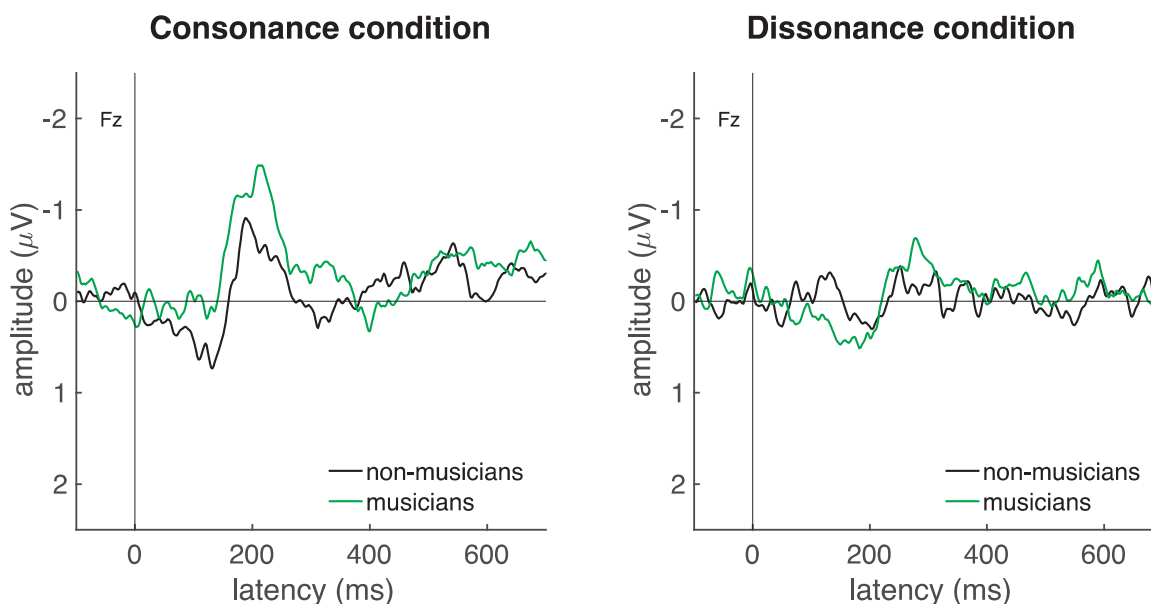

Fig. 6. Difference waves after changes in consonant and dissonant sequences for musicians and non-musicians.

present work complements previous research exploring the neural correlates of consonance processing in three ways. First, our results address the neural activations emerging from changes in the transition from consonance to dissonance and from dissonance to consonance. They thus provide direct evidence about the processing asymmetries along the consonance-dissonance continuum and how they are implemented at the neural level (Minati et al., 2009; Bidelman and Grall, 2014). Second, in line with previous findings (Koelsch et al., 1999) our results highlight the influence of musical expertise on auditory processing. The different neural activations we observed between musicians and non-musicians in response to changes in consonance and dissonance suggests that formal musical training enhances the extraction of information from relevant acoustic stimuli. Third, participants in the present study were not required to explicitly report when they had detected a change. Thus, the brain responses were not recorded under conditions in which attention was focused on the acoustic stimuli (Regnault et al., 2001; Schön et al., 2005). This allowed us to explore pre-attentive processing of consonant and dissonant changes.

The responses observed in our study demonstrate early neural processing benefits for consonance. These responses were elicited in the absence of explicit attentional focus to the sound sequences, as participants in our study were asked to watch a silent movie, and not asked to perform any task over the musical stimuli. Consonant intervals presented as standards triggered a response with more amplitude than dissonant intervals presented as standards in both musicians and non-musicians (see Fig. 5, left panel). This might suggest a more accurate representation of consonant than of dissonant intervals. More importantly, we observed a MMN in both musicians and non-musicians in the consonance condition (repetitive consonant intervals interrupted by dissonant intervals). Thus, our results provide evidence that changes from consonance to dissonance are represented at a cortical level very early on, triggering neural responses (the MMN) independently of musical training. However, the latency for the MMN after changes in consonant sequences was smaller in musicians than in non-musicians. This suggests that the perceived contrast between consonance and dissonance might be easier to perceive for listeners with prolonged musical training, as the peak latency gets shorter with the increasing magnitude of stimulus change (Amenedo and Escera, 2000; Tiitinen et al., 1994). Even more, an enhancement of the N5 component was observed only for musicians in the consonance condition. In the music domain, the N5 has been associated to violations of harmonic expectations (Koelsch et al., 2000; Koelsch and Siebel, 2005). Modulation of the N5 might indicate a strong representation of a clear consonant context for participants with formal musical training. The violation of such consonance context by the presentation of a dissonant interval would be clearly detected by these participants and be reflected by the N5 component. In the present study, the N5 component could thus be linked to a facilitatory effect of musical expertise for the detection of context violations. In the dissonance condition (repetitive dissonant intervals interrupted by consonant intervals) we did not observe any significant changes in brain responses in non-musicians. In this condition, a late MMN was elicited only in musicians. The fact that the MMN was not observed in non-musicians might reflect the difficulty of perceiving changes in dissonance as has been suggested by behavioral studies (Schellenberg and Trehub, 1994, 1996). Concurrently, changes in sequences of dissonant intervals elicited only a late MMN in musicians. The late MMN has been associated with the detection of changes in difficult tasks (Goydke et al., 2004), over complex auditory stimuli (Ceponiene et al., 1998) and under long-term memory conditions (Zachau et al., 2005). So, our results provide evidence at the neural level that detecting changes in dissonant sequences is a more demanding task than detecting changes in consonant sequences. A decreased latency and increased amplitude of the MMN does not necessarily indicate greater neuronal firing but rather a more accurate representation of standard stimuli in the brain (Gaeta et al., 1998). Thus, the late MMN observed in musicians in the dissonance condition

suggests that musical experience might provide listeners with richer acoustic information that facilitates the detection of changes in dissonant sequences. Both the familiarity with dissonant sounds and a general improvement in pitch processing skills (Bidelman, 2013) could make them easier to process (McLachlan et al., 2013), triggering a change-detection component only in musicians. Importantly, although formal musical training allowed the pre-attentive detection of changes in the dissonant context, the longer MMN latency in the dissonant condition compared to the consonant condition indicates once more a processing benefit for consonance even after prolonged formal musical training.

In the consonance condition, we also observed an enhancement of the P1 component only in non-musicians. In the auditory domain, this component has been related to attentional processes and level of arousal (Key et al., 2005). The P1 latency appears to be reduced by acoustic training in adults (Bosnyak et al., 2004). Our findings are consistent with EEG (Virtala et al., 2011) and magnetoencephalography (Kuriki et al., 2006) (MEG) studies in which the amplitude of P1 responses to changes in successive harmonic tones was significantly smaller for musicians compared with non-musicians. Given that an increased activity in the P1 latency range is related to a higher level of arousal to incoming auditory information, it has been argued that a decreased activity in the P1 window might reflect a musician's learned ability to modulate responses after interfering stimuli (Nikjeh et al., 2009). Larger P1 amplitudes as the ones observed for non-musicians in the present study, would thus suggest an increase in processing demands, while smaller P1 would suggest increased processing efficiency. Thus, in the present study, this early positivity would signal that processing a dissonant sound embedded in a consonant sequence might be more demanding to naïve listeners than to musicians. Interestingly, for the musicians group, there seems to be a positive deflection peaking around 180–210 ms in the dissonance condition. Although this positive deflection was not statistically significant, its amplitude might suggests an added difficulty while processing changes in a dissonant context for musicians.

Much work is still needed to understand all the factors underlying the processing advantages of consonance over dissonance. The present study could have benefited from behavioral data that could be correlated to amplitude of ERP responses to confirm the processing advantage for consonance over dissonance. Despite this limitation, in this study we advance in this line of research by showing early neural responses (a P1, a MMN) to consonance changes (but not to dissonance changes) in non-musicians. Importantly, we observed this difference under incidental listening conditions, as participants were not explicitly asked to pay attention to the sounds. This suggests that the processing advantage for consonance does not require higher cognitive levels involving conscious processing of sounds. Its roots could be found at early processing stages. Importantly, our results also reveal a long-term training effect on how the brain reacts to consonance. Contrary to non-musicians, participants with extended musical training showed automatic neural responses (as marked by the emergence of a MMN) in both consonant and dissonant sequences, suggesting that experience allows for more efficient processing of dissonant intervals. But even in musically trained participants, the latency of the MMN revealed a more robust processing of consonance over dissonance.

5. Conclusions

Our results show that brain responses elicited for the transition from consonance to dissonance differ from brain responses to the transition from dissonance to consonance. This pattern of different neural responses might underlie the processing advantages for consonance reported in behavioral studies. Moreover, results from the present study suggest that the processing benefits for consonance might be found already at an early stage of auditory processing and do not depend on attention. Finally, we have also observed a facilitator effect of musical

expertise at a neural level.

Acknowledgments

Ethics

The experimental procedure was approved by the ethical committees of the funding body (European Research Council) and the Universitat Pompeu Fabra (reference number 4852/1). All participants signed an informed consent.

Declaration of interests

None.

Data, code and materials

Article's supporting data is provided as supplementary material.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2018.06.005.

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