BIOLOGICAL FOUNDATIONS OF CONSONANCE PERCEPTION: EXPLORING PHYLOGENETIC ROOTS AND NEURAL MECHANISMS

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A mi familia, en especial a mis padres

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ABSTRACT

Consonance is one of the most salient features of music. Despite its central role in Western music, its origins remain controversial. Thus, understanding the mechanisms involved in the perception of a chord as consonant (stable) or dissonant (unstable), have become an outstanding issue in music perception research. The present dissertation is devoted to explore the biological bases of consonance perception through a comparative and a neurophysiological approach. Results from several experiments showed that rats, a species with no documented vocal learning abilities, share with humans the capacity to discriminate consonance from dissonance. The animals however lack the ability to generalize to new stimuli and do not exhibit processing benefits for consonance as humans do. Moreover, musicians' neural responses triggered by changes in consonance and dissonance differed from those of non-musicians. Together, the results reported in the present dissertation highlight that experience with harmonic stimuli, such as vocal production and musical training, is an important factor to account for the emergence of consonance within our musical system.

RESUMEN

La consonancia es una de las características más salientes de la música. A pesar de su papel fundamental en la música occidental, sus orígenes siguen siendo controversiales. Por lo tanto, la comprensión de los mecanismos implicados en la percepción de un acorde como consonante (estable) o disonante (inestable), se ha convertido en una cuestión pendiente en la investigación de la percepción musical. La presente tesis doctoral está dedicada a explorar las bases biológicas de la percepción de la consonancia a través de dos enfoques, comparativo y neurofisiológico. Los resultados de varios experimentos mostraron que las ratas, una especie sin habilidades vocales, comparten con los humanos la capacidad de discriminar la consonancia de la disonancia. Sin embargo, los animales carecen de la capacidad de generalizar a nuevos estímulos y no presentan beneficios para el procesamiento de la consonancia como lo hacen los humanos. Por otra parte, las respuestas neuronales desencadenas por cambios en la consonancia y disonancia difieren entre músicos y no músicos. En conjunto, los resultados reportados en esta tesis ponen de manifiesto que la experiencia con estímulos harmónicos, tales como la producción vocal y la formación musical, es un factor importante para explicar el fenómeno del a consonancia dentro de nuestro sistema musical.

PREFACE

The evolutionary origins and adaptive significance of music ability have long intrigued scholars. In *The Descent of Man* (1871), Darwin already stated that our musical abilities "must be ranked among the most mysterious with which humans are endowed". There is no evidence that any other species has developed musical skills. Thus, music has been considered as one of the abilities that define us as humans (Patel, 2008). Despite the central role of music in human culture, its origins and adaptive function remain a mystery. There has thus been an increasing interest in the understanding of the cognitive bases that support the faculty of music, and over the past few years music has been an active topic of empirical studies within the field of cognitive science.

At a first glance, it may seem that music is not specific to humans. Other species do produce "songs". However, the context of their singing differs by far from that of humans. While this is the topic of many discussions, humans' singing is at least partially produced for pure enjoyment, with no clear adaptive consequences. Animals' songs on the contrary are tightly linked to their communicative functions and there is no evidence of performances for entertainment in non-human species (Hauser & McDermott, 2003). In fact, animal singing has been defined by its adaptive role, being mainly used in the context of territory defense and mate attraction (Catchpole & Slater, 1995; Marler, 1999).

Throughout human history, music has been present in every known culture. It is precisely because the universality and uniqueness of music in our species, that its study has grown in importance to understand human cognition and evolution. The study of the evolution of music has followed mainly two approaches. The first one favors the view that musical abilities are a direct target of natural selection (e.g. Wallin et al., 2000; Balter, 2004; Mithen, 2005). The second considers music as a by-product of other cognitive skills (e.g. Pinker, 1997). Again, even though this is a highly debated issue, hypotheses about the possible adaptive roles of music in human evolution, ranging from courtship to social cohesion, do not seem to explain all the implications of music in human culture (e.g. Miller, 2000; Cross, 2003; Morley, 2003). Thus, the origins and adaptive significance of music (if any) remain unknown and are the focus of much research (Patel, 2008).

As pointed out in McDermott and Hauser (2005), the two approaches, the one suggesting music as a by-product of other cognitive skills and the one considering music as a biological adaptation, might not be mutually exclusive. Rather, it could turn out that some aspects of music emerge from general-purpose auditory mechanisms, while other aspects are the result of music-specific adaptations. One way to disentangle the relative contributions of each one and advance our knowledge of the biological foundations underlying our musical ability is to explore the initial state of music knowledge prior to experience and how relevant experience alters this state (Hauser & McDermott, 2003).

A fruitful approach to explore the initial state of music knowledge is through comparative studies. Comparative data from non-human animals can thus provide much information on the evolutionary origins of music that is difficult to obtain in any other way.

In the present dissertation, we wanted to explore the biological bases underlying the perception of consonance, a salient aspect of music related to aesthetics. To this end, comparative and neurophysiological approaches were used. The comparative work explored whether animals lacking experience with harmonic stimuli process consonance in a similar way as humans do. The neurophysiological study explored the underlying mechanisms of consonance processing in listeners with varying degrees of experience with music (non-musicians and musicians). Importantly, both lines of study addressed the question of whether consonance perception might be influenced by the previous experience that the listener had with harmonic and musical stimuli.

The present work will have the following organization. In a first *Introduction* section, relevant literature about the consonance-dissonance phenomenon will be presented and the studies will be framed within current theories of music cognition. Importantly, in this section a special attention is given to describe recent research on consonance processing in humans and other species. Next, there will be two experimental sections. In *Experimental Section I* two manuscripts addressing consonance perception from a comparative perspective are presented. The *Experimental Section II* encompasses

one manuscript exploring the neural responses underlying the processing of consonance in humans. Then, in a *General Discussion* section the findings we observed in the experiments and their potential impact on consonance processing theories are reviewed. We also propose possible directions for future studies in this field of research. Finally, in the *Summary and Conclusions* section the findings of the present dissertation are briefly recapitulated.

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1. INTRODUCTION

Although music has been claimed to be a faculty unique to our species (Patel, 2008), little is known about its evolutionary history and the cognitive mechanisms essential for perceiving and appreciating it. One way to advance our knowledge of the basic mechanisms that allow the emergence of the musical ability is to explore the initial state of music knowledge prior to experience and how relevant experience alters this state (Hauser & McDermott, 2003). The present work aims to understand the underlying mechanisms involved in the perception of consonance, one of the most salient features of music associated with pleasantness and deeply rooted in how people experience music.

To tackle this issue we will advance along two lines of research. The first line will take a comparative approach exploring the extent to which non-human animals might share with humans some of the mechanisms responsible for consonance processing. The second line of research will explore the neural responses involved in consonance perception in humans. Similarities in music processing between humans and other species would shed some light on the origins of musical structures. It is feasible that perceptual competencies in non-human animals play a substantial role in music perception and cognition in humans. Likewise, findings of brain-based mechanisms involved in the cognitive processes underlying music perception can tell much about the biological roots of music. The present dissertation encompasses three studies. Two of them

explore consonance processing from a comparative perspective. The third study takes a complementary neurophysiological approach to explore the neural activity underlying the perception of consonance in humans.

Before describing the experimental work, a general overview of consonance-dissonance phenomena will be presented. First it will be described what are consonant and dissonant intervals, followed by a summary of the main theories proposed to explain the perception of consonance. Next, there will be a description of recent and relevant research for this work on consonance processing in humans and other species.

1.1 The phenomenon of consonance – dissonance

"Agreeable consonances are pairs of tones which strike the ear with certain regularity; this regularity consists in the fact that the pulses delivered by the two tones, in the same interval of time, shall be commensurable in number, so as not to keep the ear drum in perpetual torment"

Galileo Galilei

The term "consonance" comes from the Latin *consonare* that means "sounding together". Harmony, the sound of two or more tones played simultaneously, is a basic element of Western music that can be defined in terms of its relative harshness. A smooth-sounding harmonic combination is considered to be consonant (pleasant)

while a harsh-sounding harmonic combination is considered as dissonant (unpleasant). Consonant intervals are usually described as more pleasant, euphonious and beautiful than dissonant intervals that are perceived as unpleasant, discordant, or rough (Plomp & Levelt, 1965). Thus, the terms "consonance" and "dissonance" make reference to the degree of pleasantness or stability of a musical sound as perceived by an individual.

1.1.1   Consonant and dissonant intervals

An interval in music is the distance between two pitches (tones). When intervals are presented in a musical context, their perceptual quality is modulated by the context in which the intervals are heard (e.g. chords composing a melody). This is known as *musical consonance* (Cazden, 1980). Different from this, when intervals are presented in isolation, the perceived smoothness or harshness is referred as *sensory consonance* (Krumhansl, 1990). To better understand what the intervals are, we will first briefly explain the use of the diatonic scale in Western culture.

In Western music, the diatonic scale makes use of 7 tones out of 12 possible tones from the chromatic scale (C, C#/D♭, D, D#/E♭, E, F, F#/G♭, G, G#/A♭, A, A#/B♭, B). These 7 tones are used to construct the diatonic (major/minor) scales that define tonality and musical key (e.g. the C major scale: C, D, E, F, G, A, B; see Figure 1.1). The distance between a note and the next higher instance of

that note is called the octave (e.g. the distance between C and C'). Each note has a specific frequency (how fast it vibrates). The relationship between two notes (the interval) is defined in terms of the ratio of frequencies of the two notes. For instance, the frequency ratio of the octave interval is expressed as 1:2 (the frequency of the higher note is exactly the double of the frequency of the lower note). One of the most common explanations for the perceptual phenomena of consonance and dissonance is related to the simplicity of the frequency ratios of the intervals. It was the Greek mathematician and philosopher Pythagoras who first attributed consonance to simple frequency ratios. The simpler the ratio between two notes the more consonant (stable) the sound. Conversely, the more complex the ratio between two notes the more dissonant (unstable) the sound.

Notes of the chromatic and diatonic scales
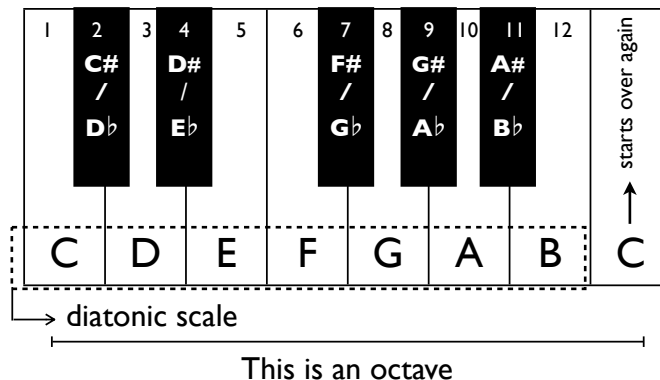
Figure 1.1 A one-octave portion of the piano keyboard indicating the twelve chromatic and seven diatonic notes.

Intervals are usually identified in their short name by a letter and a number. The letters denote the quality of the interval. They can be called perfect (P), major (M), minor (m), augmented (A), and diminished (d). Perfect intervals are considered perfectly consonant while major, minor, augmented and diminished intervals are considered to be less consonant (Weber, 1981). The numbers (1, 2, 3, 4, 5, 6, 7 and 8) make reference to the distance between two notes of the diatonic scale. Thus, for instance, a perfect fifth (P5) is so-called because it is considered as a perfect consonance and there are 5 tones (C, D, E, F, G) between the lower and higher note (e.g. from C to G). The bottom note is known as the root. In table 1.1, intervals are listed in ascending number of semitones.

Interval naming				
Number of semitones	Interval name	Short name	Upper Note	Interval ratio
0	Unison	P1	C	1:1
1	Minor second	m2	C#	15:16
2	Major second	M2	D	8:9
3	Minor third	m3	D#	5:6
4	Major third	M3	E	4:5
5	Perfect fourth	P4	F	3:4
6	Tritone	TT	F#	32:45
7	Perfect fifth	P5	G	2:3
8	Minor sixth	m6	G#	5:8
9	Major sixth	M6	A	3:5
10	Minor seventh	m7	A#	9:16
11	Major seventh	M7	B	8:15
12	Octave	P8	C'	1:2

Table 1.1 The root note (lower note) is considered to be C, and upper notes are specified for each interval.

It is important to note that the perception of consonance-dissonance is continuous, a gradation from the most consonant to the most dissonant sound, rather than clearly defined categories (e.g.,

Kameoka and Kuriyagawa, 1969a; Krumhansl, 1990). Given that what is pleasing to one person may be unpleasant to other, the concept of consonance is considered to be subjective and culturally conditioned. However, several studies across different time periods and different countries have reported similar ranking judgments of the degree of consonance over tone combinations of the chromatic scale (e.g., Bowling, 2012; Butler & Daston, 1968; Guernsey, 1928; Malmberg, 1918) being some tone combinations ranked consistently as consonant and others ranked consistently as dissonant (see Figure 1.2 for a summary of these results).
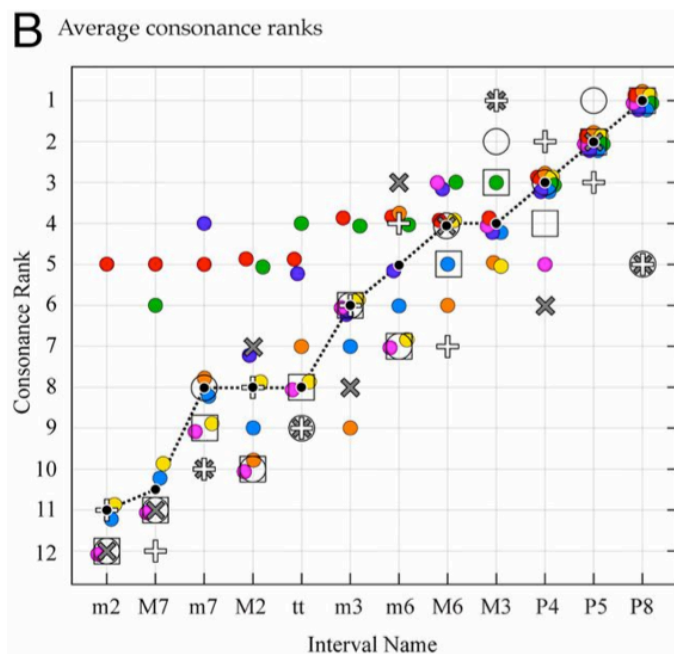
Figure 1.2 The relative consonance assigned by listeners to each of the 12 chromatic intervals played as two-tone chords. The filled black circles and dashed line show the median rank for each interval; colored circles represent data from Malmberg (1918); open circles from Guernsey (1928); crosses from Butler and Daston (1968); open squares from Bowling (2012). These data were collected between 1898 and 2012, in Germany, Austria, the United Kingdom, the United States, Japan, and Singapore. Reproduced from Bowling & Purves (2015).

Based on these studies and different theories emphasizing the physical features of the sound as the basis for consonance (e.g. Helmholtz, 1877), intervals have been classified according to their perceived degree of consonance (see Table 1.2). Though the consonance ranking is often considered as factual, it could vary depending on musical styles and different cultures.

Consonance ordering of tone combinations		
Interval evaluation	Interval name	Interval ratio
Absolute consonances	Unison	1:1
	Octave	1:2
Perfect consonances	Fifth	2:3
	Fourth	3:4
Medial consonances	Major sixth	3:5
	Major third	4:5
Imperfect consonances	Minor third	5:6
	Minor sixth	5:8
Dissonances	Major second	8:9
	Major seventh	8:15
	Minor seventh	9:16
	Minor second	15:16
	Tritone	32:45

Table 1.2 Ordering of consonances for two-tone intervals from Helmholtz (1877, pp. 183 and 194) as accepted in the Western musical culture in decreasing order of 'perfection' from most consonant to most dissonant.

Although this perceptual phenomenon has been studied for centuries, there is not a unique explanation of what are the factors that influence the perception of consonance and dissonance. Several theories have been proposed throughout the years.

1.1.2 Main theories on consonance perception

The perception of consonance and dissonance are among the oldest and more debated phenomena in music history. As pointed out by Hindemith "the two concepts have never been completely explained, and for a thousand years the definitions have varied" (Hindemith 1942, p.85). Broadly, the main theories explain the perception of consonance-dissonance in terms of acoustics, psychophysics and enculturation. In this section we will present a brief review of the main historical theories that have been proposed to explain these perceptual phenomena.

Acoustic theories

Acoustic theories rely on the physical properties of the acoustic signal as the basis for consonance perception. Early attempts linked the degree of consonance-dissonance of an interval (two tones sounding simultaneously) to frequency ratios (the relation between the frequencies of the two notes). The *number ratio theory* has been traditionally attributed to Pythagoras (around 500 BC; Stanley, 1655) and states that simple interval ratios between two tones (e.g. 1:2, the perfect octave) result in consonance while complex interval ratios between two tones (e.g. 15:16, the minor second) result in dissonance. Plomp & Levelt (1965) note that this first approach has occupied scholars for years and that later in time scientists such as Euler, Lipps and Polak have supported this hypothesis. Another approach based on the physical properties of the sound is the

roughness theory proposed by Helmholtz (1877). The author claimed that the perception of dissonance is due to a sensation of roughness that comes from rapid amplitude fluctuations called "beats". The beats are produced when some notes are combined. Helmholtz observed that at the distance of an octave (1:2; considered a perfect consonance), the partials of the two harmonic complex tones did not produce beats, and consequently no sensation of roughness. Thus, it was deduced that the more beats contained within a sound, the more rough will be the sound leading to an increased perception of dissonance (Terhardt, 1974). In line with these acoustic approaches, the *periodicity length theory* developed by Irvine (1946), suggests that consonance and dissonance are related to the length of the periodicity of a cycle. The length of a repetition for a combined signal (two tones) depends on the simplicity of the frequency ratio. When two tones are related by simple frequency ratios, the cycle of repetition is relativity short. On the contrary, when tones are not related by simple frequency ratios, the cycle of repetition for the combined signal is long.

Psychophysiological theories

These theories base the perception of consonance-dissonance on psychophysiological aspects of the auditory system. For instance, the *critical-band hypothesis* by Plomp and Levelt (1965) propose that the degree to which an interval is perceived as consonant or dissonant is related to cochlear mechanisms. The hypothesis suggests that the degree of consonance of a musical interval

depends on the interaction of frequency components within single auditory filters. Intervals with a frequency difference exceeding critical bandwidth are judged as consonant while the most dissonant intervals correspond with frequency differences of about a quarter of the bandwidth. As explained in Bidelman and Heinz (2011), the pitches of consonant intervals have fewer partials that pass through the same critical bands (giving pleasant percepts) than pitches of dissonant intervals whose partials compete within individual channels. The *synchrony of neural firings theory* by Boomsliter and Creel (1961) proposes that musical intervals are governed by inherent properties of the auditory system. According to this theory, consonance arises when neural impulses in the auditory system are synchronized.

Enculturation theories

These theories propose that consonance-dissonance perception is due to social, cultural and stylistic norms that listeners are exposed to. From this point of view the perceptual difference for tone combinations would be learnt, developed over time and emerged in the context of a given culture. According to the *adaptation theory* of Moore (1914) and Odgen (1924) listeners are more likely to judge an interval as consonant depending on the amount of exposure that they and their ancestors have had to that interval. The more they have been exposed to certain intervals, the more consonant would be perceived those intervals. This theory was discarded because it is based on the inheritance of acquired characteristics (Hargreaves, 1986). However, the idea that the amount of exposure to intervals

determines the evaluative response to them was supported later by other studies (e.g. Guernsey 1928; McDermott, Lehr, & Oxenham, 2010; McLachlan, Marco, Light, & Wilson, 2013; Valentine, 1962).

In Valentin (1962), children of different ages were tested for aesthetic judgments for intervals. Results showed that older as well as musically trained children approximate more to the adults' pattern of evaluation for intervals than younger children, suggesting a strong role of experience. These findings are corroborated by the study of MacLachlan and collaborators (2013). The authors provide evidence that adaptation through experience plays a central role in the development of harmony perception and propose that recognition mechanisms underlie consonance judgments. The experiments showed that listeners' familiarity with chords facilitated pitch processing, increasing the perception of a sound as consonant. Similarly, Guernsey (1928) reported a series of experiments that led to the conclusion that consonance was associated with familiarity for commonly used chords. McDermott and collaborators (2010) also report that exposure to music amplifies preference for harmonic frequencies because of their musical importance. All these studies coincide in the idea that the perception of consonance and dissonance emerges from cognitive processes, such as the categorical perception of musical intervals and recognition mechanisms linked to learning. From this perspective, exposure, familiarity and learning are all important aspects of consonance (Cazden, 1980). But not only experience perceiving certain sounds is important for consonance perception,

experience producing harmonic sounds might also play a role. For example, human vocalizations have also been considered to account for consonance perception (Schwartz, Howe, & Purves, 2003). In Schwartz and collaborators (2003), an analysis of the speech signal revealed that the probability distribution of amplitude-frequency combinations in human utterances predicts consonance ordering. Because human vocalizations are the periodic acoustic stimuli to which humans are more exposed to and mostly produce, this extensive experience would lead to a preference for consonant intervals.

Enculturation theories also take into account the current convention of the musical culture (Lundin, 1967) and the specific context of a given musical passage (Gardner & Pickford, 1944) for the evaluation of consonance and dissonance of an interval. Given that musical styles are ever changing, not only differences between cultures (e.g. Western and Eastern) but also different ages in the same culture are considered as factors influencing perceptual differences for pitch combinations. In the same way, unlike isolated chords, the context of an entire melody can affect the perceived gradation of consonance/dissonance of chords. Therefore, from the perspective of enculturation, consonance and dissonance are a matter of individual preference molded through culture.

1.2 Human research on consonance processing

Over the past years, there has been an increased interest on the mechanisms underlying music perception and cognition. Among these studies, understanding those mechanisms involved in consonance as one of the most salient features in music, have become an outstanding issue in this research field. In the next sections we will present the most relevant recent findings on consonance processing research in humans.

1.2.1 Preferences

Is consonance equivalent to preferences for certain tone combinations over others? A study by Butler and Daston (1968) provided consistent evidence that judgments for the distinction between consonance and dissonance can be described in terms of preference. In this study, naïve American listeners were presented with a list of pairs of dyads (two-note chords). Participants were asked to state a preference for one dyad of each pair. Results showed a high degree of agreement among all the participants in preference for some dyads over others. Importantly, the ordering of preferences observed in this study highly correlated with the ranking of the musical intervals with respect to the degree of consonance performed by musical "experts" (Malmberg, 1918). Malmberg sought to experimentally standardize the perception of consonance and dissonance by asking expert listeners to rank dyads based on four factors: fusion, blending, smoothness and purity. The fact that the ordering of preferences of naïve listeners fairly

matched the rank based on experts' judgments led to the conclusion that preference for certain tone combinations over others can be considered as an equivalent to consonance.

The fact that listeners were so consistent in their ordering of tone combinations according to consonance rankings led to the idea that consonance preference did not change over development. The question of whether preferences for consonance are innate or developed over time has been addressed empirically recently. Studies have focused on infants' responses (in terms of looking times) to consonant and dissonant stimuli. Results revealed that the preferential bias for consonant over dissonant sounds arises already in early stages of development (e.g. Trainor & Heinmiller, 1998; Trainor, Tsang, & Cheung 2002; Zentner & Kagan, 1998; see Figure 1.3) ranging from 2 to 6 months of age. Conclusions from these studies pointed to the idea that such preference for consonant sounds might be present from birth and is not dependent on experience.
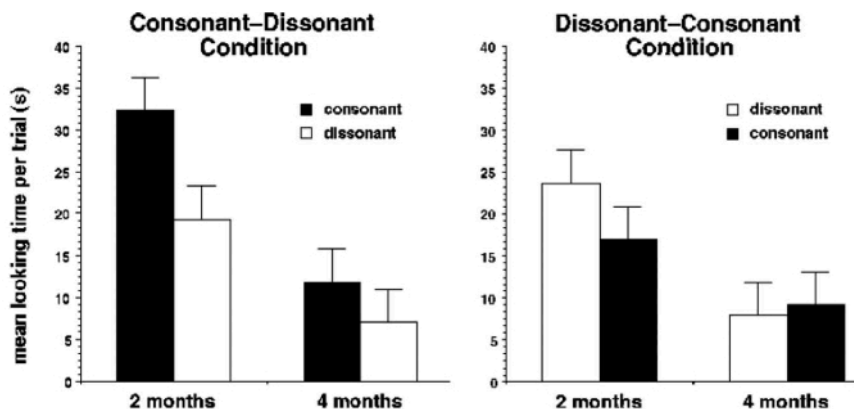
Figure 1.3 Mean looking times to consonant and dissonant stimuli for 2- and 4-month-old infants. Reproduced from Trainor et al. (2002).

Nevertheless, recent studies have highlighted the central role that experience plays in the emergence of consonance preference. A study with 6-month-old infants showed that after a short pre-exposure to consonant or dissonant stimuli infants do not show a preference for consonance over dissonance. Infants paid more attention to the stimuli they were pre-exposed to (the familiar stimulus), independently of whether it was consonant or dissonant (Plantinga & Trehub, 2014; see Figure 1.4). A more recent study with a native Amazonian society provided additional empirical support to the idea that experience plays a pivotal role in preferences for consonance. Indigenous participants, with minimal exposure to Western culture, rated consonant and dissonant chords equally pleasant, suggesting that consonance preferences might not arise from innate biases (McDermott, Schultz, Undurraga, & Godoy, 2016). In this study, McDermott and collaborators compared ratings of pleasantness of sounds in populations varying in their exposure to Western music. Participants in the study were residents of the United States and three different populations from Bolivia. Results showed cross-cultural variations. Preference for consonance depended on the degree of exposure to harmonic music (see Figure 1.5), with participants more exposed to Western harmonic music (residents of the United States) showing a clear consonance preference, while participants with no exposure to Western harmonic music (indigenous participants from the Amazonian tribe) showing no preference for consonance. This pattern of results observed across cultures highlights the importance of studies testing non-Western populations to gain insight about the

origins of consonance perception. Together, the results from these studies on the role of experience bring further support to the idea that familiarity with chords facilitates pitch processing, leading to an increased perception of a sound as consonant (McLachlan et al. 2013).
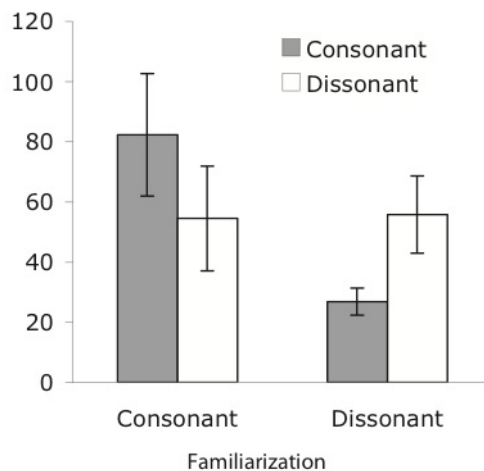
Figure 1.4 Mean cumulative looking (seconds) to consonant and dissonant stimuli as a function of familiarization with consonant and dissonant stimuli. Error bars are standard errors. Reproduced from Plantinga & Trehub (2014).

As evidenced from these recent results, the origins from consonance perception still remain controversial. However, these studies illustrate that sensitivity to consonance and dissonance not only implies a perceptual difference between them but also a preference.
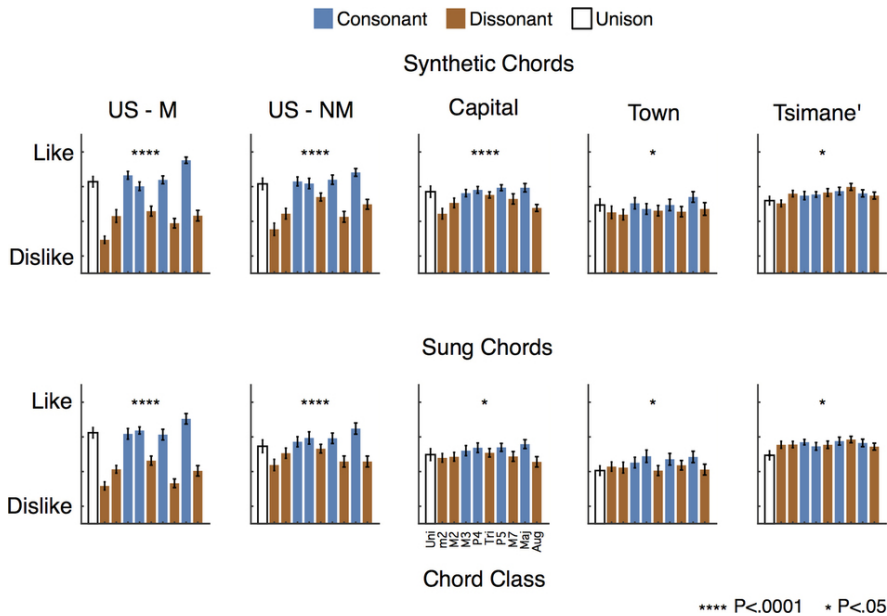
Figure 1.5 Ten chords were presented: the unison, minor second, major second, major third, perfect fourth, tritone, perfect fifth, major seventh, major triad, and augmented triad. The composite ratings plotted were averages of those for consonant (blue) and dissonant (brown) chords. Ratings are from 23 US musicians (US-M), 25 US non-musicians (US-NM), 24 Bolivian city-dwellers (capital), 26 Bolivian town-dwellers, and 64 Tsimane'. Asterisks denote statistical significance of a repeated-measures ANOVA across all chord ratings. Data are mean and s.e.m. Reproduced from McDermott et al. (2016).

1.2.2 Processing differences

As we argued above, perceptual differences and preferences for tone combinations are well established. Most people perceive some intervals as pleasant or consonant and other intervals as unpleasant or dissonant. These aesthetic differences lead to preferences for the former over the latter. Beyond the perceptual differences, some evidence suggests that the distinction between consonance and dissonance also triggers processing differences. Behavioral studies

testing human adults (Komeilipoor, Rodger, Craig, & Cesari, 2015; Schellenberg & Trehub, 1994) and infants (Schellenberg & Trehub, 1996) have demonstrated that there are processing advantages for consonance over dissonance. In the studies of Schellenberg and Trehub (1994, 1996) adult and infant participants detected changes in patterns containing simple frequency ratios (consonant intervals) easier than changes in patterns with complex ratios (dissonant). Similarly, in a recent study Komeilipoor and colleagues (2015) found that participants' performance in a movement synchronization task, using a finger-tapping paradigm, was better after the presentation of consonant stimuli than after the presentation of dissonant stimuli. Results showed a higher percentage of movement coupling and a higher degree of movement circularity after the exposure to consonant sounds than to dissonant sounds. Together, these studies add a strong contribution to the understanding of the phenomenon of consonance. Their findings suggest that consonance perception goes beyond aesthetic preferences and might even facilitate cognitive processing. Despite this outstanding evidence, little research has been devoted to explore the extent to which cognitive performance in other tasks is influenced by the degree of consonance in auditory stimuli.

1.2.3 Neural correlates

Modern neuroimaging and electrophysiological studies have tried to identify the encoding mechanisms for consonant and dissonant pitch

relationships in brain activity. Evidence from functional magnetic resonance imaging (fMRI) have shown that the cerebral blood flow changes as a function of the perceived consonance and dissonance in different brain areas such as the premotor cortex, the cingulate and the frontal gyrus (e.g. Foss, Altschuler, & James, 2007; Minati, Rosazza, & D'Incerti, 2009; Tillmann, Janata, & Bharucha, 2003). Studies with event-related brain potential (ERPs) have determined as well that the modulations of cortical activity in response to musical chords change as a function of the degree of consonance (Minati, et al. 2009; see Figure 1.6). In fact, these neural representations for pitch combinations correlate with the hierarchical ordering of musical pitch; that is, the degree of consonance/dissonance of pitch combinations (Bidelman & Grall, 2014; Brattico, Tervaniemi, Näätänen, & Peretz, 2006; Itoh, Suwazono, & Nakada, 2010; Krohn, Brattico, Välimäki, Tervaniemi, 2007).
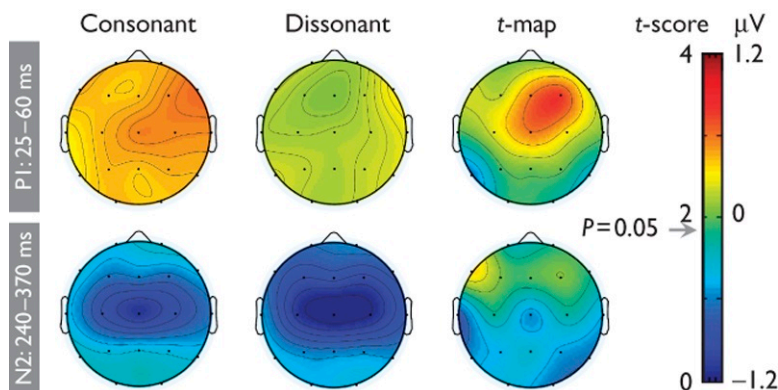
Figure 1.6 Topographic maps of average potential and *t*-scores (obtained with two-tailed paired *t*-tests over both musicians and non-musicians) for the P1 and N2 time windows. Reproduced from Minati et al. (2009).

In addition, it has been found that the amplitude of the frequency following responses (FFR) triggered by consonant intervals is higher than the amplitude of responses following dissonant intervals (Bidelman & Krishnan, 2009). Even more, evidence from both neuroimaging and electrophysiological studies has shown that neural correlates for consonance and dissonance can change as a function of musical expertise (for a review see Bidelman, 2013). As revealed from fMRI data, the areas of activation for consonant chords are right lateralized for non-musicians and less asymmetric for musicians (Minati, et al., 2009; see Figure 1.7). Likewise, different ERPs components elicited for musicians and non-musicians when processing harmonic intervals suggest that musicians discriminate intervals at earlier processing stages than non-musicians (Schön, Regnault, Ystad, & Besson, 2005; Regnault, Bigand, & Besson. 2001).
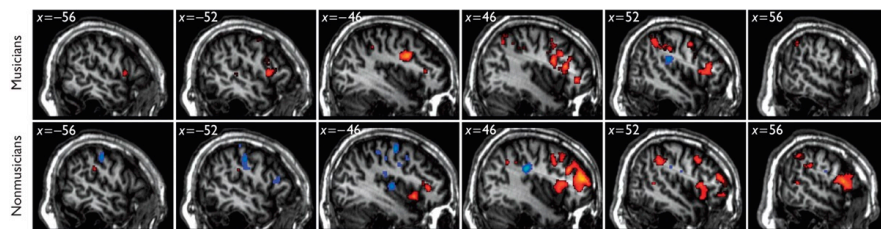
Figure 1.7 Group-level activations (at $P< 0.01$) for musicians and nonmusicians on sagittal selections for the left (x=-56, -52 and -46) and for the right hemispheres (x=56, 52 and 46). Red-yellow indicates larger response for consonant chords, blue-cyan the converse. Reproduced from Minati et al. (2009).

These studies demonstrate that indeed the brain responds differently to consonant and dissonant musical chords. Moreover, the fact that

there are changes in brain functions due to musical expertise provides strong support to the idea that experience does influence the perceptual attributes of consonance and dissonance. So far, electrophysiological and neuroimaging studies that address consonance processing have advanced much our understanding of the cerebral bases of consonance perception. However, there is still much to be learned about the neural underpinnings of the advantage of consonance over dissonance observed in behavioral studies (Komeilipoor et al., 2015; Schellenberg & Trehub, 1994; 1996).

1.3   Animal research on music perception

What is the importance of animal research on music perception? Findings from comparative work might be central to answer questions about the evolutionary origins of music. More precisely, comparative work is central to explore three major questions (Hauser and McDermott, 2003) very similar to the ones posed by Chomsky regarding research on the understanding of evolution and development of language (for example, Chomsky, 2005). Authors consider that from a comparative perspective one would know: which is the initial state of knowledge of music prior to experience with music, how this initial state is transformed by relevant experience, and the evolutionary history of the initial state. Thus, comparative work in music perception is a powerful tool to investigate the evolution of music.
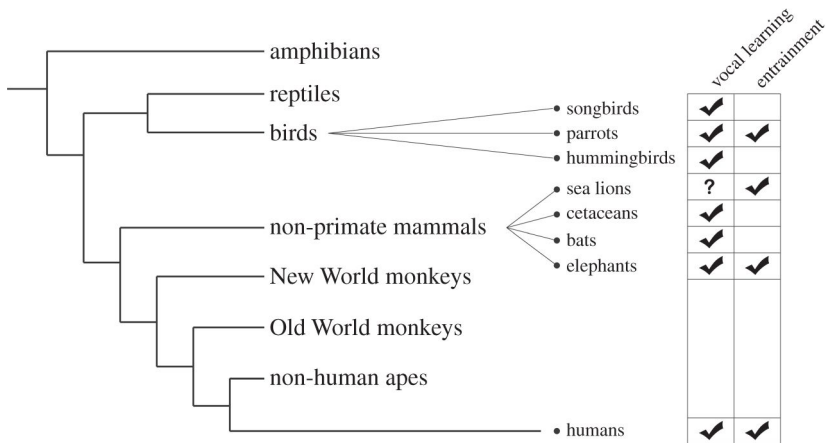
Experiments testing nonhuman animals are also essential mainly for two reasons (McDermott and Hauser, 2005). First, musical exposure can be carefully controlled under laboratory conditions. Unlike experiments with human adults and infants, animals can be deprived from any musical stimuli from birth. Thus, any music-related perceptual biases found in animals cannot be the result of musical exposure. Second, since animals do not produce music, musical biases present on them would have evolved for general auditory mechanisms rather than as adaptation to music. Hence, the comparative approach can provide data that would be challenging to obtain in other way.

Comparative studies addressing music perception have already shown that animals are able to respond to several aspects of music stimuli in a similar way as humans do. For example, in Porter and Neuringer (1984) study, pigeons were trained to differentiate between excerpts of musical pieces from Stravinsky and Bach. Pigeons learnt the discrimination and generalized to new musical excerpts of these composers. Even more, pigeons were able to distinguish the new Stravinsky's and Bach's musical excerpts from excerpts belonging to other composers. Similarly, carps were able to discriminate blues from classical music and transfer the learnt discrimination to new pieces (Chase, 2001). These experiments demonstrate animals' capacity to tell apart music from different composers and genres. However, it is difficult to tell which musical features guided the discrimination. Further studies have addressed this issue by exploring basic elements of music individually (such

as pitch, meter, timbre and rhythm) and in different species (for a review see Hoeschele, Merchant, Kikuchi, Hattori & ten Cate, 2015).

Research has revealed that processing of some musical traits, such as pitch (a property of sounds that allows to judge them as "higher" or "lower" depending on frequency) and rhythm (a regular pattern in time) might vary importantly across species. For example, studies on pitch processing suggest that birds are better than mammals (Friedrich, Zentall, & Weisman, 2007; Weisman, Njegovan, Sturdy, Phillmore, Coyle, & Mewhort, 1998; Weisman, Njegovan, Williams, Cohen, & Sturdy, 2004), including humans, in the ability to perceive sounds varying in frequency. Regarding rhythm processing, studies have shown that some avian species (Hasegawa, Okanoya, Hasegawa, & Seki, 2011; Patel, Iversen, Bregman, & Schulz, 2009; Schachner, Brady, Pepperberg, & Hauser, 2009) but not primate species (Hattori, Tomonaga, & Matsuzawa, 2013; Honing, Merchant, Háden, Prado, & Bartolo, 2012; Zarco, Merchant, Prado, & Mendez, 2009) have the capacity to synchronize to a beat. Primate species were not able to display synchronization to a sequence of regular beats on different tempi even after a long period of training while avian species developed this behavior without any formal training (but see Cook, Rouse, Wilson & Reichmuth, 2013 for evidence of rhythm synchronization in a Sea Lion).

The production of complex vocalizations has been proposed as one of the constraints to develop or not the capacity to synchronize rhythmic movements to a beat (Patel, 2014). This vocal learning hypothesis suggests that the aforementioned capacity is determined by changes in brain structure driven by evolution of complex vocal learning. Brain structure of vocal learners has been shown to be associated with specialized neural circuitry involving connections of pre-motor areas and the basal ganglia (Petkov & Jarvis, 2012). Few species have been identified as vocal learners and possessors of entrainment, and none of them are closely related to humans (Hoeschele et al., 2015; see Figure 1.8). Beyond rhythm perception, vocal production learning has been suggested as one of the five fundamental constraints –including cultural transmission, generativity, entrainment and motivation– for the structure of music in general (Merker, Morley, & Zuidema, 2015). Thus, a very important area of research in comparative cognition is to explore similarities and differences in music processing across species that are considered as vocal learners and species that are not vocal learners.

amphibians

reptiles

birds
- songbirds
- parrots
- hummingbirds

non-primate mammals
- sea lions
- cetaceans
- bats
- elephants

New World monkeys

Old World monkeys

non-human apes

- humans

	vocal learning	entrainment
songbirds	✔	
parrots	✔	✔
hummingbirds	✔	
sea lions	?	✔
cetaceans	✔	
bats	✔	
elephants	✔	✔
humans	✔	✔

Figure 1.8 Species with vocal learning and entrainment abilities and their relationship in a phylogenetic tree. Reproduced from Hoeschele et al. (2015).

Animal research certainly provides a different and useful approach to explore the underlying mechanisms of music perception, as revealed by the findings explained above. They have shown that some basic abilities involved in music processing might be the result of general acoustic biases, like those involved in perceiving rhythm. But more important for the present work, besides studies exploring pitch and rhythm perception across species, some work has also been devoted to understanding whether consonance perception is also observed in non-human animals. In the next section, studies addressing consonance perception in non-human animals will be presented.

1.3.1 How general is the perception of consonance and dissonance in other species?

Comparative studies exploring the perception of consonance and dissonance, and the variety of species tested for this purpose, have been scarce. However, research tackling consonance perception in non-human animals has explored the phenomenon from different perspectives including discrimination, preference and neurophysiological studies.

Discrimination studies have tested the perception of sensory consonance and dissonance primarily in avian and primates species. In these studies, Java sparrows (Watanabe, Uozumi, & Tanaka, 2005), and Japanese monkeys (Izumi, 2000) were trained to discriminate between consonant and dissonant chords. Both species successfully discriminated consonance from dissonance and transferred the learned behavior to other chords with novel frequencies. Similar findings were reported from studies whose main objective was not focused directly in the perception of consonance and dissonance per se, but in chord discrimination tasks based on relative pitch changes. Results from these studies suggested that the chord discrimination performance of black-capped chickadees (Hoeschele, Cook, Guillette, Brooks, & Sturdy, 2012), pigeons (Brooks & Cook, 2009), and European starling (Hulse, Bernard, & Braaten, 1995) was guided for the sensory dimension of consonance and dissonance in the acoustic structures.

Neurophysiological studies corroborate the results of behavioral experiments showing the ability of animals to discriminate musical intervals based on sensory consonance. Different neural responses for consonant and dissonant stimuli have been observed in the auditory nerve (Tramo, Cariani, Delgutte, & Braida, 2001) and inferior colliculus (McKinney, Tramo, & Delgutte, 2001) of cats as well as in the primary auditory cortex of monkeys (Fishman et al., 2001).

Beyond perceptual differences, studies have also revealed spontaneous preferences for consonance over dissonance in non-human animals. In these studies, newly hatched domestic chicks (Chiandetti & Vallortigara, 2011) and an infant chimpanzee (Sugimoto et. al., 2010) were presented with consonant and dissonant versions of complete melodies. Results showed that chicks preferentially approached to a visual imprinting object associated with consonant melodies over an identical object associated with dissonant melodies. Similarly, the infant chimpanzee constantly produced, with the aid of a computerized setup, consonant versions of melodies for longer periods of time than dissonant versions of those same melodies. However, no preferences have been observed in other species when tested with isolated consonant and dissonant chords. Cotton-top tamarins (McDermott & Hauser, 2004) and Campbell's monkeys (Koda et al., 2013) showed to have preferences for some characteristics of acoustic stimuli such as softness over loudness, but not for consonance over dissonance. The fact that some species showed

preference for consonance and others did not might be explained by the type of stimuli used in the experiments. Preferences were observed when stimuli included complete melodies but not when the stimuli were isolated chords.

Together these findings demonstrate that at least some sensitivity to the degree of consonance defining a musical interval is not uniquely human. However, research in this area has just begun and much work is still needed to understand all the factors underlying the perception of consonance. For instance, as most of the results come from avian species, which have a complex vocal system, one could think of exploring the role of vocal learning hypothesis in consonance perception. As mentioned before, this hypothesis considers vocal production as a constraint for structure of music (Merker, Morley & Zuidema, 2015), thus using non-vocal learners species would shed light on whether consonance perception is affected by vocal production. Another issue regarding consonance processing that has not been tested in nonhuman animals thus far, is the processing advantage for consonance over dissonance observed in human infants (Schellenberg & Trehub, 1994) and adults (Schellenberg & Trehub, 1996).

1.4   Scope of the present dissertation

Explanations for the consonance and dissonance phenomena are still debated. Recent research has focused on the role that experience might play on the perception of this musical trait. The

present work is aimed to add insight to this issue by exploring the biological bases of consonance perception through the use of two different methods. First, through comparative work with other species, which allows us to fully control for musical exposure and tackle issues on music evolution. Second, using neurophysiological techniques to explore the neural mechanisms involved on the perception of consonance in humans.

The experimental part of this dissertation is composed by 3 studies. The first study assesses how pitch combinations varying on the degree of consonance are processed by different species. The second study explores whether the processing advantages for consonance over dissonance observed in humans are also present in other species. Finally, the third study explores the neural responses underlying the processing benefits for consonance in humans.

2. EXPERIMENTAL SECTION I

Exploring the phylogenetic roots of consonance processing: cross-species studies

In order to gain insight about the evolutionary roots of consonance perception, two cross-species studies were carried out. These studies explored whether perception of consonant and dissonant stimuli in animals resemble that of humans. The Long-Evans rat (*Rattus norvegicus*), a non-vocal learner species and distant from humans in terms of phylogeny, was used as experimental model. This species, lacking processing of harmonic sounds and reared in a controlled environment, was particularly useful to test the role of experience in consonance perception.

The first study explored the extent to which this organism with no extensive experience producing and perceiving harmonic stimuli properly perceives and discriminates consonance from dissonance. It was hypothesized that if consonance processing were based only on the physical properties of the sound, this species that lacks experience with harmonic sounds, would display an accurate discrimination and generalization of consonant and dissonant stimuli. Conversely, if experience were a factor influencing consonance perception, rats would not be able to perform such task.

The second study moved beyond perceptual experiments and sought to determine whether the processing advantages for consonance over dissonance would be observed in a demanding pattern detection task across species. If processing benefits for consonance extend to other species, rats might process sequences more accurately if they contain consonant rather than dissonant intervals. Importantly, this study would explore whether experience producing and perceiving harmonic stimuli is necessary to benefit from differences between consonance and dissonance.

2.1 Manuscript 1

Crespo-Bojorque P, Toro JM. The use of interval ratios in consonance perception by rats (Rattus norvegicus) and humans (Homo sapiens). J Comp Psychol. 2015 Feb;129(1):42–51. DOI: 10.1037/a0037991

2.2   Manuscript 2

Crespo-Bojorque P, Toro JM. Processing advantages for consonance: A comparison between rats (Rattus norvegicus) and humans (Homo sapiens). J Comp Psychol. 2016 May;130(2):97– DOI: 108. 10.1037/com0000027

3. EXPERIMENTAL SECTION II

Neural mechanisms of processing advantages for consonance: an ERP study

Electroencephalography (EEG), a method to record electrical activity of the brain, was used in the third study to explore brain responses triggered by consonant and dissonant sounds. This study explored the neural mechanisms underlying the processing advantages for consonance over dissonance and how experience, in form of musical training, might modulate these neural responses. To this end, highly trained musicians and naïve listeners participated in the study.

3.1 Manuscript 3

Crespo-Bojorque, P., Monte-Ordoño, J., & Toro, J. M. (Submitted*). Musical training modulates benefits for consonance processing.

Musical training modulates benefits for consonance processing

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Abstract

Consonant and dissonant musical intervals differ in how pleasant they are perceived and how easily they are processed. Consonant intervals tend to be rated as more pleasant and are more readily processed than dissonant intervals. In the present study, we explore how the brain responds after changes in consonance and dissonance, and how experience modulates these responses. Event-related brain potentials (ERP) 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 or musically naive volunteers. Results showed that changes in a sequence of consonant intervals are processed at a pre-attentive level of auditory processing independently of musical expertise, as revealed by a MMN elicited in both musicians and non-musicians. Changes in a sequence of dissonant intervals elicited a late MMN only in participants with extensive musical training. Even more, a P100 was elicited only in non-musicians when a dissonant sound appeared in a consonant sequence. Our results demonstrate processing asymmetries for consonance and dissonance at the neural level. They also provide support to the idea that experience enhances processing of musical intervals varying in their degree of consonance.

1. Introduction

In music theory, the relationship between two pitches played simultaneously (i.e. harmonic intervals) can be described as consonant or dissonant. In Western music, consonant pitch relationships are associated with pleasantness and stability as opposed to dissonant pitch relationships that are associated with unpleasantness and instability. Importantly, the perception of consonance-dissonance is continuous, a gradation from the most consonant to the most dissonant sound, rather than clearly defined categories [1, 2]. Although much has been discussed about the origins of consonance, there is mounting evidence that a listener's experience with a given musical system is a key factor in the emergence of consonance preferences[3].

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[4] and the event-related brain potentials[5-7] (ERP) change depending on the perceived consonance and dissonance of the auditory stimuli. Consonant chords elicit a larger N1 component than dissonant chords, while dissonant chords elicit a larger P2 component than consonant chords[7]. Also, the difference between consonance and dissonance has been observed at a pre-attentive level of auditory processing as reflected by a mismatch negativity (MMN) component elicited when a dissonant triad chord appears in a sequence of repetitive major triad chords[8]. At the brainstem, different responses to consonant and dissonant intervals have been

observed. 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[9]. Interestingly, these subcortical responses match the ordering of consonance for tone combinations as it is often listed in Western music theory[2]. 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 ran so far have tested Western listeners. There is thus the possibility that brain responses to sensory consonance and dissonance emerge as a result of long-term enculturation[10].

Several studies addressing the role of experience in the emergence of consonance preferences suggest that a sound can be rated as more consonant or dissonant depending on the musical context[12], the culture of the listener[13] and long-term exposure to harmonic stimuli[14]. Evidence from behavioral and neurophysiological studies highlights that experience with a given musical system is an important factor underlying consonance and dissonance processing. For instance, electrophysiological recordings have shown that neural correlates for consonant and dissonant pitch relationships are modulated by musical expertise[6, 15-17]. Different latencies of the ERP components suggest that musicians differentiate consonant and dissonant chords earlier (100-200 ms) than non-musicians (200-300 ms)[18]. 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[17]. Recent experiments across cultures have demonstrated that preferences for consonance depend on the degree of exposure to harmonic music. Listeners exposed to Western harmonic music (musicians and non-musicians residents of the United States) show a clear consonance preference, while participants with no exposure to this musical system (indigenous members of an Amazonian tribe) show no preference for consonance over dissonance[3]. Experiments with 6-month-old infants have shown that familiarity, not consonance, is what drives the infants' preferences. After being familiarized with either consonant or dissonant sequences, infants listen longer to the familiar stimulus, independently of whether it is consonant or dissonant[19]. It is thus a listeners' familiarity with a chord what leads to an increased perception of consonance[20]. Thus, evidence available so far provides support to the idea that musical enculturation and training correlate with the strength of consonance judgments in adults[14, 21], children[22] and infants[19].

The distinction between consonance and dissonance seems to extend beyond aesthetic considerations and also involve at least some processing differences. Studies with adults[23] and infants[24] have shown it is 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[25]. A recent study showed that humans benefit from consonance as to facilitate the detection of

abstract patterns in a rule learning task[26]. Participants learned a 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 such advantages are modulated by experience. 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 experience might modulate these responses, both musically-trained participants and naive listeners 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 musical training, alters the brain's responses to changes in consonant and dissonant stimuli. 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 MMN, an ERP component related to the detection of changes in a pattern or a sequence. The MMN has been observed after the violation of rules embedded in auditory stimuli[27]. There were thus 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 highly trained musicians and musically-naive participants.
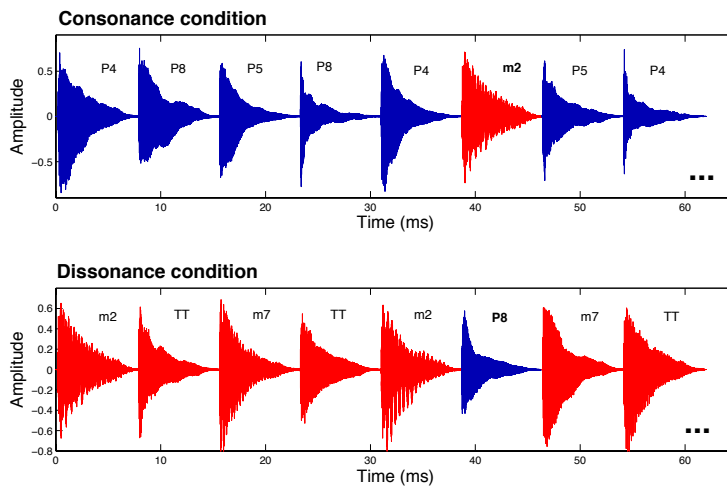

Fig. 1. Graphical depiction of interval sequences used in the present study. In both the Consonance condition and the Dissonance condition, sequences of standard, frequent, stimuli are interrupted by deviant, infrequent, stimuli.

2. Results

2.1 Consonance condition

In non-musicians, a significant positive component from 96 to 150 ms (cluster mass permutation test, p = .036; see Fig. 2; for the mean amplitude after consonant and dissonant intervals see Table1, 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 P100 component, which has been associated to an increased level of arousal after the presentation of a deviant auditory stimulus[28, 29]. This positivity was followed by a negative component from 172 to 250 ms (cluster mass permutation test, p = .007; see Fig. 2, Table 1, and Supplementary Fig. S2 online).

In the group of musicians, a significant negative component from 160 to 240 ms (cluster mass permutation test, p = .008; see Fig. 3, Table 1, and Supplementary Fig. S3 online) was also observed. Timing of the negativity observed in both musicians and non-musicians is consistent with a MMN. This neural response was elicited when a dissonant interval was presented in the context of a sequence of consonant intervals. Emergence of a MMN in both groups of participants suggests that changes in consonance are readily detected independently of extensive musical training.
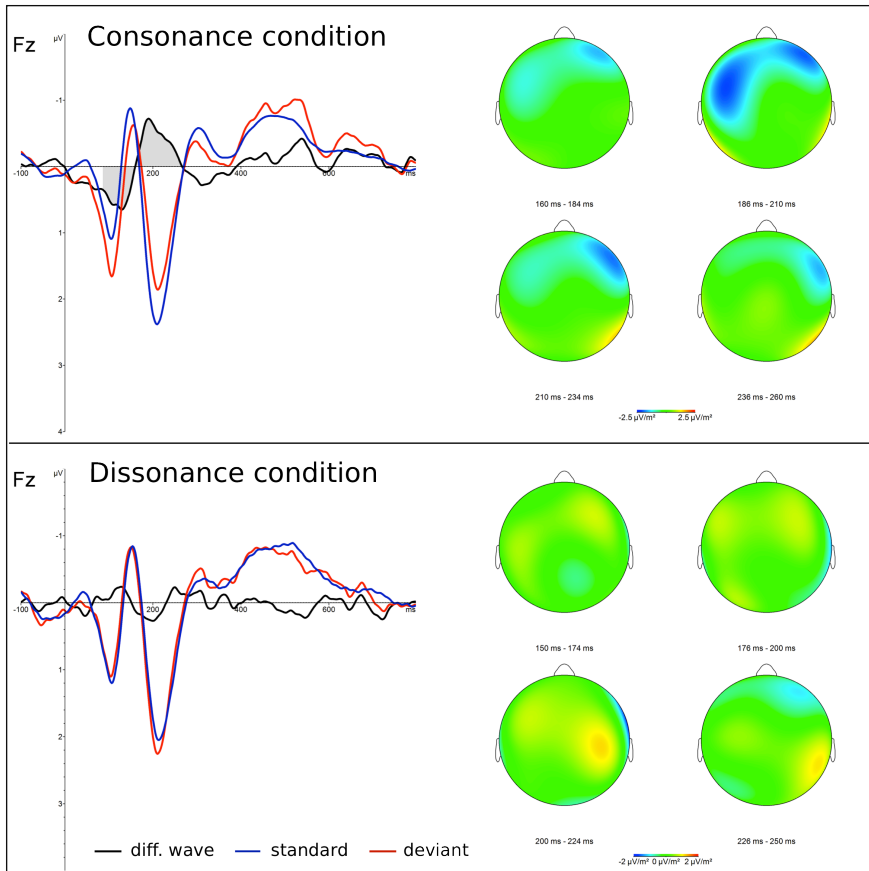
Fig. 2. ERPs and polarity maps elicited for changes in consonant and dissonant sequences for non-musicians. Difference waves (black line) are the result of substracting the averaged response to standard stimuli (blue line) from the averaged response to deviant stimuli (red line) in the Fz electrode. In the consonance condition two significant components were observed, an early positivity (P100) and a later negativity (MMN). For the dissonance condition no significant components were found.

2.2 Dissonance condition

No significant differences between standard and deviant stimuli were observed for non-musicians (see Fig. 2, Table 1, and Supplementary Fig. S2 online). The change from dissonance (standards) to consonance (deviants) did not produce any distinct neural activation in these participants.

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However, in the group of musicians, a negative component from 232 to 314 ms (cluster mass permutation test, $p = .021$) was observed when a consonant interval was presented within a sequence of dissonant intervals (see Fig. 3, Table 1, and Supplementary Fig. S3 online). Timing of this negative response is consistent with a late MMN component. This component has been previously observed in the context of especially difficult tasks[30].

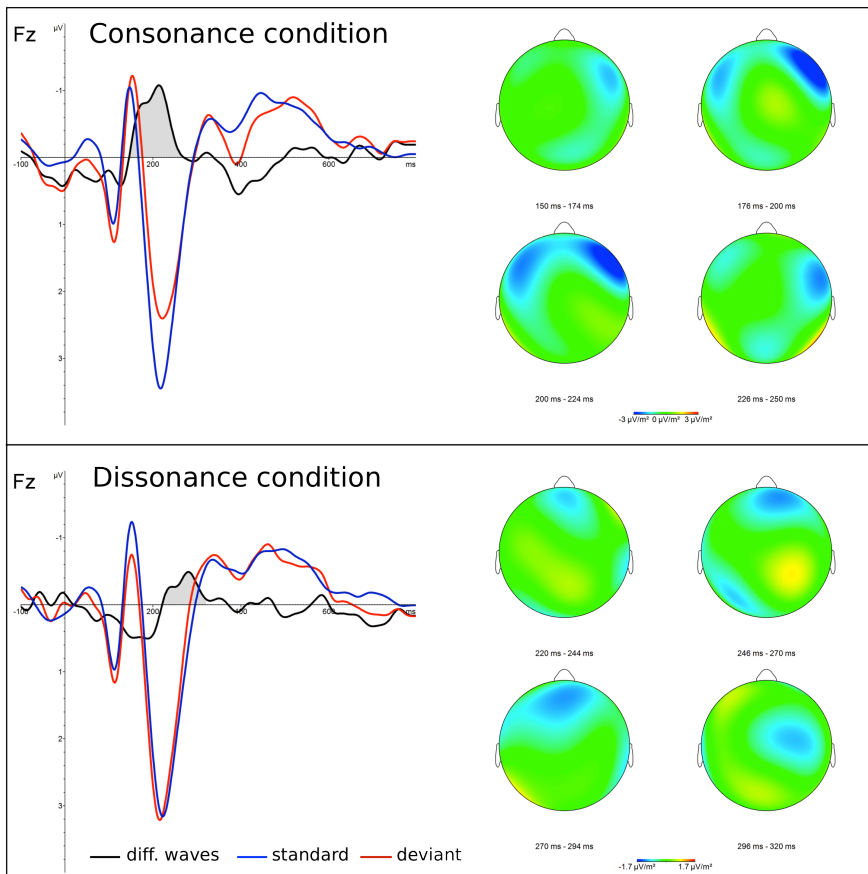
Fig. 3. ERPs and polarity maps elicited for changes in consonant and dissonant sequences for musicians. A MMN was elicited in both the Consonance and the Dissonance conditions.

2.3 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 1). A Region x Position x Condition ANOVA showed that there were no differences between conditions (see Supplementary Table S4 online). So, in listeners with extensive musical experience, the amplitude and the distribution of the negativity response was similar independently of whether the deviant stimulus was consonant or dissonant. Next, the latencies of the difference waves were compared. A Region x Position x Condition ANOVA demonstrated a difference across conditions ($F(1,15)=197.04$, $p<.001$; see Supplementary table S4 onlinel), with the negativity appearing much later when a consonant interval was presented after a sequence of dissonant intervals (Dissonance condition) than when a dissonant interval was presented after 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 x Condition interaction (F(1,571)=11.57, *p*=.001). The pairwise comparisons showed that there was a difference between the Consonance and the Dissonance condition in the frontal region (*p*=.044). Analysis over the latency of the MMN response did not show any significant main effect or interactions.

	Time window	Standard amplitude (SD)	Deviant amplitude (SD)
Musicians			
Consonant condition	P100	.76 (.83)	1.17 (1.05)
	MMN	2.82 (1.01)	2.09 (1.18)
Dissonant condition	P100	.74 (.74)	.98 (1.08)
	MMN (late)	1.69 (.77)	1.23 (1.07)
Non-musicians			
Consonant condition	P100	.40 (1.10)	1.05 (1.35)
	MMN	1.91 (.97)	1.39 (1.15)
Dissonant condition	P100	.51 (.87)	.32 (1.19)
	MMN (late)	1.47 (1.02)	1.56 (.94)

Table 1. Means of amplitude in μV for the MMN and the P100 time windows. All the data refers to the Fz electrode.

A P100 component was also observed in the Consonance condition (but not in the Dissonance condition) in non-musicians. A Region x Position x Condition ANOVA on the difference wave's peak voltage in the P100 time window showed a Region x Condition interaction (F(1,359)=5.62, *p*=.02; see Supplementary Table S5 online). Pairwise comparisons showed a significant difference between Consonance and Dissonance conditions in the frontal

region (p=.012). Thus, in non-musicians, the comparisons across the Consonance and Dissonance conditions confirm that deviant stimuli trigger different neural responses (a P100 and a MMN) only in the former, but not in the latter condition.

Next we wanted to explore possible differences across conditions 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 x Condition repeated measures ANOVA was conducted with the between-subjects factor Group. There was a Region x Condition interaction (F(1,742)=8.28, p=.001). Pairwise comparisons showed that in the frontal region the negativity was greater in the Consonance condition than in the Dissonance condition (p=.009). Also, a Group x Region x Condition interaction was observed (F(1,742)=5.18, p=.012). Pairwise comparisons did not show differences between groups in the frontal region. Instead, there was a greater negativity in the Consonance condition than in the Dissonance condition only in musicians (p<.001). Complementarily, a significant difference between conditions (Consonant and Dissonant) in the frontal region was observed only in the group of non-musicians (p=.037), likely because the MMN was only observed in the Consonance but not in the Dissonance condition.

The analysis conducted over the latencies of the MMN showed a main effect of Condition (F(1,30)=91.46, p<.001) and a significant

Group x Condition interaction $(F(1,30)=59.13,\ p<.001)$. The pairwise comparisons showed that in both the Consonance $(p=.031)$ and the Dissonance condition $(p<.001)$ 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 MMN response was only observed in musicians (see Fig. 4).
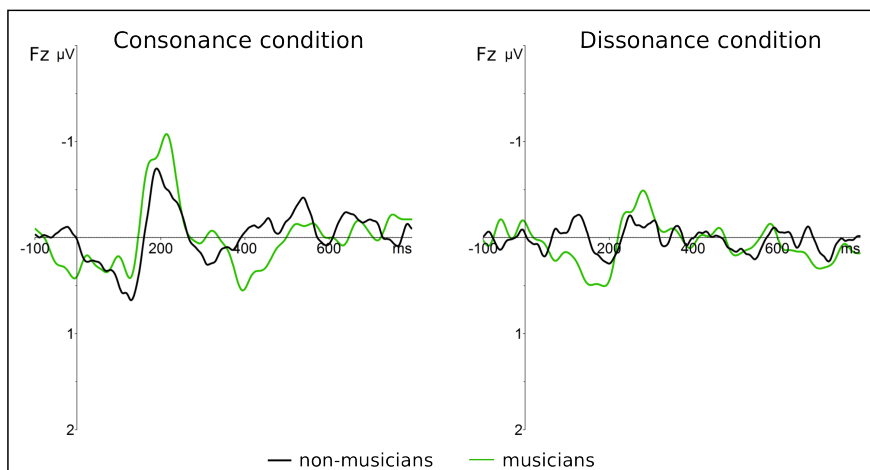
Fig. 4. Difference waves elicited for changes in consonant and dissonant sequences for musicians and non-musicians.

The visual analysis of the Grand-average data suggested that musicians and non-musicians might be responding differently to the highly frequent standard stimuli. To explore this possible difference across groups, a Position x 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.

3. 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[31]. Understanding this phenomenon is one of the outstanding issues in music cognition. The aim of the present study was to investigate how the brain responds after a change in consonance or after a change in dissonance, and how experience might modulate these responses. Event-related brain potentials suggested that differences in how the cerebral cortex responds to changes in the degree of consonance and dissonance might contribute to the processing advantages observed in behavioral studies for the former over the latter. While changes in consonant sequences elicited a MMN component in both musicians and non-musicians, changes in dissonant sequences elicited a late MMN only in participants with extensive musical experience. In addition, the results highlight how experience modulates very early responses during consonance processing. Responses to changes in the dissonant context differed depending on the degree of musical expertise of the listeners. The MMN in response to changes in a dissonant sequence was triggered only in listeners with prolonged musical training. The fact that the MMN was not observed in naïve listeners might reflect the difficulty of perceiving changes in dissonance as has been suggested by behavioral studies[23, 24].

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[9], the cerebral blood flow[4] and event-related brain potentials[5-7] (ERP) change depending on the perceived consonance and dissonance of the auditory stimuli and on musical expertise. The present work complements previous research exploring the neural correlates of consonance processing in two 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 evidence regarding processing asymmetries along the consonance-dissonance continuum and how they are implemented at the neural level[17, 32]. Second, 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[7, 18]. 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. 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 typical pre-attentional neural responses (the MMN) independently of musical training. However, 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 late MMN has been associated with the detection of changes in difficult tasks[30], over complex auditory stimuli[33] and under long-term memory conditions[34]. So, detecting changes from dissonance to consonance seems to be a more demanding process than detecting changes from consonance to dissonance. However, musical experience might provide listeners with richer acoustic information that facilitates the detection of changes in dissonance sequences. Both the familiarity with dissonant sounds and a general improvement in pitch processing skill[10] could make them easier to process[20], triggering a change-detection component only in musicians.

In the consonance condition, we also observed a P100 component only in non-musicians. In the auditory domain, this component has been related to attentional processes and level of arousal[35]. The P100 latency appears to be reduced by acoustic training in adults[36]. Our findings are consistent with EEG[28] and magnetoencephalography[29] (MEG) studies in which the amplitude of P100 responses to changes in successive harmonic tones was significantly smaller for musicians compared with non-musicians. Given that an increased activity in the P100 latency range is related

to a higher level of arousal to incoming auditory information, it has been argued that a decreased activity in the P100 window might reflect a musician's learned ability to modulate responses after interfering stimuli[28]. Larger P100 amplitudes would thus suggest an increase in processing demands, while smaller P100 would suggest increased processing efficiency. 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. The fact that this component was observed only in participants with no extensive musical training highlights the role of experience on consonance processing. Participants with musical expertise would have more efficient responses to interfering stimuli.

Much work is still needed to understand all the factors underlying the processing advantages of consonance. In this study we advance in this line of research by showing early neural responses to consonance changes (but not to dissonance changes) in non-musicians. Importantly, we observed this difference under incidental listening conditions (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. Even more, a P100 component, which is linked with processing demands, was elicited after the presentation of deviant dissonant stimuli only in musically naive participants. This suggests that experience allows for more efficient processing of dissonant intervals.

4. Methods

4.1 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.

4.2 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 2). 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.

Intervals used during the experiment

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

Table 2. 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.

4.3 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 the stimuli 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 minutes between conditions. In each condition there were 4 blocks. 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 to 9 standard stimuli before each presentation of a deviant stimulus. 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.

4.4 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 control 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 10kΩ and EEG was recorded during the familiarization phase of the experiment.

4.5 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 0μV at

EOG channels and with an amplitude >100µV at EEG channels were rejected. For both conditions, epochs of 900 ms were extracted with a baseline from -100 to 0ms relative to the stimulus onset. The permutation test described in Maris and Oostenveld[30] 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, 1,000 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).

Moreover, further analyses were conducted 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 x Position x 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.

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Competing interests

We declare no competing finantial interest.

Supplementary note

Musical training modulates benefits for consonance processing

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S1   Polarity maps (P100 component)

80 ms - 100 ms   100 ms - 120 ms

120 ms - 140 ms   140 ms - 160 ms

-2 µV/m² 0 µV/m² 2 µV/m²
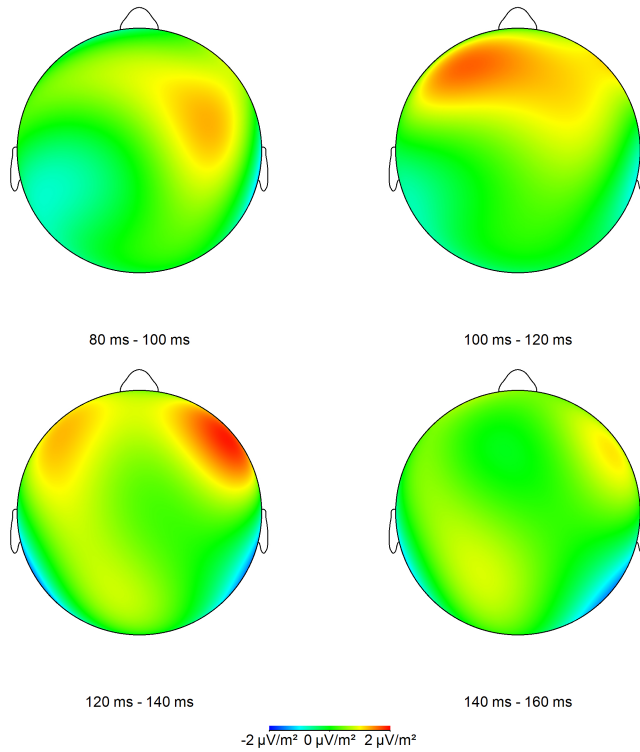
Supplementray Figure S1. Polarity maps for non-musicians in the Consonance condition in the 80 to 160ms window. An early positivity (P100 component) was elicited when the dissonant intervals were played in the context of consonant intervals.
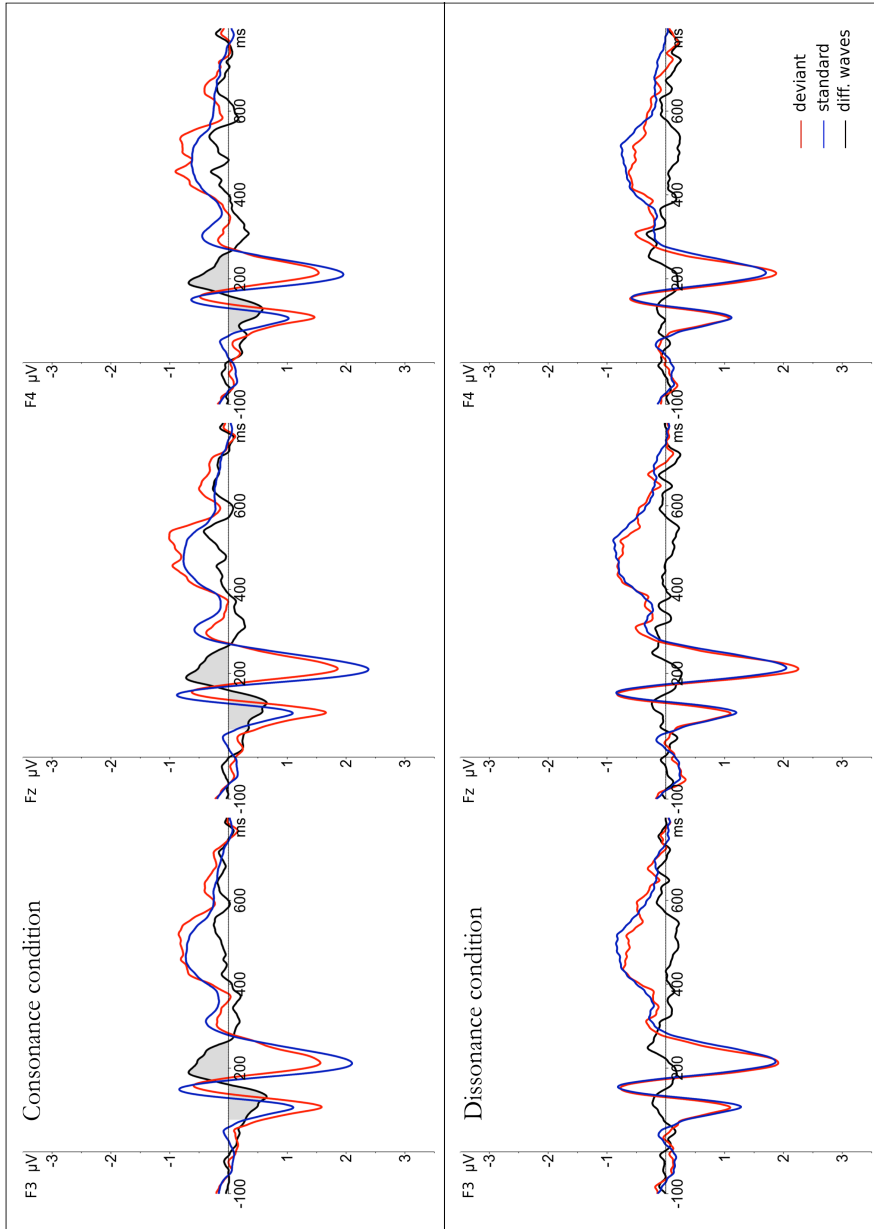
Supplementary Figure S2. ERPs for non-musicians in central eloctrodes. In the consonance condition, differences between standard and deviant stimuli are observed in an early positivity (P100) and a later negativity (MMN) as highlighted in the difference waves. No differeces between standard and deviant stimuli were observed in dissonant sequenes.
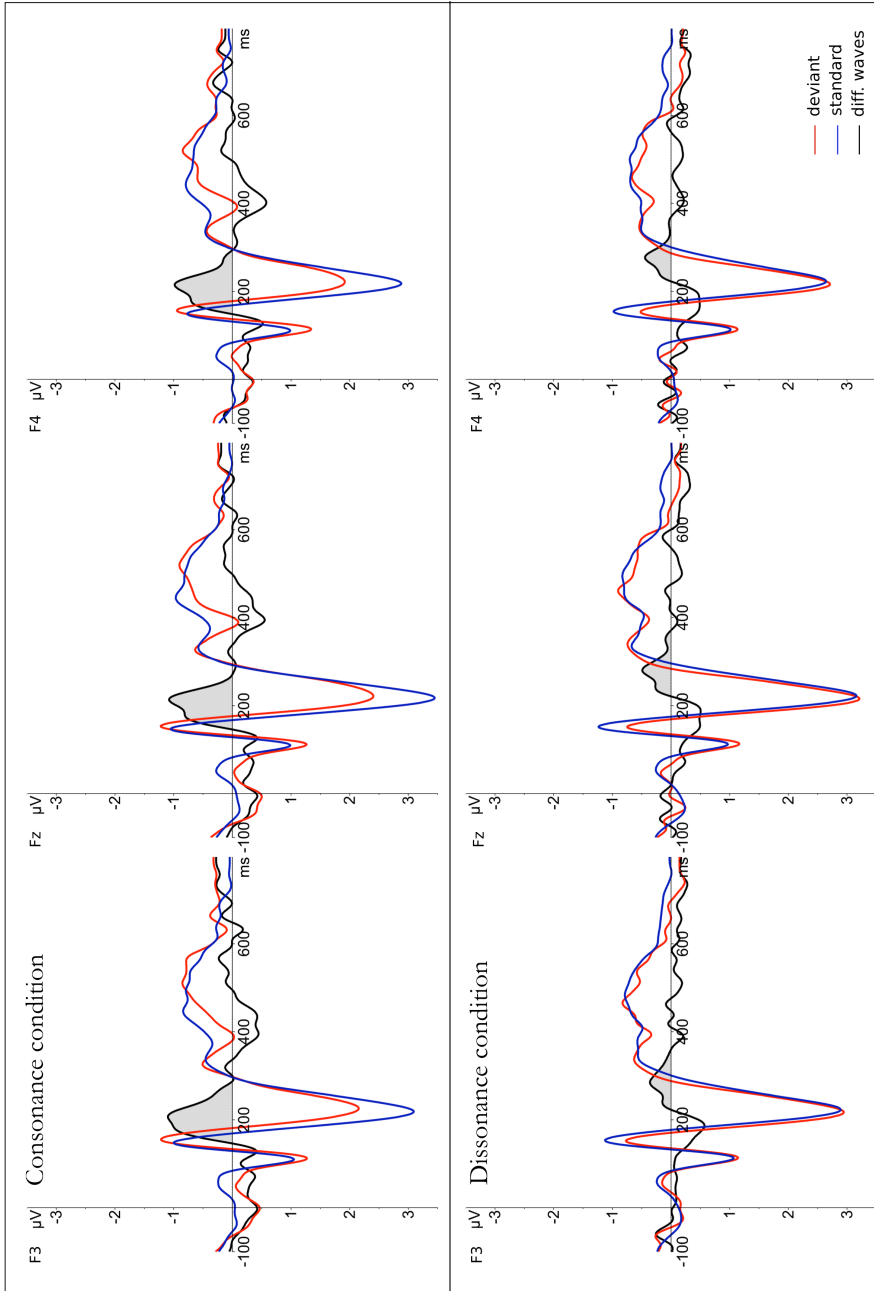
Supplementary Figure S3. ERPs for musicians in central electrodes. In both conditions, differences between standard and deviant stimuli are observed in an early negativity (MMN component) as highlighted in the difference waves.

S4

Musicians group	MMN peak voltage		MMN peak latency	
	F	p	F	p
Region	.36	.614	.31	.663
Position	2.72	.106	.90	.393
Condition	2.99	.104	197.04	<.001
Region x Condition	.25	.675	.56	.534
Position x Condition	2.80	.097	.36	.664
Region x Condition x Position	.48	.691	.20	.913

Supplementary Table S4. Results of the repeated measures ANOVA on the MMN peak voltage and the MMN latency of the Musicians Group

S5

Non-Musicians group	MMN peak voltage		MMN peak latency		P100 peak voltage	
	F	p	F	p	F	p
Region	6.05	.006	.24	.764	2.19	.143
Position	.49	.560	.65	.525	.40	.586
Condition	.90	.356	1.41	.253	2.66	.124
Region x Condition	11.57	.001	.93	.396	5.62	.020
Position x Condition	.34	.654	.21	.772	.55	.573
Region x Condition x Position	.48	.658	.32	.780	.70	.562

Supplementary Table S5. Results of the repeated measures ANOVA on the MMN peak voltage, the MMN latency, and P100 peak voltage of the Non-musicians Group

S6

	MMN peak voltage		MMN peak latency		Standard peak voltage	
	F	p	F	p	F	p
Region	3.02	.072	.45	.597	-	-
Position	1.62	.211	.25	.755	.33	.716
Condition	3.48	.072	91.46	<.001	.76	.389
Region x Condition	8.28	.001	1.48	.234	-	-
Position x Condition	.52	.566	.57	.542	.21	.048
Region x Condition x Position	.37	.753	.47	.710	-	-
Region x Group	2.77	.087	.12	.850	-	-
Position x Group	1.47	.240	1.35	.266	.65	.518
Condition x Group	.21	.650	59.13	<.001	.54	.467
Region x Position x Group	.78	.504	2.32	.073	-	-
Region x Condition x Group	5.18	.012	.04	.941	-	-
Position x Condition x Group	2.29	.119	.01	.982	.77	.464
Region x Condition x Position x Group	.59	.606	.08	.973	-	-

Supplementary Table S6. Results of the repeated measures ANOVA including the between-subjects factor Group on the MMN peak voltage, the MMN latency and the Standard peak voltage.

4. GENERAL DISCUSSION

The main goal of this dissertation was to study the biological basis for the perception of consonance, a salient feature of music associated with aesthetics and which origins have been debated for centuries. Our approach was twofold. On the one hand, we sought to determine whether animals, like humans, perceive differently pitch combinations considered consonant (pleasant) from pitch combinations considered dissonant (unpleasant). On the other hand, we searched for the neural mechanisms associated to the processing of consonant-dissonant intervals in humans.

The first part of this work was devoted to explore the extent to which humans share with non-human animals certain mechanisms that could form the basis of musical organization. More specifically, we focused on the mechanisms that underlie consonance processing. Through two studies we showed that rats and humans share to some extent the ability to distinguish chords based on their interval ratios (Study 1) but differ in how they benefit from differences in the degree of consonance (Study 2). The second part of our work showed some of the neural correlates for the processing benefits of consonance (Study 3). Additionally, this third study suggested that experience is a relevant factor that modulates these neural responses. Below, findings of each of these studies will be summarized. Then, implications of these findings with respect to the literature will be discussed. Finally, future directions on this line of research will be proposed.

4.1 Summary of results

4.1.1 Study 1: A comparative approach to consonance perception

In this study, three main experiments were carried out in order to compare the animals' ability with that of humans to discriminate intervals based on their degree of consonance. Additionally, two control experiments were run with human participants to account for possible differences on the experimental procedures used across the species.

Experiment 1 explored whether animals were able to tell apart dyads (two-note chords) based on their sensory degree of consonance-dissonance. To this end, animals were trained to discriminate sequences of three consonant chords (e.g. P8-P4-P5) from sequences of three dissonant chords (e.g. m9-TT-m2). Importantly, to make sure that the principal cue for the discrimination task was the relative pitch and not the absolute pitch level, stimuli were created in three different octaves. During the discrimination training, rats were rewarded with food for lever-pressing responses after the consonant sequences, whereas no food was delivered after lever-pressing responses for dissonant sequences. Thus, by using this procedure, it was expected that lever-pressing responses were higher for consonant sequences than for the dissonant ones. In the test phase, rats were presented with sequences containing new consonant and dissonant chords

implemented at other octaves not used during training. Different from training, food was not delivered for lever-pressings responses after either consonant or dissonant stimuli. If rats succeeded in the task (discriminate consonant from dissonant chords) and were indeed able to generalize to new instances based on sensory consonance, lever-pressing responses for consonant stimuli should be significantly higher than responses for dissonant stimuli. Results showed that rats successfully learned to discriminate consonant from dissonant sequences during training. However, they were not able to generalize such discrimination to sequences containing new consonant and dissonant chords. This failure to generalize to novel stimuli led to doubts about whether rats learned the general notion of consonance and dissonance or they rather learnt only the specific chords presented during training.

Experiment 2 addressed the question raised by the previous results by testing whether rats were also able to discriminate between two sets of dissonant stimuli. That is, stimuli differed in the interval ratios between tones but not in terms of consonance and dissonance. Stimuli were also sequences of three different chords (e.g. Set A: M2-M7-m9, Set B: TT-m2-m7) implemented in three different octaves. Stimuli for the generalization test were the same as those used during training, but were implement in two new octaves. Similar to results of Experiment 1, rats learnt to discriminate but did not generalize to novel items even when stimuli differed only in their absolute frequencies and not in terms of new intervals between tones. Together, these results suggested that animals might be

memorizing the specific items used during discrimination training. Even more, they suggest that animals might be facing difficulties to perceive whole octave transpositions. A possible alternative explanation was that whole octave transpositions and the difficulty of the task we used might make the generalization impossible independently of the species tested.

As previous research has not reported problems in humans to perform whole octave transpositions (e.g. Hoeschele, Weisman, & Sturdy, 2012), in Experiment 3a human participants were tested with exactly the same stimuli presented to rats in Experiments 1 and 2. As in the experiments with rats, there was a training phase followed by a test phase. The experimental procedure replicated as best as possible the conditions under which the rats were tested. To imitate the learning motivation behind the lever-pressing responses (i.e., food), participants were informed there were two types of sequences: "correct" and "incorrect" and that they should do their best to identify "correct" sequences. To do this they should try to press a key after each "correct" stimulus and to avoid responses after "incorrect" stimuli. Feedback words "correct" or "incorrect" were presented on the screen after participants made a response. For the generalization test, a two-alternative force-choice task (2AFC) was used and no feedback was presented. Results revealed that while rats displayed almost identical performance in both training phases, humans discriminated more easily between consonant and dissonant stimuli than between different sets of interval ratios. Regarding the tests phases, unlike rats, humans succeeded to

generalize to new consonant or dissonant sequences and to different octaves. Thus, humans performed whole octave transpositions without much difficulty.

Finally, to address slight differences regarding the experimental procedures between species, two control experiments were run with human participants. In Experiment 3b participants received a higher number of training trials than in Experiment 3a. In Experiment 3c a go/no-go task was used for the generalization test (instead of the 2AFC test used in Experiment 3a). Results were consistent across the three experiments, providing evidence that humans effectively generalized the discrimination to novel stimuli implemented at different scales. The fact that humans, but not rats, succeeded in the transfer tests pointed towards important differences between species in terms of consonance processing.

4.1.2 Study 2: Processing benefits for consonance: a comparison between rats and humans

Not only aesthetic but also processing differences between consonant and dissonant chords have been identified (Komeilipoor et al., 2015; Schellenberg & Trehub, 1994; 1996). In our second study, a series of experiments explored whether processing advantages for consonance over dissonance extend to more complex tasks and facilitate the detection of abstract patterns. More importantly, this study used a comparative approach to explore

whether the processing benefits for consonance are also observed in other species. Ten experiments were run in total, three with animals and seven with human participants.

Using similar procedures, rats and humans were trained to produce responses to chord sequences following an AAB pattern, and to withhold them to chord sequences following an ABC pattern. Rats were rewarded with food for correct lever-pressing responses (i.e., after AAB sequences) and human participants received feedback on a screen with the words "correct" if they pressed a key after AAB sequences or "incorrect" if they did it after ABC sequences. After the training phase, a test session was presented with new AAB and ABC sequences. During test, food rewards or written feedbacks were not given.

Three different experiments tested rule extraction in sequences containing either consonant chords (e.g., AAB: P8-P8-P5; ABC: P5-P8-P4), dissonant chords (e.g., AAB: TT-TT-m2; m9-TT-m2) or a combination of them in a same sequence (e.g., AAB: P8-P8-TT; ABC: m2-P4-TT). Both rats and human participants succeeded to discriminate and generalize the abstract auditory rules in all the experiments. That is, they can learn abstract rule over sequences of tones. However, important differences were observed between the species. Performance of human participants was significantly better when rules included consonant chords than when the rules were implemented over dissonant chords. In contrast, rats showed no differences across experiments. Their performance was equivalent

independently of whether the rules were implemented over consonant or dissonant chords. Even more, when consonant and dissonant chords were used in a same sequence, humans but not rats showed an additional advantage. This additional advantage suggested that consonance and dissonance act as categorical anchors for humans, thereby facilitating structure abstraction.

To make sure that the processing advantages for consonance observed in humans were not due to the specific abstract patterns tested or restricted to a limited set of intervals, control experiments were run using different abstract rules and implementing the chords over different octaves and across different intervals. Results from these experiments were consistent with the previous ones. They provided further evidence that consonance helps to organize the acoustic signal as to improve the extraction and generalization of abstract rules only in humans. Although rats were able to extract the abstract rules, the difference between consonance and dissonance did not translate into a processing advantage for them.

4.1.3 Study 3: Musical training modulates benefits for consonance processing

In order to investigate the neural correlates of the processing advantages for consonance over dissonance, event-related brain potentials (ERPs) were recorded while participants were presented with sequences of consonant intervals interrupted by dissonant ones and with sequences of dissonant intervals interrupted by consonant

ones. Importantly, to compare whether experience modulates the processing benefits for consonance, naive listeners and experienced musicians were tested in the experiment.

Results showed that changes from consonance to dissonance are encoded at an early neural stage, as revealed by pre-attentional neural responses such as the MMN component, independently of musical training. That is, this component was observed in both naïve listeners and highly trained musicians. Interestingly, a P100 component was also observed only in non-musician participants when changes from consonance to dissonance occurred. In the auditory domain, the P100 latency appears to be reduced by acoustic training in adults (Bosnyak, Eaton, & Roberts, 2004). Consequently, larger P100 amplitudes are related to an increase in auditory processing demands (Nikjeh, Lister, & Frisch, 2009). Thus, it seems that processing a dissonant sound embedded in a consonant sequence is more demanding to naïve listeners than to musicians.

Conversely, changes from dissonance to consonance triggered a late MMN only in musicians. The late MMN component (similar to the one observed in this condition) has been related to change detection in difficult tasks (Goydke, Alternmüller, Möller, & Münte, 2004). This suggests that processing changes in dissonant sequences is a more complex phenomenon and that prolonged experience seems to be a requisite to process these changes.

4.2   Implications on consonance processing theories: is consonance perception experience dependent?

Our findings from comparative and electrophysiological studies highlight experience as an important factor to account for the perception of consonance. In this way, results from this dissertation are in line with the theories suggesting that perceptual differences for tone combinations are learnt as a result of exposure to harmonic stimuli (e.g., Guernsey 1928; McDermott, et al., 2010; McLachlan, et al., 2013; Valentine, 1962). In particular, our work tackled the role of exposure from two different approaches. On the one hand, we tested the perception of intervals varying in their degree of consonance in a vocal learner and a non-vocal learner species to assess whether the production and perception of harmonic sounds have an effect on consonance-dissonance perception. On the other hand, brain responses to changes in consonant and dissonant sequences were recorded in naïve listeners and highly trained musicians to explore the neural correlates of processing advantages for consonance over dissonance and whether a larger amount of experience with music modulates these responses.

4.2.1 A comparative approach to the vocal learning hypothesis

Although vocal production learning has been considered as an important constraint for the structure of music in general (Merker,

et al. 2015) few studies have been devoted to determine which features of music might be affected by this capacity. As suggested in Schwartz and colleagues (2003) consonance perception might arise from the statistical structure of human vocalizations, the periodic acoustic stimuli to which humans are more exposed to. In that study, an analysis of the speech signal revealed that the probability distribution of amplitude-frequency combinations in human utterances predicts consonance ordering. Thus, there is an initial background suggesting that perceptual differences for tone combinations are constrained by the production of complex vocalizations. Our results together with other comparative studies also point in this direction.

While some vocal learning species such as song birds (Hoeschele et al., 2012; Hulse et al., 1995; Watanabe, et al., 2005) are able to generalize to novel consonant-dissonant stimuli, rats (Study 1 in the present dissertation) and pigeons (Brooks et al., 2009), do not. This lack of generalization observed in non-vocal learning species opens the door to the possibility that experience producing and perceiving harmonic sounds are important to the creation of categories around stimuli that vary in frequency ratios. Even more, our results showed that consonance and dissonance have a modulatory effect in humans but not in rats when performing a rule-learning task (Study 2). While humans showed a clear advantage for consonance, rats performed equally well independently of whether the task contained consonant or dissonant stimuli. Thus, our comparative data provide

evidence that consonance might be one of the musical features modulated by vocal production learning.

It has been suggested that species with a complex vocal system, such as songbirds, may have converging mechanisms with those of human speech (Bolhuis, Okanoya, & Scharff, 2010). Thus, brain structure of vocal learners would be associated to specialized neural circuitry that non-vocal learner species lack. This distinction in brain circuitry between species might explain differences in consonance processing.

To date, the vocal learning hypothesis, as a constraint for the structure of music, has been primarily explored in rhythm perception (for a review see Patel, 2014). In this dissertation, we broadened the spectrum of musical features and species tested for this purpose. By exploring consonance processing in a species that has not been reported to learn complex vocalizations such as the rat, our work helps to shed some light on the relative contribution of the physical properties of the sound and experience to the perceptual phenomenon of consonance-dissonance. As we have argued before, our results show that rats do not generalize across octaves and do not benefit from processing advantages for consonance over dissonance.

4.2.2 What about pre-exposure to harmonic stimuli?

Although our main results suggest that vocal production might be an important factor in consonance perception, results from Studies 1 and 2 could also be considered under the light of the lack of pre-exposure to harmonic stimuli. The animals that participated in these experiments were reared and tested under controlled laboratory conditions. That is, the rats used in our studies did not have a long-term exposure to natural harmonic sounds or to musical stimuli prior to the experiments. Thus, the differences we observed between rats and humans when processing consonance could also arise from differences in the pre-exposure to harmonic stimuli.

For instance, the fact that rats had the capacity to discriminate consonant from dissonant intervals (Study 1) suggest that at least some perceptual aspects needed for the discrimination of chords based on their sensory consonance may not be modulated experience either in the form of producing complex vocalizations or coming from extended exposure to musical and harmonic stimuli. As suggested by McLachlan and collaborators (2013), experience allowing the creation of memory templates for harmonic stimuli might underlie consonance-dissonance perception. Experimentally disentangling the relative roles of exposure and vocal production would require a wide-ranging set of experiments. For example, an experimental design tackling these issues could involve the pre-exposure of rats (or another non-vocal learning species) from birth to harmonic music. It would then be interesting to test these animals

to explore whether this experience would lead to a different pattern of results from what we found in Study 1. That is, to explore whether animals exposed to harmonic music would be able to perform whole octave generalizations and discriminate chords on the basis of consonance. Similarly, exposure might be at the base of processing advantages for consonance. Preferences for consonance over dissonance are greatly influenced by pre-exposure to consonant stimuli (Plantinga & Trehub, 2014; McDermott et al., 2016). This preference could be a pre-requisite to benefit from differences between consonance and dissonance as human participants in our experiments did. Experiments to explore the role of exposure on processing advantages for consonance could be a next step to shed some light on this topic. For instance, one could run experiments exploring abstract rule learning over consonant or dissonant chords (as those from Study 2 in the present work) with populations that have not had extensive experience with harmonic music (as members of the Amazonian tribe tested by McDermott and colleagues, 2016). Because members of these populations do not show a preference for consonance over dissonance, their results on processing advantages would be telling regarding the idea that preference is necessary to benefit from consonance. Thus, the present research opens the door to very interesting lines of work regarding the emergence of consonance preferences and advantages. At this stage, many more experiments are needed to address the relative contribution of long-term exposure to harmonic sounds and vocal production to consonance processing.

4.2.3 Formal musical training

As observed in Study 3 in the present dissertation, cortical activity in response to changes in consonant and dissonant sequences was different not only depending on whether the context was consonant or dissonant but also as a function of musical expertise. ERPs components elicited for changes in chord sequences were different for musicians and non-musicians. These results suggest that a greater amount of experience with harmonic sounds modulates the processing of intervals varying in their frequency ratios. A change-related MMN component was elicited in highly trained musicians for changes in both contexts, consonant and dissonant, while for non-musicians this component appeared only in the consonant context. It is also possible, however, that the group differences in our study between musicians and non-musicians were due to a more general facilitating effect of music training on the auditory system, such as pitch processing skills in general, and not specifically due to experience with consonant-dissonant intervals. For instance, our results are consistent with previous studies showing different ERPs components elicited for musicians and non-musicians when processing harmonic intervals, suggesting that musicians discriminate intervals at earlier processing stages than non-musicians (Schön, et al., 2005; Regnault, et al., 2001). Similarly, fMRI data have revealed that the areas of brain activation for consonant chords are right lateralized for non-musicians and are less asymmetric for musicians (Minati, et al., 2009). Thus, together with our results, there is strong evidence that the amount of

experience with musical stimuli modulates brain responses to stimuli varying in their frequency ratios.

4.2.4   Enhancement of cognitive abilities by music: is consonance part of this boost?

Several studies have reported the influence of musical training on different cognitive skills. Reports suggest that musically trained children show increased linguistic (Moreno, Bialystok, Barac, Schellenberg, Cepeda, & Chau, 2011; François, Chobert, Besson & Schön, 2013), reading (Moreno, Marques, Santos, Santos, Castro, & Besson, 2009), mathematical (Gardiner, Fox, Knowles & Jeffrey, 1996) and spatio-temporal (Costa-Giomi, 1999; Hetland, 2000) abilities when compared with children who did not receive musical training. Research in adults has also found that musical expertise critically modifies long-term memory (Groussard et al. 2010) and enhances performance in other cognitive areas such as attentional and multisensory processes (Trainor, Shahin, & Roberts, 2009). Musicians display a more robust encoding of linguistic pitch than non-musicians (Schön, Magne & Besson, 2004; Wong, Skoe, Russo, Dees & Kraus, 2007), and speakers of tone languages have enhanced auditory processing abilities parallel to those observed after musical training (Bidelman, Hutka, & Moreno 2013). Experience with rhythm enhances phonological processing (Cason & Schön, 2012), and tempo (fast or slow) and mode (mayor or minor) influence levels of arousal and mood states, which in turn, modulate performance on nonmusical tasks (Husain, Thompson, &

Schellenberg, 2002). There is thus a growing body of evidence of complex interactions between music and other cognitive domains.

Regarding consonance, there is little evidence suggesting that besides aesthetic differences, consonance and dissonance involve some processing differences. Both adults and infants present a processing advantage for consonant over dissonant intervals, in the sense that it is easier to detect changes over the former than over the latter (Schellenberg & Trehub, 1994; 1996). This opens the door to the possibility that consonance is used as a perceptual anchor for other cognitive processes. That is, that such processing advantage over consonant intervals could also be used to find structures in the acoustic signal by cognitive mechanisms that have been shown to be important in other domains.

In Study 2 in the present dissertation, the set of experiments testing human participants explored whether consonance might be used as a cue for the extraction of abstract patterns from the acoustic signal. Results showed that abstract patterns are more readily detected when they are implemented over consonant than over dissonant intervals. Beyond that, contrasting consonance and dissonance in the same abstract pattern noticeably helped listeners to structure the signal, improving their performance during test. Thus, the difference between consonance and dissonance could be used to facilitate structure extraction. Findings from this set of experiments extend previous evidence of enhanced processing for consonant patterns.

Moreover, our results add to the evidence that certain aspects of music, such as rhythmic or temporal structure, facilitate cognitive processing. Conventional (Trehub & Hannon, 2009) and regular rhythms (Drake & Botte, 1993) are associated with preference and processing advantages relative to unconventional or irregular rhythms. Together, the results reported across several studies suggest that aesthetic preferences for musical consonance and rhythmic regularity seem to run in parallel to ease of cognitive processing.

4.3   Future directions

Our results shed some light on the biological bases of consonance processing. They also open the door to further work that could address some of the issues raised by the experiments we ran.

In the first study on the present dissertation we showed that rats do not generalize the discrimination between chords to novel stimuli that differed in fundamental frequency. It is possible that rats show no generalization across octaves because of a general difficulty described for mammals to process absolute pitch when compare to avian species (Weisman, Williams, Cohen, Njegovan, & Sturdy, 2006; although see Hoeschele, Weisman, Guillette, Hahn & Sturdy, 2013 for failure on octave equivalence in a songbird). Therefore, further work could explore whether rats process better musical

intervals in restricted pitch ranges and not across wide ranges as we already did. For instance, transpositions could be tested for different keys instead of different octaves. In this way, test stimuli would fall within the same range of stimuli from training. Although there is evidence for whole octave transposition in rhesus monkeys, a species that do not have a complex vocal system, octave transpositions were successful over complete melodies but not over individual notes (Wright, Rivera, Hulse, Shyan, & Nieworth, 2000). Thus, it could be also explored whether rats would generalize across octaves if the stimuli were implemented over tonal melodies.

In the second study on the present dissertation, we observed that unlike humans, rats did not benefit from differences in sensory consonance. Further comparative experiments with species that produce complex harmonic vocalizations could explore whether such experience is enough to trigger processing advantages for consonance over dissonance. Beyond vocal production, experience perceiving harmonic stimuli could also be address in rats and other non-vocal learner species. Hence, new experiments could focus on disentangling the relative contribution of vocal production and experience. For instance, rats could be pre-exposed from birth to harmonic music or to a set of musical intervals and tested later to explore whether this experience would lead to a different pattern of results.

Importantly, in this dissertation all the studies with human participants were conducted in the context of Western music

culture. It is thus important to acknowledge the possible impact of culture-related factors in our results. We definitely need more research exploring how general across cultures are the results we report in our studies. To date, cross-cultural investigations on the origins of consonance perception are scarce and controversial. While some evidence point to the prominence of culture-related factors as potential determinants of responses to musical intervals (Maher, 1976; Fritz, et al., 2009) other results showed a remarkable degree of concordance across cultures (Butler & Daston, 1968) suggesting that cultural differences do not have an effect on the judgments of musical intervals. As mentioned before, despite the fundamental contribution that cross-cultural data could give to the understanding of consonance-dissonance phenomenon, there are not many studies on this topic. Thus, this is an outstanding line of research that needs to be explored to tap the role experience at a fundamental level. For instance, the recent study by McDermott and colleagues (2016) pointed in this direction by exploring cross-cultural variation in consonance preferences in an Amazonian tribe that have almost no exposure to Western culture. Results from this study suggested that consonance preferences might not be innate neither driven by exposure to harmonic natural sounds such as vocalizations. Further experiments in this kind of societies with minimal exposure to Western music could test whether this lack of preference for consonant sounds translate into a lack of processing advantage for consonance over dissonance as it was observed in rats (Study 2).

5. SUMMARY AND CONCLUSIONS

Based on the data obtained in this work several conclusions about the biological basis of consonance perception are stated below.

Regarding the question to what extent non-human animals share with humans some of the mechanisms responsible for consonance processing we found that:

- Components of complex auditory processing needed to recognize chords based on their interval ratios are shared across species.
- Interval ratios, rather than sensory consonance, might guide chord discrimination in non-human animals.
- A species such as the rat is not able to generalize across octaves. Thus extensive experience with harmonic stimuli might be required for the creation of categories among stimuli varying in frequency ratios.
- There are differences across species regarding the extent to which they benefit from differences in sensory consonance.
- Consonance facilitates cognitive processing in other domains. Consonance helped to organize the acoustic signal as to improve the extraction and generalization of abstract rules only in humans.
- The perception of differences across tone combinations might be constrained by the production of complex vocalizations.

From the study exploring auditory event-related brain potentials to changes in consonance and dissonance we conclude that:

- Changes from consonance to dissonance triggers pre-attentional neural responses such as the MMN independently of musical training.
- On the contrary, to observe a change-detection component for changes from dissonance to consonance musical expertise was required, as a late MMN was found only in highly trained musicians.
- Neural responses triggered by a task exploring processing advantages for consonance over dissonance were modulated by musicianship.

Taken together, results from this dissertation suggest that the processing of harmonic intervals is modulated by experience, as reflected in different performance depending on the species tested and in different brain activity depending on musical expertise.

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ANNEX

The introduction and manuscripts (1 and 2) of the present dissertation served as the basis for the manuscript presented below. This manuscript has been submitted for publication as a part for a Special Issue on music cognition in *Comparative Cognition & Behavior Reviews*.

Consonance processing in the absence of relevant experience: Evidence from non-human animals

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