NEURAL AND EVOLUTIONARY CORRELATES OF RHYTHM PROCESSING THROUGH BEAT AND METER

Alexandre Celma Miralles

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Supervisor:

Dr. Juan Manuel Toro, Center for Brain & Cognition

DEPARTAMENT DE CIÈNCIES EXPERIMENTALS I LA SALUT

Universitat
Pompeu Fabra
Barcelona

us la dedico

als que heu cregut sempre en mi

amb amor profund

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Abstract

Time is a structural component of music. Across cultures, the sounds of music are produced and perceived as rhythmic patterns that have an underlying isochronous beat. This periodic beat is organized by meter into hierarchical patterns of strong and weak positions. Both beat and meter are cognitive constructs that work as referential temporal points to categorize and predict events, allowing, among others, for synchronized movements. This dissertation aims to explore the biological bases of the isochronous beat and the hierarchical meter through a neurophysiological and a comparative approach. The electrophysiological studies with humans have revealed that our neural populations can similarly entrain to periodic visual and auditory stimuli and synchronize to ternary meter when it is imagined in the visual modality or signaled by spatial auditory cues. Moreover, formal training in music and attention interact with the processing of rhythm by enhancing the neural entrainment to the periodicities of beat and meter. The behavioral studies in rats have revealed that other animals can recognize the rhythmic structure underlying a familiar tune and can detect isochrony in auditory sequences across tempi regardless of the absolute durations of the sounds. In contrast to humans, rats lack vocal learning abilities, which may not be necessary to process these two temporal components of rhythm. Together, these findings point out that some rhythmic aspects of music can go beyond the auditory modality in humans and that their origins can be found in other species.

Resumen

El tiempo es un componente estructural de la música. En cada cultura, los sonidos de la música se producen y se perciben como patrones rítmicos que poseen una pulsación isocrónica subyacente. Esta pulsación isocrónica se organiza mediante el compás en patrones que jerarquizan posiciones fuertes y débiles. Ambos, la pulsación y el compás, son constructos cognitivos que funcionan como puntos de referencia temporal para categorizar y predecir eventos, permitiendo así sincronizar movimientos (entre otras cosas). Esta tesis pretende explorar las bases biológicas de la pulsación isocrónica y del compás jerárquico desde un enfoque neurofisiológico y comparativo. Los estudios electrofisiológicos con humanos han revelado que las poblaciones neuronales pueden sincronizarse con estímulos periódicos visuales y auditivos; y con el compás ternario, sea imaginado en la modalidad visual o marcada por características auditivas espaciales. Además, la formación musical y la atención interaccionan con el procesamiento del ritmo y refuerzan la sincronía neural con las periodicidades de la pulsación y el compás. Los estudios conductuales con ratas han revelado que otros animales son capaces de reconocer la estructura rítmica subyacente a una canción familiar y pueden detectar isocronía en secuencias auditivas presentadas en varios tempos, independientemente de la duración absoluta de los tonos. A diferencia de los humanos, las ratas carecen de habilidades de aprendizaje vocal, las cuáles parecen no ser necesarias para procesar estos dos componentes temporales del ritmo. En conjunto, estos hallazgos señalan que algunos aspectos rítmicos de la música van más allá de la modalidad auditiva en los humanos y que sus orígenes se pueden encontrar en otras especies.

Resum

El temps és un component estructural de la música. A cada cultura, els sons de la música es produeixen i es perceben com patrons rítmics que posseeixen una pulsació isocrònica subjacent. Aquesta pulsació isocrònica s'organitza mitjançant el compàs en patrons que jerarquitzen posicions fortes i febles. Ambdós, la pulsació isocrònica i el compàs, són constructes cognitius que funcionen com a punts de referència temporal per categoritzar i predir esdeveniments, fet que permet sincronitzar moviments (entre altres coses). Aquesta tesi pretén explorar les bases biològiques de la pulsació isocrònica i del compàs jeràrquic des d'un enfocament neurofisiològic i comparatiu. Els estudis electrofisiològics amb humans han revelat que les poblacions neuronals poden sincronitzar-se amb estímuls periòdics visuals i auditius; i amb el compàs ternari, sigui imaginat en la modalitat visual o marcada per característiques auditives espacials. A més, la formació musical i l'atenció interaccionen amb el processament del ritme i reforcen la sincronia neural amb les periodicitats de la pulsació i el compàs. Els estudis conductuals amb rates han revelat que altres animals són capaços de reconèixer l'estructura rítmica subjacent a una cançó familiar i que poden detectar isocronia en seqüències auditives presentades a diversos tempos, independentment de la durada absoluta dels tons. A diferència dels humans, les rates no tenen habilitats d'aprenentatge vocal, les quals semblen no ser necessàries per processar aquests dos components temporals del ritme. En conjunt, aquestes troballes assenyalen que alguns aspectes rítmics de la música van més enllà de la modalitat auditiva en els humans i que els seus orígens es poden trobar en altres espècies.

Preface

Sometimes I wonder how I ended up investing so much time in the topic of the evolution of syntactic structures in both music and language without losing the motivation for it. The answer becomes clear to me when I look back on my past and notice three aspects of my life that may have directly influenced this interest in cognition and its evolution across species. The first has been an incessant learning of musical skills since I was a child, from playing instruments and singing to conducting children's orchestras. The second relates to the constant presence of animals in my life. The last was a genuine passion to solve enigmas and logical pattern sequences as a kid. I will try to briefly explain these influences and how they may have paved the way leading to the present work.

I was 8 years old when I first enrolled in the music school of my city, Reus. I remember that I chose to play the violin because I felt a good connection with the violin teacher. It is hard to describe how tedious and frustrating the synchronization of your arms and fingers to play this instrument can be, and even more so when one must keep the beat at the tempo of the song. Besides the teachers, there was always the infamous metronome, which not always aligned with one's own musical performance. It is interesting to point out here how important the beat is in the instruction of classical music, and how persistent the training of beat flexibility is. Even one song covers a great range of tempi because practicing consists firstly of playing it at a slow tempo and gradually speeding it up until reaching its actual tempo. Indeed, the only reliable way to play quickly is when movements are accurately synchronized at slow tempi, which may reflect how the brain integrates the precise fine-grained motor actions involved in playing. Furthermore, I will never forget the obsession that the violin teachers had in forbidding me to tap along with the beat of the music I was playing. They insisted on telling me that proficiency in playing is achieved when one succeeds in only externalizing the movements related to the violin and mentally keep the beat 100% of the time (which may fit an embodied cognition approach). In fact, I could not play syncopated off-beats unless I tapped with my foot, and sometimes I still substitute the missing on-beats with subtle breathings. My mind needed to reinforce the beat by filling in the metrically relevant missing sounds. I think that these experiences with the musical rhythms are quite common in learning music and reflect the neural processes underlying beat perception and motor synchronization.

During my childhood I had a special interest in understanding other animal species. Since I was born, there has always been a dog at home, with whom I played and enjoyed teaching smart tricks. I was fascinated by their cognitive abilities and their social-emotional aptitudes. In addition to our dogs, several Chinese striped hamsters shared their lives with my family as well. I remember spending many evenings with my sisters and cousins building labyrinths with Lego bricks to test the abilities of these hamsters. As in the scientific method, there was always a sunflower seed or a yogurt pellet that worked as reward and that I placed hidden in the labyrinth, protected by fake walls and traps that they had to pass. Twenty years on, I still do similar things in the lab, though now with bigger rodents, homologated pellets and controlled stimuli to observe animal responses in conditioning paradigms that explore musical traits in rats. The harmless "experimentation" with animals has no age restrictions. In fact, I once presented the rhythmic abilities of Snowball and Ronan to my summer camp kids, and few weeks after some parents told me that they started to teach beat perception and synchronization to their pets: dogs, cats, budgerigars and rabbits. Although they may have failed, these children are now sensitive to the particularity of the beat in music. Behind this casual anecdote, however, highlights the relevance of communicating scientific findings to all society, because it can reach kids' interests and trigger their curiosity to unsuspected topics.

Finally, the last aspect that may have led me to studying the processing of musical structures in the brain comes from my obsession on detecting patterns in structures. My favorite subject in school was "Logic", which consisted of solving puzzling, visuo-spatial tasks, and numeric series that followed sequential pattern rules. This was transformed in high school into an innate passion to analyze linguistic syntactic structures, eager to discover their rules and breakdowns. It was this curiosity that made me switch from chemistry and biology to linguistics and cognitive sciences. Even in the music school and the conservatorium, my favorite subjects were harmonic theory and composition classes (subjects hated by everyone else) because I wanted to understand the syntactic rules underlying music in order to play with their limits. Curiously, it was this passion that pushed me every day to check for new findings in linguistic and musical syntax and motivated me to design paradigms to test their boundaries with neuroscientific methodologies.

I consider that these three aspects of my nature and life experience are fundamental to illustrate the motivational origins of the research included in this dissertation tackling the origins of rhythm. The etymology of *rhythm* comes from the Latin *rhythmus*, 'movement in time', and the Greek ῥυθμός, 'measured flow or movement, proportion, symmetry, order, form, structure', related to the Proto-Indo-European root **sreu*, 'to flow' (online Ethimology Dictionary). The present thesis therefore aims to explore the biological bases of the structured flow of music. More specifically, we aimed to study the processing of the isochronous beat and its metrical organization in our brain as well as beyond our species. To achieve this, we used electrophysiological methodologies and comparative cognition paradigms. The neurophysiological studies explored neural entrainment to beat and meter beyond the prototypical auditory modality and explored meter projection in vision and meter induction in the auditory spatial domain. These studies also tackled the role of formal training in music and attention in rhythmic perception. The comparative work focused on the discriminatory abilities of rats regarding isochrony and rhythmic organization. The thesis is divided into four chapters. Chapter 1 presents a biological approach to music, in which we discuss the universal traits of music, neural correlates of music in the brain, and the musicality components that can be present in other species. It is here that we introduce the main theories about rhythmic cognition and findings regarding the processing of beat and meter. Chapter 2 encompasses two electrophysiological studies in humans about the neural bases of beat and meter and the role of formal training and attention in these processes. Chapter 3 contains two studies that address the discrimination of isochrony and the recognition of rhythmic organization in rats. Chapter 4 discusses the main findings of our studies and connects them to the current literature and some possible future lines of research. Chapter 5 closes the thesis listing the main conclusions from our work.

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1. INTRODUCTION

The musical faculty "must be ranked amongst the most mysterious with which [humanity] is endowed" (…) and "the perception, if not the enjoyment, of musical cadences and of rhythm is probably common to all animals, and no doubt depends on the common physiological nature of their nervous system"

(Charles Darwin, 1871, The Descent of Man)

Music is a universal human trait. It occurs in all cultures around the world under the form of social interactions that involve dance or other performances (Honing, 2018; Trehub, Becker and Morley, 2015). The relationship between the rhythms of music and the coordinated actions of dance is so deep that some cultures do not even have separate linguistic terms to distinguish them (Peretz, 2006). Although music can be enjoyed individually, most of the times it occurs in social events. As such, music needs to be predictable to some extent. This seems to be the main function of the beat, which establishes equally-spaced points in time that can be predicted and used to join and align actions among individuals. A metrically-organized beat is therefore a core feature of music, fundamental for interpersonal synchronization.

During many decades, music has been studied from social sciences as a cultural entity. However, the latest advances in experimental psychology and cognitive neuroscience approached music as a biological entity, developed under the pressure of evolution and constrained by the neural structures of the brain. On the one hand, comparative research has devoted much effort to explore what components of music appear in other species, aiming to shed some light onto the evolutionary origins of musicality (Honing, ten Cate, Peretz, Trehub, 2015; Fitch, 2005; Bispham, 2006). On the other hand, neuroscientific research has persistently pursued the understanding of the neurocognitive mechanisms underlying the processing of music (Zatorre, Chen Penhune, 2007; Peretz, 2002; Thaut, 2013; Clynes, 2013; Patel, 2010; Koelsch, 2006; Vuust et al., 2009).

The present work aims to study the processing of the rhythms of music, an endeavor that has attracted research from multiple disciplines, from musicologists and linguists to cognitive neuroscientists and physical engineers. We will present our studies following two lines of research. The first line tackles rhythmic perception from a comparative cognition approach, aiming to shed some light onto the rhythmic processing mechanisms that are shared between human and non-human animals. The second line explores the bases of cross-modal beat perception and meter induction in humans using a frequency-tagging approach on neural entrainment. This dissertation is made of four studies: two of them tackling isochrony and rhythmic organization from a comparative perspective and two of them studying beat perception and meter induction from a neurophysiological approach. The finding of similar abilities between species may bring insights about the evolutionary origins of certain rhythmic properties of music, as well as their functions in every species. The finding of similar neural responses to beat and meter across modalities may elucidate the extent to which the brain is capable of organizing temporal information depending on the features relevant to each modality. Finally, the finding of effects of formal training in music on the perception of rhythms may account for brain plasticity to long-term experience.

In the present section we will present a general overview of the musical rhythm. First, we will describe music and its rhythmic components, and how it modulates the brain and relates to language and dance. Second, we will summarize research about the brain mechanisms underlying the processing of rhythms, models and theories behind them, and the oscillatory bases of neural entrainment to rhythmic stimuli. Third, we will review musicality features present across species, evolutionary theories behind them and the most relevant abilities regarding rhythm and tune discrimination found in non-human animals. Finally, we will state the scope and the experimental settings of the present work.

1.1. Music, musicians and rhythm

1.1.1. *The universal music faculty*

It has not been until recently that the biological foundations of music have obtained a relevant spot in research, putting together the advances of genetics, cognitive neuroscience, developmental and comparative psychology, linguistics and musicology. The fertile research across fields led to the birth of *biomusicology* (Wallin, Merker and Brown, 2000), a discipline that aims to study from a biological approach the emergence of musical traits across cultures and species, and the neural mechanisms and sociocultural environments sustaining and triggering them. The presence of music in old human societies (d'Errico et al., 2003), and of musicality traits in non-human animals (Honing et al., 2015), reinforces the idea that music may be an ancient capacity rather than a recent creation, with innate mechanisms underlying common principles across cultures regardless of time and place (McDermott and Hauser, 2005).

What is music?

Music is the intentional arrangement of sounds (and movements) over time occurring in a sociocultural context and following aesthetical frameworks. Music evokes emotional states (sadness, happiness, energy, calm…) and usually involves dance: people that move in synchronized performances coordinating body gestures. Similar to language, music is found across cultures around the world, is learned effortlessly via cultural contact and share neural substrates with other cognitive domains. Parallel to language and speech, music has musical idioms, which are instances of music that depend on the cultural background (Western music, Indian ragas…) and individual tastes (genres and styles). As speech and sign language, music goes beyond the auditory modality and involves the visual, vestibular and proprioceptive modalities as well as motor skills (Herholz and Zatorre, 2012; Schlaug, 2009; Phillips-Silver and Trainor, 2008; Brochard et al., 2008). It is this cross-modality that allows us to either follow the visual cues of the orchestra conductor or to synchronize with each other when we dance or play an instrument. Finally, the processing of music might be constrained by genetic, developmental and physical factors, as well as by long-lasting experiences, such as musical training.

What is music made of?

Music is mainly made of the sounds coming from the voice or musical instruments, but contemporary styles can also incorporate other acoustic materials and effects. These sounds are "governed by structural principles that specify the relationships among notes that make up melodies and chords, and beats that make up rhythms" (Fedorenko et al., 2012). Fitch (2013) proposes that the relationships between harmonic melodies and metrical rhythms represent two superposed hierarchical structures that interact with each other during the processing of any musical excerpt. These structures are the tonal-harmonic structure (Lerdahl and Jackendoff, 1983; Lerdahl, 2001, 2013) and the metrical structure (Longuet-Higgins, 1979; Temperley, 2004; Honing, 2012). The former structure categorizes the tones and the chords of music in terms of tonal-harmonic functions (i.e. tonic, dominant, subdominant) that depend on the relationship and distance to a stable tonal center (Figure 1a, modified from Rohrmeier, 2011). The latter structure categorizes the rhythms in relation to an isochronous beat that is hierarchically organized in patterns of strong and weak positions (Figure 1b, modified from Fitch, 2013).

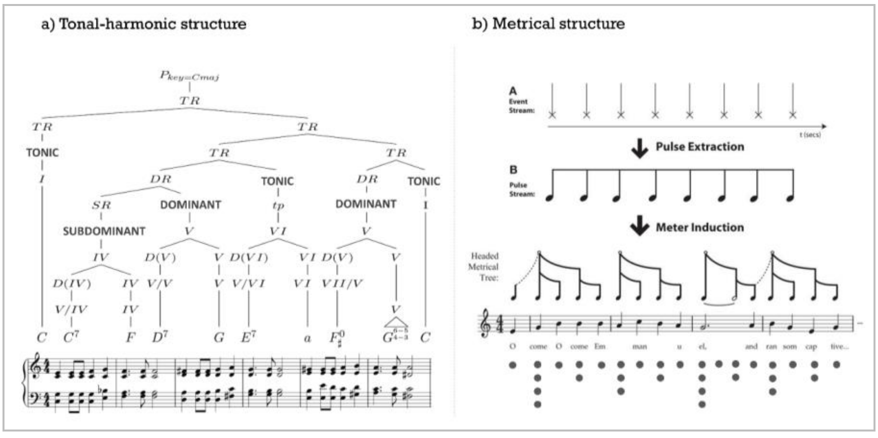

Figure 1 The hierarchical structures of music. Examples of (a) the tonal-harmonic relationships between the tonic, subdominant and dominant functions (adapted from Rohrmeier 2011) and the metrical groupings of isochronous beats with disticnt degrees of prominence, marked by the dots (adapted from Fitch, 2013).

What are the evolutionary functions of music?

More than a century ago, Darwin (1871) observed that music, as a whole, did not show any obvious function in nature, despite requiring a physiological cost and playing an important role across societies. It is for this reason that he proposed that music could be a fossil remaining from a former adaptation, a communication system of earlier hominids whose function was later overtaken by language. This idea was followed later by researchers that discussed the existence of this musical protolanguage (Jespersen, 1922; Livingstone, 1973; Richman, 1993; Brown, 2000; Mithen, 2005; Fitch, 2006; Masataka, 2006; Celma-Miralles, 2014). However, some aspects of music seem to have important roles in human societies, because they sustain social group cohesion and coordination in collective activities (Cross, 2007; Merker, 200, Mithen, 2005), can work as sexual attractors for mating (Darwin, 1871; Miller, 2000), establish emotional parent-offspring connections through infant-directed speech (Dissanayake, 2008), and support individual well-being.

The approaches to music evolution can be classified across a continuum. At one extreme, music is seen as an evolutionary adaptation shaped by natural selection and governed by genes and their development. From this position, natural, sexual or kin selection may have selected musical traits that had a role in survival (for detailed reviews of the advantages and weaknesses of evolutionary approaches, see Peretz, 2006; and Fitch, 2006). At the other extreme, musical abilities stem from general-purpose learning capacities shaped by the environment, and music is a by-product of other selected mechanisms (Pinker, 1997) or a transformative invention (Patel, 2010). A more plausible position falls between these two extremes. Music may therefore be composed by independently-evolved musicality features, such as rhythm and pitch, selected for distinct purposes. Therefore, a better way to approach the evolution of music is by splitting it into several independent musicality components, whose mechanisms evolved as cognitive traits selected for specialized functions (Honing and Ploeger, 2012). These cognitive components of musicality might be essentially involved in the perception, production and appreciation of music, and externally affected by sociocultural and psychobiological factors. For instance, Trainor (2008) proposes that music has deep evolutionary roots in the underpinnings of human sound processing, which constrains rhythmic and harmonic structures, and permits variation of these features across cultures. From this view, temporal and spectral properties of music derive from general auditory functions, while scales, rhythmic patterns and harmonic structures depend on learning and environmental exposure.

What elements are found across cultures?

The music faculty seems to be unique to our species (Hauser and McDermott, 2003; Fitch, 2006; Peretz, 2006). Similar to language (Jackendof, 2009; Patel, 2008, 2010; Fitch, 2005), music identifies us as humans and is found across all the societies of the world (Harwood, 1976; Peretz and Zatorre, 2001; Savage et al., 2015; Brown and Jordania, 2013). During the last decades, several ethnomusicologists and psychologists pursued the discovering of universals in music, that is, traits that are common to all musical cultures. Before this quest for music universals, Lomax (1977, 1980) had already classified 148 musical cultures into 10 families that could be grouped into Arctic hunters and fishers, with male-dominated unison singing of irregular rhythms, and African gatherers, with feminized polyvoiced singing of repetitive regular rhythms (Peretz, 2006).

One of the first ethnomusicologists that identified music universals was Nettl (2000), who reported three main cross-cultural characteristics: vocal music, the meter and the sense of pulse, and the use of at least 3-4 pitches. The list of potential music universals increased since then, including observations of cross-cultural musical features even found in previous ethnomusicological studies, such as those reported in Carterette and Kendall (1999): a deep-structural idea, auditory grouping, reference pulses, rhythmical patterns by asymmetrical subdivisions of time pulses. The psychologists Dowling and Harwood also identified four universals (Dowling and Harwood, 1986; Dowling, 2001): discrete pitch level, octave equivalence, 5-7 pitches within the octave, and tonal hierarchy. Trehub (2000) proposed to include relational pitch and time features, small integer frequency ratios, unequal scale steps, and lullabies for infants. Fitch (2006) pointed out that recursion and unbounded combinatory were also universals present in music, because a small set of elements can generate an infinite number of musical structures. All these properties of music were therefore proposed and discussed as possible universal traits of the musical idioms of the world.

The most recent research on the universal features of music was developed by Savage et al. (2015). They analyzed a corpus of 304 musical excerpts covering 9 world-wide regions: North America, Central-South America, Europe, Africa, the Middle East, South Asia, East Asia, Southeast Asia and Oceania. They found that 18 out of 32 features could be considered statistical universals, comprised in the subcategories of pitch, rhythm, instrumentation, performances style and social context. Relevant to this dissertation are those regarding rhythm. As Savage and colleagues (2015) states, "music tends to use an isochronous beat organized according to metrical hierarchies based on multiples of two or three beats —especially multiples of two beats. This beat tends to be used to construct motivic patterns based on fewer than five durational values". These statistical rhythmic universals also emerged in iterated learning paradigms of culturally transmitted rhythms (Ravignani, Delgado and Kirby, 2017). Finally, although these rhythmic features could be independently present in other species, it is the combination of all of them that makes music unique to humans.

1.1.2. *Music in the brain and its relation to language and dance*

Music offers the possibility to study how the brain transforms a sequence of pitches and chords into a hierarchically-organized percept that assembles temporal and harmonic information. Long experience with music can modulate these activations and the structures underlying them. Thus, the study of expert musicians can improve our understanding of brain plasticity in skilled human behaviors. Other human abilities seem to be related to music skills. For instance, language and dance activate similar brain mechanism to process and temporally predict events and synchronize with them. Here, we review studies that revealed structural and functional changes due to training in music, as well as some brain commonalities between the processing of music, language and dance.

Processing of musical sounds

Music perception is a complex process that involves a mixing of bottom-up and top-down processes. Many brain regions are precisely activated in a coordinated manner to process the simplest melodic intervals that build up a chord and the simplest temporal intervals that lead up to the beat. This processing of melodic and temporal intervals is computed in prefrontal and temporal regions of the brain, but the first step to perceive music is the translation of acoustic information into neural activity in the cochlea (for a review, see Koelsch, 2011). Subsequently, the auditory brainstem, the superior olivary complex and the inferior colliculus process these neural impulses depending on properties such as timbre, pitch, intensity, and interaural disparities (Geisler, 1998). The perceptual grouping and separation of such properties are a fundamental to establish the cognitive representation of the acoustic object. Afterwards, the neural responses are sent from the medial geniculate body of the thalamus to the primary and secondary auditory cortex, the amygdala and medial orbito- frontal cortex (Cardoso et al., 1994; LeDoux, 2000; Öngur and Price, 2000). It is at this point that more abstract computations occur, and that the auditory processes are connected to motor regions, working memory and emotions.

Structural and functional changes in the musician brain

Music expertise is the refinement of multiple sensorimotor skills due to an extensive formal training in music: singing, playing a musical instrument or even dancing. A hot topic in research is whether there are differences between musicians and non-musicians due to the learning and practice of music. Some functional and structural changes were found in the neural structures of musicians and non-musicians due to the plasticity of the brain (for a review, see Dalla Bella, 2016; Schlaug, 2009; Herholz and Zatorre, 2012). These changes in the neurocognitive mechanisms underlie sensorimotor integration, feedback readjustments and the generation of expectancies, and are boosted by the repetitive planning, execution and correction of sounds and movements to perform music accurately and expressively (Brown, Zatorre and Penhune, 2015). Although structural and functional differences between the brains of musicians and non-musicians were found, it is still debated up to what point these differences are a consequence or a prerequisite for music skill learning. What seems to be clear is that instrumental practice plays a role in this brain changes by reinforcing an auditory-visual-sensorimotor network (Bangert and Altenmuller, 2003). This network can also be engaged as a mirror system during the listening of the performance of a musical piece that one knows how to play (Lahav, Saltzman and Schlaug, 2007).

Some structural differences relate to the sensorimotor integration of multimodal features, which involves regions such as the inferior lateral and superior parietal lobe, the inferior frontal gyrus and the cerebellum (Sluming et al., 2002; Gaser and Schlaug, 2003). These brain changes occur because practicing music involves the processing of multisensory information and the precise engagement of motor skills. More specifically, learning to play a musical instrument involves the repeated association of body/hand/finger movements to acoustic properties of the sounds, the visual patterns of reading music scores and the continuous multisensory feedback. The comparison of the brain of musicians and non-musicians showed structural differences in the primary auditory cortex, the premotor and supplementary motor regions, and the corpus callosum; together with associated micro-structural changes (see Schlaug, 2009, for a review). The earlier and the longer musicians practiced, the greater these brain changes were (Bangert and Schlaugh, 2006; Gaser and Schlaugh, 2003). For instance, the anterior part of the corpus callosum was larger in musicians, especially for those musicians who started earlier (Schlaug, et al., 1995), which seems to connect motor regions that are involved in the complex bimanual movements of playing music. Besides, musicians had larger symmetrical motor cortices (Amunts, et al., 1996, 1997) and higher relative cerebellar volumes in males (Schlaug, 2001). All these differences support the idea that the training in music and the cross-modal practice of a musical instrument triggers structural changes in the brain.

Changes in brain structure not always imply more brain activity. For instance, brain imaging techniques revealed that musicians have more gray matter than non-musicians in the premotor region, the perirolandic region, the posterior superior parietal region, the posterior mesial perisylvian region bilaterally and the cerebellum (Gaser and Schlaug, 2003). However, although musicians had more gray matter in the primary auditory cortex (Schneider et al., 2002), some studies showed that non-musicians had stronger activations in the auditory and motor cortices (Trainor et al., 1999; Hund-Georgiadis and von Cramon, 1999; Jancke et al., 2000). This apparent contradiction could be explained by attributing a more efficient network to musicians, related to their gray matter increases that may require fewer resources to solve the tasks. Other studies also found functional differences between musicians and non-musicians depending on the task (Schlaug, 2015; Jongsma, Desain and Honing, 2004). For instance, activations of the left inferior parietal lobe appeared only in musicians for passive harmonic and melodic processing (Schmithorst and Holland, 2003) or were enhanced in the processing of slow, medium and fast tempi (Liu et al., 2018). MEG responses to piano tones were also 25% larger in musicians (Pantev et al., 1998) and distinct regions of the brain were activated when musicians that possessed or lacked absolute pitch had to recognize tones categorically (Peretz and Zatorre, 2005).

Clear evidence for brain plasticity comes from comparisons of musicians that play distinct instruments or children that pursue musical lessons. For instance, the precentral gyrus of musicians playing string instruments (with left hand fine motor control) develops the shape of an inverted Omega in the right hemisphere, while in musicians playing keyboard instruments the shape appears in both hemispheres (Bangert and Schlaug, 2006; see Figure 2a). In the same line, trumpet and string players had more cortical activity when they were presented to the sounds of their musical instrument (Pantev et al., 2001). Similarly, the brain of singers, who particularly train vocal skills, had increases of gray matter volumes and functional activations in primary somatosensory cortices, which were connected to specific activations of the right anterior insula and that depended on their musical expertise (Kleber et al., 2009, 2013, 2016).

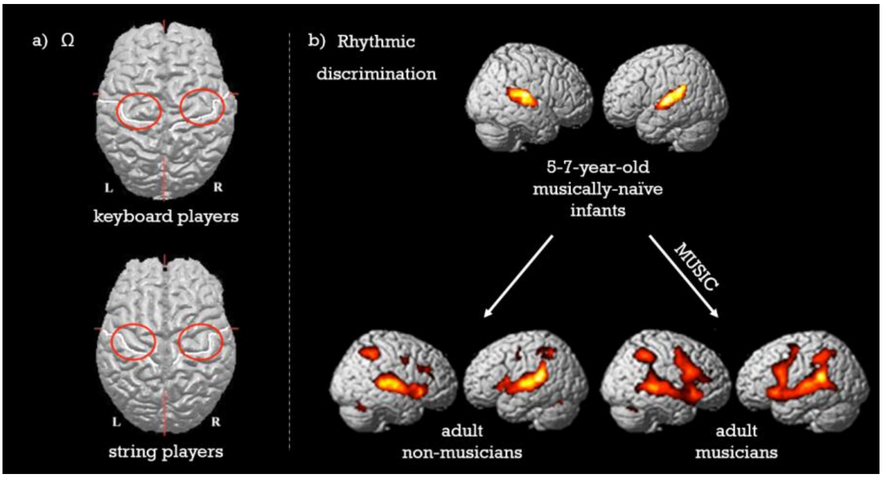

Figure 2 Brain plasticity due to music practice. An inverted Omega shape appears in the precentral gyrus of musicians (a), in the hemisphere that monitors the playing of each musical instrument (adapted from Bangert and Schlaug, 2006). The fMRI responses during a rhythmic discrimination task (b) differ between adult musicians and musically-naïve adults and children (adapted from Schlaug, Norton, Overy and Winner, 2005).

Other changes were tracked in the initial stages of musical training, by comparing 5-7-year-old children during the learning of a musical instrument with a control matching group (Overy et al., 2004; Norton et al., 2005; Schlaug et al., 2005). After 15 months of training, better fine-motor skills and melodic/rhythmic discrimination skills were found in the musically-trained children. These improvements were claimed to be associated to an enhancement of verbal skills (Forgeard et al., 2008). Similar research showed that keyboard or voice lessons improved the IQ of 6-year-old children, compared to controls that received either no training or lessons in drama (Schellenberg, 2004). These improvements may be related to the demands of attention, memory and technical skills needed to play music. The comparison of the fMRI of musically-naïve children, non-musician adults and musician adults can help to disentangle the functional and structural changes caused by normal maturation from those changes caused by training in music. A good example of these functional changes was revealed in a rhythmic discrimination task (Figure 2b), which showed that the brain of musicians had additional activity in the parietal lobe, the posterior middle frontal gyrus and the inferior frontal gyrus, compared to non-musicians or musically-naïve children (figure 2b; adapted from Schlaug et al., 2005).

Commonalities between music, language and dance in the brain

The cognitive processes behind the formation of harmonic and rhythmic structures are generally referred as music syntax. Similar to language, music is organized following a set of principles that control the combination of discrete elements (Patel, 2003; Koelsch, 2011). In fact, both systems may share some of the syntactic resources underlying this combinatorial ability (Patel, 2010, 2012), but they may operate on distinct structural representations: words or tones. An example of syntactic overlap between music and language is the P600 event-related potential, which appeared for both linguistic and musical syntactic incongruences (Patel et al., 1998). The authors sustain that this P600 may reflect the syntactic integration processes. Based on this overlap, Patel (2003) came up with the "Shared Syntactic Integration Resource Hypothesis", proposing that frontal brain areas work as 'processing regions' that integrate and provide resources to more posterior brain areas, which work as linguistic or musical representation regions. The relationship between the syntax of music and language seems to be supported by a MEG study that observed activations of left frontal areas (including Broca's area) and its right homologue during the harmonic processing of music (Maess, Koelsch, Gunter, and Friederici, 2001). Finally, a behavioral study with children by Gordon et al. (2015) highlights the links between music and language, more specifically, between rhythmic perception skills and morpho-syntactic production.

There are some commonalities between the underlying structure of music and speech regarding the temporal processing of hierarchically structured rhythms (Haegens and Zion-Golumbic, 2018). Paralleling the metrical structure found in music, a similar pattern of strong and weak elements occurs in speech, where stressed and unstressed syllables offer relevant prosodic information. Although speech does not have the same degree of regularity as language, the stressing patterns of the prosody helps listeners to generate predictions. Beyond phonology, the model of metrical trees proposed by Fitch (2013) equates rhythmic syntax to linguistic syntax, and considers them as sub-types of hierarchical processing. In music downbeats dominate upbeats and they occupy a higher prominent position in the stream. As it happens to linguistic phrases in sentences, the prominence of a musical event depends on its place in the overall metrical hierarchy, rather than just on its serial temporal position.

There are studies supporting links between linguistic and rhythmic abilities (Grube, Cooper and Griffiths, 2013). Language-related deficits are accompanied with temporal-processing deficits in clinical populations suffering from dyslexia (Leong and Goswami, 2014), specific language impairment (Cumming et al., 2015), stuttering (Wieland et al., 2015) or aphasia (Grube et al., 2016). Interestingly, rhythmic training can improve phonological and reading skills in these populations (see Schon and Tillmann, 2015). In fact, the oscillatory rhythms of the brain are also related to the parsing of linguistic information, with distinct frequency bands associated to the processing of phonemes, syllables, phrases and sentences (Giraud and Poeppel, 2012; Ding et al., 2017). In addition, the temporal organization of sounds following structured rhythms can play an important role in poetry and songs, in which rhyme and rhythm are used for their mnemonic effects that boost the auditory working memory (see Fritz et al., 2013). The relationship between the processing of speech and rhythm reinforces the idea that shared cognitive structures may underlie the temporal processing of language and music.

Music might have evolved inseparably from dance (Arbib and Iriki, 2013). Both abilities could be seen as manifestations of the same cognitive faculty, which organizes sounds and actions over time with social, emotional and aesthetical purposes. Music and dance are not dissociable in many group activities and cohesive events, and some cultures even lack terms that distinguish between them (Peretz, 2006). What may allow humans to dance in synchrony with the music is the presence of isochronous beat organized in metrical hierarchies (Fitch, 2013, 2016), because it facilitates the prediction of actions at relevant points in time. The rhythmic behavior associated to music and dance engages a motor cortico-basal ganglia-thalamo-cortical circuit, which controls voluntary skeletomotor movements and involves the supplementary motor areas and the putamen (Coull et al., 2011). The evolution of this network, affording sequential processing and temporal predictions, is discussed in detail in Patel and Iversen (2014) and Merchant et al. (2015). Finally, Lee et al. (2015) found that dance reflects the metrical structure of music and that dance cues can shape sound perception. Other studies found that changes in posture, spatial location, and movement velocity mark the underlying beat of music and are related to its metrical organization (Toiviainen, Luck and Thompson, 2010; Burger et al., 2014). Together, all these studies support the idea that there are cognitively deep connections between music and dance (Koelsch, 2011).

1.1.3. *Rhythmic cognition*

Rhythmic cognition can be divided into distinct domains: beat, meter, tempo and grouping. Several temporal-processing mechanisms allow us to extract these structural properties from music and interpret them in multiple contexts (Ravignani et al., 2014). A musical rhythm is a pattern of time intervals in a stimulus sequence. These sequences are perceived as having an underlying isochronous beat, a stable mental periodicity that provides reference points in time to categorize the perception of the events (Patel, 2008). Meter organizes beats in hierarchically-structured patterns of strong and weak positions (Fitch, 2013). Tempo relates to the speed of the beat, and can modulate the grouping and metrical structures perceived by the listeners. Tempo itself can be modulated as an expressive timing tool by gradually advancing or delaying upcoming beats. Finally, rhythmic grouping corresponds to the perceptual segmentation of the musical stream into motives, phrases and sections, categorizing patterns of durations on a discrete symbolic scale (Lerdahl & Jackendoff, 1983; Honing, 2013).

What is the musical beat?

The beat is a cognitive construct representing events that occur at isochronous intervals (London, 2004, 2012). Beat perception is therefore a psychological response that arises from the perception of regularities in a rhythmic pattern (Benjamin, 1984; Lerdahl and Jacekndoff, 1983; Palmer and Krumhansl, 1990) and that boosts the generation of expectations of upcoming events (Large and Jones, 1999). It is not a property of the objective sensory stimulus, but the product of endogenous neural mechanisms processing it (London, 2004; Nozaradan et al., 2018). The beat is fundamental to keep the time and it is normally associated with motor entrainment (Patel, 2010). It corresponds to the frequency at which we easily tap our feet, clap our hands or move our body (see the "clapping test", by Arom, 1991). Present in most of the cultures around the world, the beat is also associated to dance and group coordination (Savage et al., 2015). Interestingly, the beat is not always present in the signal, but inferred from it, what gives to the listener the feeling of groove (Stupacher, Hove and Janata, 2016; Madison, 2006; Madison, Sioros, 2014; Sioros et al., 2014). This feeling of groove may result from the fulfilling of generated rhythmic predictions structuring complex rhythms (Vuust and Witek, 2014). We have to keep in mind, however, that music is never purely isochronous, but rather quasi-periodic, and that the brain flexibly adapts to changes in speed to generate effects like accelerando or ritardando (Fitch, 2013). Finally, the beat helps to encode temporal intervals as multiples or subdivisions of itself. This chunking mechanism results in a better reproduction and discrimination of rhythms, because it reduces complex patterns to simpler components (Ravignani, Delgado and Kirby, 2017).

Meter and the metrical hierarchy

Fitch (2013) emphasizes the importance of two distinct steps in rhythmic perception. The first step consists of perceiving a beat. The second step consists of assigning a metrical structure to the pulses of the beat, to categorize them in levels of perceptual prominence. This metrical structure generates hierarchical patterns of strong and weak positions. This hierarchical metrical processing is also found in language phonology, especially in poetry (Liberman and Prince, 1977; Fabb and Halle, 2012), but likely absent in other animal species (Fitch, 2013).

The meter is normally marked by salient acoustic features, such as pitch, amplitude or timbre, that modify the prominence of musical events (London, 2012). The level of the primary strong beat is traditionally called the tactus or downbeat. Interestingly it can also be assigned voluntarily by the listener (Nozaradan et al., 2011). The metrical grouping of the beat normally is based on small integer ratios, such as 2:1 (march-like) or 3:1 (waltz-like) in Western-cultures, or (5:1) and (7:1) in non-Western cultures. Humans are able to synchronize motor actions to distinct levels of the metrical hierarchy: to the beat, its subdivision or its metrical grouping, which are normally related by small integer ratios (Honing, 2013).

The levels of the metrical hierarchy depend on the grouping or the subdivision of the perceived beat, and are used as a mental framework. The distinct levels of the metrical hierarchy periodically coincide. Beats at lower levels of the metrical hierarchy (subdivisions) are faster than beats at upper levels (meter grouping). The metrical context arises from the interaction between the preceding musical context and the expectations generated by the proficient listener. Metrical perception is therefore active, mixing top-down and bottom-up processes. Deviations from the metrical structure, like syncopations, elicit effects of surprise in the listeners, that can lead to the feeling of groove (Stupacher, Hove, Janata, 2016).

The tempo of the beat

The tempo stands for the frequency of the beat, normally specified in beats per minute in musical scores and metronomes. In general terms, the tempo range of the beat usually falls between 1 and 2 Hz, at IOIs between 500 and 700 ms (Parncutt, 1994), but preferred tempi varies across individuals, depending on their age and musical expertise (Drake et al., 2000a; Iversen and Patel, 2008). Relative tempo (analogous to relative pitch in transposed tunes) is the ability to identify a tune that is slowed down or speeded up across tempi. Interestingly, most individuals excel in absolute tempo detection and production (Gratton, Brandimonte and Bruno, 2016). When the tempo accelerates, the individuals tend to tap to slower temporal levels that are higher in the metrical hierarchy of the beat, and therefore slower (Repp, 2005). This suggests the existence of a preferred tempo range, likely linked to spontaneous motor tapping, walking rates and dance music (Drake et al., 2000b; McAuley et al., 2006; Whittle, 1996; van Noorden and Moelants, 1999). In fact, an optimal pulse-tempo frequency was identified at 2 Hz after comparing the magnitudes of Steady-State Evoked-Potentials (henceforth, SSEPs) at distinct tempo (Will and Berg, 2007), which supports that SSEPs are not just reflecting the spectral transformations of the auditory signal.

Beat perception and its key aspects

Beat perception is a form of perceptual categorization that has the property of degeneracy (Nozaradan et al., 2018), which means that inputs and outputs can establish many-to-one and one-to-many relationships. This property underlies the invariance and flexibility of beat perception. When applied to rhythmic perception, this physical property allows us to perceive structurally different elements as the same, or structurally identical elements as different. As Nozaradan and colleagues (2018) state, "a single musical rhythm can lead to different perceived beat frequencies and phases (e.g. Desain and Honing, 2003) and, in turn, various rhythmic patterns can give rise to a similar perceived beat frequency and phase (Povel and Essens, 1985)". What is relevant here is that this property may help the brain to extract the same beat from distinct rhythmic excerpts, which reduces perceptual complexity, as well as may allow the brain to entrain to distinct metrical periodicities of the same stimulus, which enhances perceptual flexibility.

Beyond this property, Patel and Iversen (2014) identified six aspects of beat perception that are crucial in the processing of musical rhythms in humans, and that not always are shared with other animal species.

a) Beat perception is predictive:

The synchronized movements to the beat fall, within few tens of milliseconds, very close in time to the perceptual stimuli (Rankin et al., 2009; van der Steen and Keller, 2013; Iversen and Patel, 2008). This tendency to tap simultaneously to a perceptual event (or even in advance) is known as phase-alignment and seems to be lacking in our closest relatives (Zarco et al., 2009) but present in distantly-related species (Patel et al., 2009; Cook et al., 2013).

b) Beat perception is flexible across a wide range of tempi

Humans have a preference for beats occurring at 600 ms. Although beats can be perceived between 200 and 2000 ms, the strongest sense of beat occurs between 400 and 1200 ms (London, 2012). Similarly, most dance pieces have a beat ranging at intervals between 400 and 500 ms (van Noorden and Moleants, 1999).

c) Beat perception is constructive

The beat perceived by the listener provides an internal temporal reference which is imposed on the stimulus and reshapes how it is perceived (Iversen, Repp and Patel, 2009). This establishes the grouping boundaries of rhythmic patterns, guides attentional resources in time and modulates the perception of accents (Repp, 2007; Locke, 2009). Listeners can flexibly synchronize to the period of the stimulus at distinct phases (Merchant and Honing, 2014; Repp, Iversen and Patel, 2008).

d) Beat perception is hierarchical

The strong and weak patterns in which the beats are organized lead to higher level periodicities. These hierarchical groupings follow small integer ratios, like 2:1 (binary meter) or 3:1 (ternary meter). Among the periodicities of these groupings, listeners tend to choose those that fall closer to a preferred tempo range (Patel, 2008).

e) Beat perception is modality-biased

The sense of a beat underlying a rhythmic pattern depends on the modality in which it is perceived. For instance, sequences of sounds are perceived different than flashing lights (Patel et al., 2005; McAuley and Henry, 2010; Grahn et al., 2011), but not moving visual stimuli (Grahn, 2012; Repp, 2005; Repp and Su, 2013). While humans have a tapping bias favoring auditory over visual metronomes (Repp and Penel, 2002; Iversen et al., 2015), monkeys do not have a clear preference (Merchant and Honing, 2014; Zarco et al., 2009).

f) Beat perception engages the motor system

The passive perception of a beat engages motor regions such as the premotor cortex, the basal ganglia and supplementary motor areas (Grahn and Brett, 2007; Chen et al., 2008a; geiser et al., 2012; Teki et al., 2012), with an enhanced auditory-motor coupling (Kung et al., 2013; Zatorre et al., 2007) which is reinforced in musicians (Grahn and Rowe, 2009). The role of this network is the processing of temporal sequences and the generation of temporal predictions (Schubotz, 2007). We will review these findings in more detail in section 1.2.

Taking into account some of these properties, several models attempted to simulate beat perception and compute the frequency of discrete pulses (see Zuk, Carney and Lalor, 2018), either using an internal clock (Povel and Essens, 1985), pattern matching (Parncutt, 1994), an internal resonator (van Noorden and Moelants, 1999) or several neural oscillators (Large, Herrera and Velasco, 2015). Some of the models received evidence from EEG and MEG studies regarding time-locked cortical activity to the perceived beat of a stimulus and its metrical levels (Nozaradan et al., 2011; 2012; Snyder and large 2005; Iversen, Repp and Patel, 2009; Tal et al., 2017; Tierney and Kraus, 2014; Fujioka, et al., 2012; Fujioka, Ross and Trainor, 2012, 2015; Celma-Miralles, de Menezes and Toro, 2016). We will review some of these studies and theories in section 1.2.

Sensorimotor synchronization to rhythms

Finally, a fruitful way to study rhythm perception and production is by asking participants to tap with the finger along with a beat (de Pretto, Deiber and James, 2018). The boundaries of motor synchronization to rhythms have been studied across cultures, ages, tempo ranges and modalities (see Repp, 2006; Repp and Su, 2013). In human sensorimotor synchronization, phase correction and period correction are strategies to compensate deviations from isochrony, and almost no differences between musicians and non-musicians were found in short time intervals (Madison and Merker, 2004).

Sensorimotor synchronization can also be used to study perceptual and motor impairments in certain diseases. The existence of areas specialized for rhythmic perception became evident after the discovering of a disorder affecting the processing of rhythms: beat deafness, a type of congenital amusia (Phillips-Silver et al. 2011; Dalla Bella and Sowiński, 2015). This motor-perceptual disorder consists of the difficulty to synchronize and find a beat underlying a musical excerpt. Similarly, Parkinson's disease patients are found to be impaired in processing isochronous intervals or more complex beat-based rhythms (Grahn and Brett, 2009; Harrington, Haaland and Knight, 1998), suggesting a role of the basal ganglia in detecting and generating an internal beat. The study of these affected populations can complement and confirm the results found in the laboratory.

1.2. Human research on rhythm processing

1.2.1. *Time, rhythm and beat in the brain*

A crucial dimension of music is the organization of tones and chords over time. We have already discussed the main aspects of our rhythm cognition: beat, meter, tempo and grouping. *Grosso modo*, timing mechanisms could be based on interval model, that estimate and compare memorized durations, or entrainment models, that take oscillatory peaks as referential points in time. Likewise, the processing of rhythm can be approached by interval-based timing models or beat-based timing models. In this section, we want to review these approaches and the theories behind the processing of the beat, as well as to present relevant research on the brain structures that underlie the processing of the musical beat and meter.

Models and brain substrates for the processing of timing

There are several models trying to explain the processing of timing. These models and the neuroscientific evidences supporting them are reviewed and discussed in Grondin (2010) and McAuley (2010). Here we present them into two groups.

a) Interval models: they comprise the estimation of duration by an internal “clock”, the storing of the duration by a reference memory, and the comparison of memorized estimated durations. The internal clock can be based on a pulse-emitting “pacemaker” (e.g. Gibbon, 1977; Church, Meck and Gibbon, 1994) or a bunch of fixed oscillators that work as “coincidence-detectors” (e.g. Church and Broadbent, 1990; Matell and Meck, 2000).

b) Entrainment models: they consist of self-sustaining oscillators that have peaks in amplitude at regular time intervals (Large and Jones, 1999; McAuley and Kidd, 1998). The period and the amplitude peaks of the oscillator provide referential time points to which compare the stimulus onsets. They can account for contextual effects. Differently, beat-based models rely on fixed oscillators that cannot modulate the phase or the period.

Regarding the neural basis of timing, neuroimaging studies and brain-damaged patients revealed the involvement of areas such as prefrontal cortex, parietal cortex, premotor cortex and supplementary motor areas, the basal ganglia and the cerebellum (see Grahn, 2012). The role of the cerebellum was attested with duration discrimination and finger-tapping tasks (Kawashima et al., 2000; Teki et al., 2011). The role of the basal ganglia in timing tasks was revealed by patients with Parkinson’s disease, who had impaired duration discrimination and poor finger-tapping synchronization (Artieda et al., 1992; Elsinger et al., 2003). In fact, the cerebellum is more associated to interval-based (absolute) timing while the basal ganglia are more associated to beat-based (relative) timing (Teki et al., 2011; Grube et al., 2010).

Models and brain substrates for the processing of rhythm and its beat

Similar to timing, rhythm models can be divided into two groups: ruled-based models and real-time models (Grahn, 2012). The former relies on an internal clock that regularly ticks within a pacemaker-accumulator mechanism (Povel and Essens, 1985). The latter is based on the entrainment of multiple neural oscillators to the periodicities at distinct metrical levels of the rhythm (Large and Snyder, 2009). Several fMRI studies report a distributed network to process rhythm and its beat, which seems to overlap with timing mechanisms. An important characteristic for the models is if the rhythms are metrical or non-metrical, because they would be respectively explained by metric (beat-based) coding models or figural (grouping-based) coding models (Essens & Povel, 1985; Povel and Essens, 1985). Based on this metrical feature, the processing of temporal intervals may distinctly activate two neural substrates: a beat-based timing network, consisting of striato-thalamo-cortical connections, and a duration-based timing network, involving the inferior olive and cerebellum (Teki et al., 2011).

The involvement of motor areas in the processing of rhythm has been reported in several fMRI studies, which identified activations in premotor cortex, supplementary motor areas, basal ganglia, striatum and cerebellum (Grahn and Brett, 2007; Chen, Penhune and Zatorre, 2008; Bengtsson et al., 2009; Teki et al., 2012; Kung et al., 2013; Merchant and Honing, 2014). These neural substrates of rhythm perception and production mostly overlapped with the brain areas activated by timing experiments. The activity in the basal ganglia was found to reflect the processing of beat across modalities (Grahn and Brett, 2007, 2009; Grahn, Henry and McAuley, 2011), together with the auditory-motor coupling (Chen, Zatorre and Penhune, 2006). Interestingly, these auditory-motor coupling was bilaterally enhanced in musicians (Grahn and Rowe, 2009).

The electrophysiological responses to beat and meter have been studied using event-related potentials and the frequency-tagging approach. For instance, Geiser et al. (2009) manipulated the metrical structure of a rhythm by inserting or deleting a note, and found that listeners detected these metrical changes only when they were paying attention. In contrast, larger ERPs and better omission detection was found for participants listening to repeating rhythms with random silent gaps placed in strong beat positions, compared to weak beat position, even without attention to them (Ladinig, et al., 2009). By means of magnetoencephalography, Vuust et al. (2009) found that the brain of musicians, compared to non-musicians, responded faster and more strongly to metrical violations of predicted upcoming events. The internal entrainment to beat and meter has been studied (i) indirectly, analyzing the EEG responses to violations of expected metrical structures (Winkler et al., 2009), and (ii) directly, observing the EEG recordings of rhythmic excerpts in the frequency dimension (Nozaradan, 2014). Winkler et al. (2009) proposed that the mechanisms underlying rhythmic perception may be innate, because the EEG responses of newborns were different depending on whether sound omissions disrupted the beat or not. However, these responses could be influenced by previous experience, like bouncing, to which infants are very sensitive (Phillips-Silver and Trainor, 2005). During the presentation of periodic stimuli, the neural populations of the brain fluctuate generating a stimulus-related response modulating the ongoing cortical activity (Nozaradan, 2014). With the frequency-tagging approach, Nozaradan and colleagues (2011, 2012, 2017, 2018) demonstrated a selective enhancement of the periodicities related to the beat and meter in these fluctuations, across modalities, rhythmic paradigms and populations.

Another line of research focuses on the neural oscillatory changes happening at higher frequencies. There is evidence suggesting that beta- and gamma-band activity relates to the endogenous generation of beat and meter. For example, beta-band activity (13-30 Hz) was found for motor tasks in sensorimotor cortices and basal ganglia and cerebellum (Salmelin and Hari, 1994; Salmelin et al., 1995; Baker, 2007). Gamma-band activity (>30 Hz) was found for attention, memory, anticipation and feature-binding processes (Jensen, Kaiser and Lachaux, 2007; Bhattacharya, Petsche and Pereda, 2001). Fujioka and colleagues (2009) found an increase of beta and gamma activity during beat perception. Similarly, the omission of isochronous sounds occurring at strong or weak positions of a binary structure induced distinct oscillatory activity, with greater neural responses to omitted on-beat positions (Snyder and Large, 2005). Finally, the projection of an internal meter was correlated to increases of beta activity at beat positions (Iversen, Repp and Patel, 2009). It seems therefore that beta-band activity is related to the prediction of upcoming beats (Fujioka et al., 2009, 2012). In sum, EEG and MEG studies revealed neural markers for the anticipation of metrically-structured beats, which are reflected in event-related responses and beta- and gamma-band activities.

Theories for beat perception

Large and Snyder (2009) propose a theory to explain beat perception based on general neural mechanism: non-linear oscillations of the neural system that synchronize with the rhythms of an external stimulus. This view is known as the Neural Resonance Theory and poses that auditory sequences trigger oscillations in the cortical and subcortical areas of the brain that lead to the perception of beat and meter. This theory relies on the intrinsic mechanisms of the neural systems that are involved in perceiving, attending and responding to sensory signals (see Jones, 2008), in line with the Dynamic Attending Theory (Jones, 1976; Jones and Boltz, 1989; Large and Jones, 1999). However, the neuroscientific evidence we reviewed above suggests that there is an interaction between sensory and motor regions, working as a predicting sequence timing mechanism (Schroeder et al., 2010; Morillon et al., 2019). The role of motor areas was included in some theories of rhythmic perception (Todd, O'Boyle and Lee, 1999; Todd and Lee, 2015), acknowledging their contribution in generating predictions (Schubotz, 2007). In a more recent version of the neural resonance theory, Large, Herrera and Velasco (2015) included auditory-motor coupling in their model of beat perception. In this line, Patel and Iversen (2014) also incorporated the motor areas in the "action simulation for auditory prediction" hypothesis, which proposes that beat perception relies on the bidirectional communication between the auditory and motor planning regions of the cortex that simulate (even in the absence of overt movement) the neural signal of a temporally-predicted action. According to these authors, these auditory-motor connections may rely on the dorsal auditory pathway crossing the parietal cortex, which could have been strengthened by the emergence of the vocal learning ability in humans (see the vocal learning hypothesis by Patel, 2006).

Selected studies revealing metrical effects of rhythmic processing

Several studies focused on the processing of meter using EEG or MEG. A seminal study showed that isochronous sound sequences are automatically processed as binary, which is known as the tick-tock effect (Brochard et al., 2003). Since then, some studies compared the responses elicited by metrically organized sequences of sounds to similar sequences in which either the strong or the weak beat was omitted (Snyder and Large, 2005; Ladinig et al., 2009) or no beat was accented (Iversen, Repp and Patel, 2009). Furthermore, other studies tackled the imagery of meter on non-accented isochronous rhythms, comparing the projection of binary and ternary meter (Fujioka, Ross and Trainor, 2015; Nozaradan et al., 2011). These studies focused on distinct frequency ranges, revealing the importance of the beta-band in the generation of predictions of the metrical beat and the sub-delta-band in the neural entrainment to imagined metrical groupings.

To study the gamma-band with MEG, Snyder and Large (2005) presented participants with an isochronous sound accented every two beats. Induced gamma-band activity normally preceded the onsets of the upcoming beats (even when the sounds were omitted), while evoked gamma-band activity depended on the presence of the sound. The evoked activity had larger responses to loud tones than to soft tones, and it was sensitive to the omissions of these tones (see Figure 3a). The differences between evoked and induced activities reflected the combination of stimulus-driven and expectancy-based representations of the binary meter. The modulation of beta- and gamma-band activity was also compared in Iversen, Repp and Patel (2009). In one condition, participants had to listen to sequences of two tones in which the accent was either on the first or on the second sound. The physical accent increased gamma- and beta-band activity. In another condition, participants listened to the same rhythms without any accent and had to impose a mental accent either on the first beat or on the second. The imagined accent increased only beta-band activity, which means that gamma-band activity depended on the physical stimulus (see Figure 3c). In an EEG study (Ladinig et al., 2009), sounds at the metrical strong or the metrical weak positions of complex rhythms were randomly omitted. In this case the omission of a strong or a weak beat elicited a mismatch negativity response. Compared to weak-beat omissions, strong-beat omissions elicited earlier and higher-amplitude MMNs (see Fig 3b). Interestingly, these responses to metrical deviations appeared regardless of attention, in both unattended and passive listening conditions, and were independent from the participants' formal training in music.

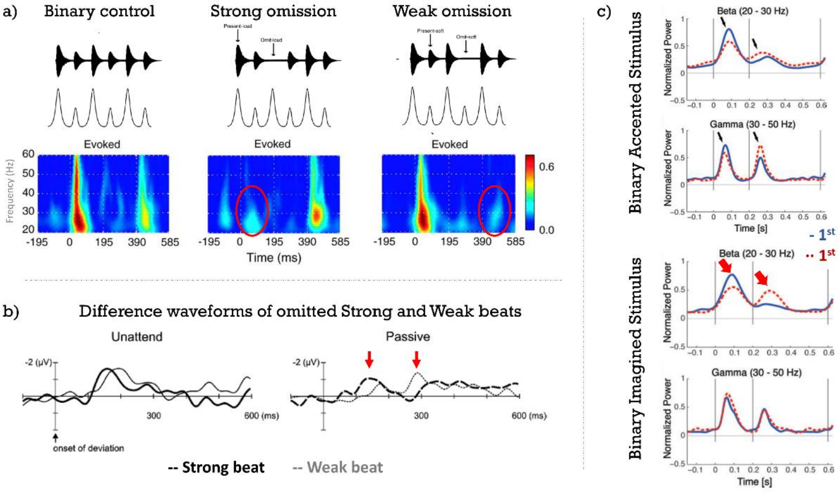

Figure 3 Neural activity distinguishing strong and weak metrical positions. Evoked gamma-band activity (a) was larger for omissions of strong beats (see the circles, adapted from Snyder and Large, 2005). Strong beat omissions elicited earlier MMNs (b) regardless of auditory attention (see the arrows, adapted from Ladinig, Honing, Háden and Winkler, 2009). The beta-band activity (c) increases when a binary accent that is not present in the signal is imagined by the participant (see the arrows, adapted from Iversen, Repp and Patel, 2009).

Regarding metrical imagery, Fujioka and colleagues (2015) studied in a MEG study the modulation of the beta-band activity when musicians were either processing or imagining binary and ternary metrical structures. As in a previous study (Fujioka et al., 2012), the beta-power decreased after the tone onset and increased predicting the following beat. These increases and decreases depended on the metrical position of the beat, in both perception and imagery conditions. The beta-power decrease for the imagined downbeat was greater than the decrease for the upbeat, in the binary meter, and the decrease for the middle-beat, in the ternary meter (see Figure 4a). These findings link beta-band modulations to internal representations of meter. Finally, in the EEG study by Nozaradan et al. (2011), participants had to listen to an isochronous beat, and imagine binary meter or ternary meter on it. The analyses in the frequency-domain revealed peaks at the slow imagined frequencies, which may stand for some populations synchronized to the binary and ternary metrical structures (see Figure 4b).

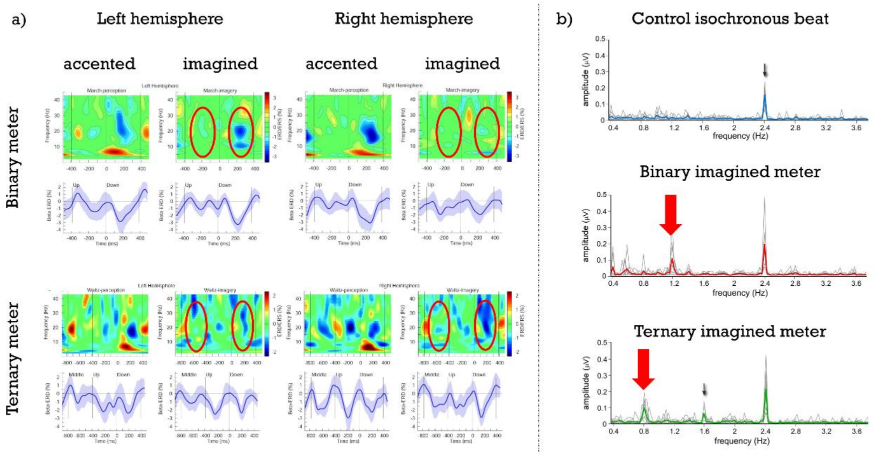

Figure 4 Neural activity related to imagined binary and ternary meter. MEG-responses in the time-frequency domain (a) for accented and imagined binary and ternary metrical structures (see the circles, adapted from Fujioka, Trainor, Large and Ross, 2012). EEG-responses in the frequency domain (b) for imagined binary and ternary metrical structures (see the arrows, adapted from Nozaradan, Peretz, Missal, and Mouraux, 2011)

1.2.1 Brain oscillations, neural entrainment and the frequency-tagging approach

The synchronization of neural activity to the rhythms of the stimulus is fundamental to explain many theories, from sensorimotor synchronization (Merker, Madison and Eckerdal, 2009) and attentional selection (Lakatos et al., 2008), to music perception (Doelling and Poeppel, 2015) and linguistic parsing (Giraud and Poeppel, 2012). Here we will review how rhythmic stimuli trigger brain oscillations, what makes them different from transient event-related potentials, what are the benefits of neural entrainment in perception, and how these neural oscillations relate to the processing of music and its rhythm. Finally, we will briefly present the frequency-tagging approach as a tool to study the synchronized activity of the brain in the frequency-domain.

What are brain oscillations?

Brain oscillations are rhythmic fluctuations that constantly occur in the brain due to the high and low excitability states of its neuronal populations (Bishop, 1932; Buszáki and Draguhn, 2004). Brain oscillations arise from the combination of three neural mechanisms: the intrinsic oscillatory fluctuations of the sensory system, the automatic entrainment to external rhythmic inputs across modalities, and the top-down modulation of these oscillations during goal-directed tasks (Haegens and Zion-Golumbic, 2018). In fact, these mechanisms are not mutually exclusive, and they could share the same underlying neural bases. These fluctuations occur in neocortical and thalamic brain regions (Steriade et al., 1993; Slézia et al., 2011) in the frequency ranges of delta (1-4 Hz), theta (4-8 Hz), beta (13-30 Hz) and gamma (30-70 Hz; Buzáki, 2006). Recent research supports that these oscillations reflect brain operations (Schroeder and Lakatos, 2009; Buszáki, 2010; Wang, 2010; Arnal and Giraud, 2012) that interact with the processing of sensory information and with the performance of actions in particular ways (for a review, see Haegens and Zion-Golumbic, 2018; and Zoefel, ten Oever and Sack, 2018). Regarding the rhythm of music, the beat tends to fall within the delta range, the meter tends to fall within the sub-delta range and the harmonics tend to fall within the theta range (see Large, Herrera and Velasco, 2015; Musacchia, Large and Schroeder, 2014).

What is neural entrainment?

Entrainment describes the synchronization of two oscillators in frequency and phase. Therefore, neural entrainment refers to the synchronization of a group of neurons to the rhythm of a sensory input. When neurons adjust the high-excitability oscillatory phase with the predicted timings of natural events, the sensory input receives an optimal processing (Schroeder and Lakatos, 2009). These oscillatory dynamics engage and modulate sensorimotor networks enhancing attention and temporal prediction, which improve sensory detection and discrimination (Jones, Kidd and Wetzel, 1981; Busch, Dubois and VanRullen, 2009). This cognitive benefit is known as rhythmic facilitation and is linked to neural entrainment.

The rhythmic facilitation phenomenon

Rhythmic facilitation refers to the improved processing effects caused by either the spontaneous intrinsic rhythms or the entrainment of neurons to external rhythms. Normally, the brain responds to external rhythms by automatically entraining to their temporal properties (Herrmann, 2001). The neural coupling to the frequency of the stimulus can even persist several cycles after the presentation of the signal, and it influences behavioral tasks (Hickok, Farahbod and Saberi, 2015; Lakatos et al., 2013). For instance, the spontaneous brain oscillations preceding the presentation of a stimulus biases the way it is processed across sensory modalities (VanRullen, 2016). Rhythmic facilitations effects are also bond to certain frequency ranges, such as theta- and alpha-band in vision, delta- and theta-band in audition or alpha- and beta-band in tactile (Haegens and Zion-Golumbic, 2018).

Multiple temporal organizations of the events can be dynamically tracked by the phase of low-frequency oscillations (Costa-Faidella et al., 2017). In general, the processing of events is more effective when they occur at high-excitability phases of the oscillations (VanRullen, 2016). However, although the phase of the ongoing oscillations facilitates detection performance (Mathewson et al., 2012; de Graaf et al., 2013), there is controversy about the specific phase (in-phase and out-of-phase) that improves or detriments the performance of visual and auditory detection tasks (e.g. Spaak et al., 2014; Hickok, Farahbod and Saberi, 2015). For instance, neural phase-locking to rhythms that are informative about the timing of upcoming events enhances sensitivity to visual and auditory targets (Rohenkohl et al., 2011, 2012; ten Oever et al., 2014, 2017). These regular temporal expectations influence the encoding of the sensory stimulation to form and predict the auditory object (Costa-Faidella et al., 2011). This means that neural entrainment to external rhythms may help the generation of temporal expectations and thus help perceptual detection tasks.

The effects of top-down modulations on the processing of target events have also been studied to explore whether they can alter the strength of the neural coupling to some periodicities of the rhythms. There is evidence for top-down rhythmic facilitation due to attentional enhancements across modalities (Kim et al., 2006; Keitel, Thut and Gross, 2017; Lakatos et al., 2008, 2016). The top-down control of neural entrainments is also supported by studies in which the system selectively entrains to one of two competing rhythmic inputs, even across modalities (Gray et al., 2015; Lakatos et al., 2016). It seems, therefore, that neural oscillations can automatically entrain to external rhythms and be modulated by top-down factors, depending on context and task demands.

Evidence supporting neural entrainment

The brain response to a periodic stimulus is termed as steady-state evoked potentials (SSEPs, Chatrian, Petersen and Lazarte, 1960; Regan, 1966). Most studies assume that they involve endogenous neural oscillations (i.e. neural entrainment) reflecting predictive processes (Zoefel, ten Oever and Sack, 2018). However, there is a debate about whether these SSEPs reflect intrinsic neural oscillations (Herrmann, 2001; Notbohm and Herrmann, 2016; Notbohm, Kurths and Herrmann, 2016; among others) or just transient evoked responses that temporally superpose due to their fast occurrence (Capilla et al., 2011; Keitel et al., 2014; Galambos and Makeig, 1981; Hari et al., 1989). To disentangle this, Haegens and Zion-Golumbic (2018) and Zoefel and colleagues (2018) propose to look at phase-locking increases and power decreases that cannot be explained by bottom-up processes, as well as to design paradigms exploring the internal construction of rhythms, the detection of subthreshold stimuli or the responses post stimulus. Indeed, our first EEG study followed a design in which the metrical grouping had to be imagined, by endogenously modulating the oscillations related to the beat.

There is plenty of evidence for neural entrainment in the rhythmic studies carried out by Nozaradan and colleagues (2011, 2012, 2016, 2017). These studies showed a selective enhancement of the frequencies related to the beat and the meter, as it happened for the "missing beat" rhythms in Tal et al. (2017). In the linguistic domain, Ding et al. (2016) tracked the rhythmic structures of phrases and sentences that did not appear in the acoustics of the stimuli, made of isochronous monosyllabic words. Besides, the tracking of these phrases and sentences was only found for native speakers, and disappeared during sleep (Makov et al., 2017). There is evidence for neural entrainment coming from subthreshold studies in which undetected stimuli maintained oscillatory activity and lowered detection thresholds (ten Oever et al, 2014, 2017; Will and Berg, 2007; Zoefel and Heil, 2013). Even when the spectral energy fluctuations of the signal were reduced, the oscillatory activity persisted (Zoefel and VanRullen, 2015). More evidence supporting neural entrainment is the fact that the perception of a beat quickly emerges after the presentation of few rhythmic cycles (Fraisse, 1982; Desain and Honing, 1999) and can last some cycles after the stimulus (Bauer et al., 2015; Correa and Nobre, 2008; Barnes and Jones, 2000; Lakatos et al., 2013; Mathewson et al., 2012).

This evidence suggests that neural entrainment goes beyond stimulus-driven processes and synchronizes with expected timings of upcoming events, which may be essential for temporal prediction mechanism (Schroeder and Lakatos, 2009). Finally, recent research found that MEG data from participants better matched the predictions of an oscillatory model than that of an evoked model, supporting that the auditory cortex relies on oscillatory mechanisms coordinated with bottom-up evoked responses (Doelling et al., 2019). Thus, the presented evidence suggests that SSEPs reflect bottom-up neural synchronization to the frequencies of the rhythmic input, which can be modulated by top-down goal-directed tasks, such as the induction of meter.

Music and neural oscillations

The rhythms of music are more complex than isochronous sounds, because they arise from the combination of sounds at multiple temporal levels, and therefore cannot be modeled by a single oscillator. Listeners can synchronize to the multiple time scales of a rhythmic pattern to extract underlying temporal reference points and generate expectancies. This ability may involve the coupling of several neural oscillators to the complex hierarchically-organized rhythms (Large, Herrera and Velasco, 2015). Despite this temporal complexity, one frequency arises as the main reference point to organize fast and slow tones (i.e. the beat), and normally elicits automatic body motion coupled to it (Nettl, 2000). The cognitive percept of a periodic beat emerging from the processing of non-periodic stimuli is explained in the computational model of the neuronal resonance theory (Snyder and Large, 2005; Large, 2008; Large and Snyder, 2009). The beat may emerge from the non-linear interactions of two oscillating systems (the physical stimulus and the dynamic neural system), that produce oscillatory activity at the stimulus' frequencies and their combinations: the (sometimes missing) beat and its harmonics. Interestingly, these non-linear computations can explain the generation of neural activity to frequencies that are not present in the stimulus itself, as in studies with a "missing pulse" (Chapin et al., 2010; Large et al., 2015; Tal et al., 2017).

There is research reporting that the metrical structure of the beat affects both neural activity and behavioral performances. Evidence for the metrical structure directing attention over points in time comes from peaks of connectivity between motor and premotor regions and auditory and visual cortices, which were elicited by audiovisual events occurring in strong-beat positions (Bolger et al., 2014). More evidence pointing towards neural entrainment to beat and meter comes from the fact that stimuli occurring at beat positions are processed better than stimuli occurring at other positions (Palmer and Krumhansl, 1990; Bower and Honing, 2015). It was also found that beta- and gamma-band activity varied depending on metrical positions (Fujioka et al., 2009, 2012, 2015). Even newborn infants show distinct neural responses depending on the sound position in the metrical hierarchy (Honing et al., 2009; Winkler et al., 2009). Other studies revealed that beat-related frequencies are enhanced when someone listens to metronomic or complex rhythms or imagines a metrical structure on them (Nozaradan, et al., 2011, 2012, 2016; Iversen, Repp and Patel, 2009; Vlek et al., 2011).

The frequency-tagging approach

During the last decades, plenty of research has advanced in identifying the neural correlates of rhythmic processing. One way to fruitfully study the neural entrainment to beat and meter consisted of recording electroencephalographic recordings and interpreting them in the frequency domain (Nozaradan, 2014; Zhou, et al., 2016). As Nozaradan et al. (2018) reviews, this technique was initially used to measure visual sensory processes (Regan, 1966, 1989) and was posteriorly extended to measure the synchronization of neuronal populations to the envelope of acoustic streams (Galambos, Makeig and Talmachoff, 1981; Pantev et al., 1996) and higher-level processes in vision (Rossion, 2014) and other modalities (Moungou et al., 2016).

This approach allows researchers to compare the increases of neural activity at distinct frequencies of interest, like the beat and its meter (Nozaradan et al., 2011, 2012). It served as the bases for experiments to study the imagery of a metrical beat (Nozaradan et al., 2011; Stupacher, Wood and Witte, 2017; Tal et al., 2017; Celma-Miralles, de Menezes and Toro, 2016), the manipulation of an internal beat by body movement (Chemin et al., 2014), the involvement of subcortical brain regions in beat perception (Nozaradan et al., 2016a), the presence of beat perception in infants (Cirelli et al., 2016) and the detrimental effects of lesions in the cerebellum and the basal ganglia on beat processing (Nozaradan et al., 2017a). With this approach one can also compare the physical properties of the input with the physiological properties of the neurally-transformed output (Lenc et al., 2018; Nozaradan et al., 2017b) and other behavioral measures, such as finger-tapping (Nozaradan et al., 2016b). This paradigm also allows to study whether there are differences in neural entrainment between musically-trained and musically-naïve participants (Stupacher, Wood and Witte, 2017; Celma-Miralles and Toro, 2019). Together, these studies show that the neural responses to the beat do not only reflect stimulus properties but are internally shaped and modulated by contextual factors, such as imagery, synchronized movements and the prediction abilities of each individual.

The idea behind the frequency-tagging approach is that beat perception is sustained by groups of neurons synchronized to the frequency of the beat, and that this synchronization can be seen as a peak of activity that reflects exogenous and endogenous processes for the prediction of upcoming events (Nozaradan et al., 2018). The frequency-tagging approach relies on the fact that the repetition of a stimulus (or a modulated property of it) at a constant rate produces periodic changes in the EEG signal (Adrian and Matthews, 1934), that are identifiable using a Fourier transform (Regan, 1966). These changes in voltage are known as steady-state evoked potentials and are supposed to be stable in phase and amplitude over time. However, the actual neural oscillations recorded with electroencephalographic methodologies are far from looking sinusoidal (Cole and Voytek, 2017); and these irregularities of the signal may introduce peaks at the frequencies of the harmonics in the frequency spectrum (Zhou et al., 2016).

The frequency-tagging approach objectively relates the stimuli input and the neural output (Nozaradan et al., 2018). It captures the non-linear transformations that the stimulus receives during the perceptual processing and that ultimately generate peaks at frequencies that are not present in the stimulus. These transformations may be also related to firing thresholds, specific frequency bandwidth or frequency-tuning functions of the neural system. Several studies by Nozaradan and colleagues corroborate that the frequency-tagging approach captures a selective enhancement of the frequencies of the beat and meter in the EEG signal (Nozaradan et al., 2012, 2016a, 2016b). Importantly, some concerns and limitations should be taken into account regarding the method (Zhou et al., 2016) and the stimulus properties (Henry, Herrmann and Grahn, 2017), because they can lead to erroneous conclusions. However, there is agreement around the idea that increases in power at certain frequencies seem to reflect both neural entrainment to the stimulus and predictive oscillatory excitability states during the processing of the rhythmic stimuli.

Some of these neural processes may not be unique to humans, because similar brain mechanisms may have evolved across species. They may help each individual animal to process environmental events accurately over time. The following section will tackle this issue and review some non-human animal abilities realetd to the rhythm of music.

1.3. Music in non-human animals

1.3.1. *Musicality traits in animals*

The comparison of distinct species can reveal what neural mechanisms and what behavioral features are connected to the development of musical components in humans. This comparison may allow us to map the emergence of these musicality traits in the phylogenetic tree and identify selective pressures that triggered their evolutionary emergence in distinct species (Ravignani, Honing and Kotz, 2017; Kotz, Ravignani and Fitch, 2018). The evolution of timing mechanisms may be linked to the necessity of all animals to identify how objects interact over time. This means that similar cognitive mechanisms could underlie the temporal processing of cross-modal information to predict the occurrence of events in the environment. In this section, we will review which aspects of music can be separately found in other species and how laboratory research and natural observations can allow us to study the animal cognitive abilities related to music.

What is musicality?

Music is composed by a mosaic of biological and cognitive traits (i.e. musicality) that allow us to perceive, produce and appreciate music. These traits are structurally separated components of music that may have been selected across species to fulfill distinct functions (Hoeschele et al., 2015). The structural and behavioral similarities present across musical cultures support the existence of a shared set of cognitive mechanisms underlying music (Savage et al., 2015). These musicality traits are constrained by our cognitive and biological system and must be distinguished from music: the acquired sociocultural construct based on the musicality components (Honing, et al., 2015). Musicality traits could have been selected for biological functions in the past differing from current functions. It is possible that they played a role in mating (Darwin, 1871), infant well-being (Honing, 2013), or group cohesion and identification (Cross, 2009). For instance, group music and dance could have substituted the social grooming typical of primates in our hominid lineage (Dunbar, 2010;

2012). Since non-human animals lack music, the common musicality traits must be related to the evolution of general-purpose auditory mechanisms driven by emotional states (McDermott, 2008). It is plausible that pitch and timing processes evolved for the identification of auditory objects in the environment, as framed in the auditory-scene analyses approach (Trainor, 2015).

Evidence for music behavior in the past is scarce because vocal music and body percussion are ephemeral immaterial objects. The earliest musical instrument is a flute that dates from 45.000 years ago (Conard, Malina and Münzel, 2009). As traces of cognitive traits are difficult to find in the archaeological record, the study of musicality components in animals may help to locate when and how these traits have arisen, spread and changed in the human lineage and other species. Comparative approaches are based on the neo-Darwinian idea that closely-related species solve similar tasks by engaging homologous mechanisms, while distantly-related species may solve similar tasks by using analogous mechanisms. Both contributions are fundamental, because they allow us to date the emergence or losses of cognitive traits across families of species, and thus account for evolutionary convergence (i.e. deep homologies) developed under similar environmental pressures. One very interesting deep homology is vocal learning, which is even found in species distantly-related to humans, such as songbirds, and might be at the bases of our language and music abilities. Finding these commonalities allows us to study the neurobiological structures underlying cognitive phenotypes, the genes and the developmental factors that regulate them.

The study of musicality components

The cognitive components making up musicality might be those involved in the perception, production and appreciation of music. Each musicality component may have an independent evolutionary history and specific brain substrates (Honing et al., 2015). Several researchers have focused on animal vocalizations and behavior looking for musicality features such as rhythm, timbre, pitch, and higher order patterning (see Hoeschele et al., 2015). Honing et al., (2015) highlight the importance of musicality traits, such as relative pitch and pitch encoding, as well as beat perception and the metrical encoding of the rhythm. However, musicality features go beyond these auditory properties and should consider social factors and affective states as well, which are directly linked to motivation, reward or group cohesion and arousal (Trehub, Becker and Morley, 2015). Fitch (2015) seems to take them into account in his division of the core components of musicality: song, drumming, social synchronization and dance; as well as the basic capacity to produce periodic motion in vertebrates (Kotz, Ravignani and Fitch, 2018).

The brain mechanisms and the evolutionary constraints that underly rhythmic entrainment (connected to vocal learning and social interactions) have extensively been studied and discussed during the last decades (Patel and Iversen, 2014; Merchant and Honing, 2014; Petkov and Jarvis, 2012). Beyond the study of entrainment and vocal learning, other constraints can guide the research on the evolution of music (and sometimes language), such as its generativity in creating infinite patterns, the effects of cultural transmission and the motivational bases to collectively sing and dance (Merker, Morley and Zuidema, 2015). It is important to incorporate these social and emotional components into the study of musicality because they can help to identify music behavior across species, which may improve our understanding about how music emerged in our lineage.

Lab studies versus natural observations

Searching musicality traits in non-human animals can be challenging. As Hoeschele and colleagues (2015) state, fruitful comparative research should take into account each species' perceptual abilities, their preferences and motivations, and their phylogenetic similarities to humans. While naturalistic studies are very informative about ecologically-driven behaviors and their motivations, laboratory studies can offer a more accurate way to tackle specific perceptual and cognitive abilities in the strategy of each species to solve a task. For instance, lab studies can control whether the success in a categorization task may depend on global or local features of the designed stimuli, on the possession or lacking of neural circuitry in the animals (such as the vocal learning or the motor cortico-basal ganglia-thalamocortical loop), or on perceptual thresholds and physiological limitations. However, lab research should move beyond prototypical scientific paradigms and adapt to more naturalistic approaches. For instance, a way to study the rhythmic drumming behavior displayed by some primates in the wild (Fitch, 2006) can consist of recording with a toy-device the percussive activity of chimpanzees (Ravignani et al., 2013) or analyzing the social interactions that involve turn-taking drumming between bonobos and humans (Large and Gray, 2015). In sum, both lab and natural studies are very informative in biomusicology; and although extensive trainings and the use of unnatural stimuli in the lab could lead to an unsuccessful learning that underestimate the capacities of the animals, they can also lead to surprising findings that reveal abilities that are not always apparent in the everyday behavior of the animals.

Animals and music

The responses to music in non-human animals have been found to vary across species. One way to approach the motivational bases of music is observing whether there are preferences towards musical sounds. For instance, Chimpanzees seem to spend more time next to a speaker playing African and Indian music than to a silent speaker (Mingle et al., 2014), but cotton-top tamarins may prefer silence over musical sounds (McDermott and Hauser, 2007). Moreover, cotton-top tamarins did not show any preference between consonant and dissonant music, while newborn chicks preferred consonant over dissonant sounds (Chiandetti and Vallortigara, 2011). Rats also discriminate consonance and dissonance (Fannin and Braud, 1971; Toro and Crespo-Bojorque, 2017; Crespo-Bojorque, 2016). Another way to study the general processing of music is by training animals with songs that belong to distinct genres and styles. For instance, both pigeons and carps are able to discriminate songs based on features related to the style of the composer or the instruments of the musical genre (Porter and Neuringer, 1984; Chase, 2001). These studies with real songs can tell us what features non-human animals can detect and may prefer in the complex auditory signal of music.

1.3.2. *Animal rhythmic perception: isochrony, beat and grouping*

Several musicality traits relate to rhythm, such as percussive drumming, beat perception, motor synchronization or metrical encoding of rhythmic patterns. Lot of research has focused on the ability to perceive and synchronize to the isochronous beat, which is apparently missing in non-human primates, but present in species distantly related to humans. This research was boosted by the finding of synchronized behavior to music in a Sulphur-crested cockatoo, Snowball (Patel et al., 2009), and in a Californian sea lion, Ronan (Cook et al., 2013). The perception and production of rhythms has also been studied in our closest relatives, apes and monkeys, and although they may sense isochrony (Honing et al., 2018), no clear beat perception was found (Honing et al., 2012). The general picture suggests that interval-based or beat-based timing mechanisms are distinctly shared across species, and that vocal learning and other brain networks may facilitate the processing of rhythmic musicality traits. In this section we will briefly review what we know about animals and isochrony, beat entrainment and rhythmic grouping.

Which species detect isochrony?

One structural aspect of music and dance is the presence of temporal regularities. The strictest regularity in a temporal pattern is isochrony, which stands for constant inter-event intervals (for a review on its evolution, see Ravignani and Madison, 2017). The beat is a perceptually isochronous construct, regardless of the irregularities present in the physical signal, so the detection of isochrony may be linked to the bases of beat perception. The discrimination of temporal regularities in rhythmic patterns has been studied in several bird species (Spierings and ten Cate, 2016). For instance, while pigeons failed to discriminate isochrony in rhythmic sequences (Hagmann and Cook, 2010), budgerigars and zebra finches succeeded, but focusing on the absolute durations of the sound sequences (Spierings and ten Cate, 2016; ten Cate et al., 2016; Van der Aa, Honing and ten Cate, 2015). Interestingly, jackdaws and starlings succeeded in the discrimination across different tempi based on the relative temporal features of the stimuli (Reinert, 1965; Hulse et al., 1984). It seems then, that some birds are able to detect isochrony. We extended a similar paradigm to a rodent model, and found that rats are also able to discriminate isochrony in new tempi regardless of the absolute durations of the tones (Celma-Miralles and Toro, 2018, 2019).

Some studies explored the issue of isochrony processing by recording neural activity in animals. For instance, two rhesus monkeys were tested with an oddball paradigm used in humans (Bouwer et al., 2016), and revealed mismatch negativities to deviant sounds in isochronous and jittered conditions (Honing et al., 2018). Contrary to what was found in humans, their mismatch negativities did not differ between onbeat and offbeat positions, which suggests that no beat was modulating their perception (Honing et al., 2012, 2018). There are three studies in rodents that indirectly tackled the detection of isochrony. A study with mice found that the presentation of irregular sequences of sounds, compared to regular sequences, elicited more activity in the amygdala and more anxiety-like behavior (Herry et al., 2007). In a pharmacological study with Wister rats, the omission of sounds elicited a late-latency positivity in the evoked potentials when the sounds were presented regularly but not when they were presented irregularly (Jongsma, Coenen and Rijn, 2002). Finally, a study with anaesthetized gerbils revealed that onbeat and offbeat positions of complex rhythms elicited distinct neuronal firing rates (Rajendran et al., 2017). All these studies suggest that there is neural sensitivity to isochrony.

Beyond perception, it is interesting to notice that some species can produce vocalizations that show a tendency towards isochrony or fixed inter-onset intervals. For instance, the complex song displays of zebra finches consist of temporally-organized syllables, whose underlying rhythmic structure looks very metronomic (Norton and Scharff, 2016). Collared doves produce sequences of rhythmic coos that, if they are manipulated in duration or temporal position, they can reduce the animal responses (Slabbekoorn and ten Cate, 2001). A tendency towards isochrony appears in the temporal structure underlying the staccato hooting of bonobos (Bermejo and Omedes, 1999), and perhaps could extend to the synchronized syllables of the geladas (Gustison and Bergman, 2017) and the rhythmic displays of the duetting of gibbons (Fan et al., 2016). Finally, synchronized behaviors that seem to tend towards isochrony or antisynchrony are found in crabs, crickets or fireflies, in distinct modalities (Kotz, Ravignani and Fitch, 2018; Wilson and Cook, 2016; Ravignani and Norton, 2017). This opens the door to study not only the perception of temporal regularities, but also the production of regular patterns in synchronized behaviors.

Which species perceive a beat and synchronize to it?

Beat perception and synchronization is a behavior rarely observed across species (Fitch, 2009), but very frequent in humans when we easily tap the foot or boob the head to the rhythms of music. Essential to this behavior is that the synchronized movements are predictive and can flexibly adapt to the frequency of the beat at distinct tempo ranges (Patel and Iversen, 2014). These two characteristics are clearly present in some parrots and a sea lion species, but they are not obvious in other species with audiomotor entrainment such as elephants, cetaceans, or even dogs and horses (Schachner et al., 2009; Fitzroy, Lobdell and Norman, 2018; Wilson and Cook, 2016; Bregman et al., 2013). While few mammals and birds show beat perception and synchronization in their normal behavior, several vertebrates and invertebrates possess a quite similar ability, sensorimotor entrainment, which consists of synchronizing vocalizations and movements to the displays of other conspecifics (Ravignani et al., 2014). The fact that this ability is widespread in the animal kingdom, from frogs and crabs to crickets and fireflies, suggests that the bases of sensorimotor entrainment could have evolved multiple times across species (Kotz, Ravignani and Fitch, 2018).

The research on animal beat perception and synchronization increased after the discovering of Snowball, a Sulphur-crested cockatoo that frequency-locked and phase-locked to the beat of a song (Patel et al., 2009). In addition, another bird species, budgerigars, was found capable of pecking a key in synchrony with a metronome and a flashing light, and can even adjust to tempo modulations after training (Hasegawa et al., 2011; Seki and Tomyta, 2018). An interesting finding in mammals was the ability of Ronan, a Californian sea lion, to entrain to the beat of a song at distinct tempi (Cook et al., 2013; Rouse et al., 2016). These findings were very controversial because Ronan, in contrast with Snowball, is not a vocal learner, so they brought doubts about the idea that only vocal learners are able to entrain to a beat (see discussion below). Beyond beat entrainment, Snowball possesses a set of "dancing" movements that can be adjusted to the metrics of the music. Interestingly, the cockatoo learned, without rewarded training, new movements that comprise not only head-body bouncing, but also combinations of movements in distinct directions These dancing steps can be classified as moving downward or side-to-side, and performing down-shake, foot-lift (sometimes with down swing), head-foot synchronization, headbang (sometimes with lifted foot), pose, semicircle low or high, body roll, counter-clockwise circle and vogue (Keehn, Iversen, Schulz and Patel, 2019). What is more, Snowball seems to flexibly improvise the dancing movements to distinct parts of the song, which reveal that they are creatively selected, as the movements of human dance.

The research on beat perception and synchronization in our closest primate relatives is scarce. Three chimpanzees were trained to tap to an auditory metronome, and only one, Ai, managed to tap in synchrony with the sound stimulus at one tempo (Hattori et al., 2013). This tempo was close to her spontaneous motor tapping preference. The fact that Ai could not synchronize with other tempi suggest that sensorimotor temporal flexibility was lacking. The phase-values of the tapping to this tempo were wider than those found in humans, which may indicate that her performance was not completely predictive (Patel and Iversen, 2014). It could be that certain species perceive the beat but are not able to synchronize with it. In a study with monkeys, Selezneva et al. (2013) found that the animals were sensitive to changes in the repeating patterns, but the authors could not disentangle whether these detections were related to the beat or more general auditory groupings. Regarding non-human primates, Honing et al. (2012) found that rhesus monkeys did not perceive a beat in sequences of rhythms, though they were sensitive to the isochrony of the stimuli (Honing et al., 2018). Interestingly, monkeys seem to have a preference for visual stimuli and could be able to predictively entrain to a visual metronome (Gámez et al., 2018; Takeya et al., 2017).

Are rhythmic groupings shared across species?

Some research has explored how rhythmic patterns are perceived and grouped across species. For instance, animals such as budgerigars, zebra finches, pigeons and rats use acoustic cues (intensity, pitch, duration…) to segment the stimulus in chunks (Spierings, Hubert and ten Cate, 2017; ten Cate et al., 2016; Hagmann and Cook, 2010; Toro and Nespor, 2015). An example of these behavioral studies consists of the perceptual grouping following the Iambic-trochaic Law found in rats, which revealed that high-low pitch alterations were perceived as trochaic rhythms, with the prominence at the second event (de la Mora et al., 2013). Regarding closer relatives, electrophysiologic studies found that macaque monkeys are sensitive to auditory grouping (Honing et al., 2012; Selezneva et al., 2013) and isochrony (Honing et al., 2018), but not to beat perception or its hierarchical meter (Merchant and Honing, 2014; Merchant et al., 2015). This may mean that they process sequences of isochronous sounds in a different way compared to humans (Kotz, Ravignani and Fitch, 2018) and that they detect regularities in rhythmic patterns (Honing et al., 2012).

Some hypotheses on the evolution of rhythmic abilities

Regarding the evolution of rhythmic cognition in animals, several hypotheses have been proposed. Besides the "auditory cheesecake" hypothesis (Pinker, 1997), which proposes that musicality traits are exaptations of independently evolved abilities, three main hypotheses aimed to explain the evolution of our rhythmic cognition based on the observations of rhythmic perception, beat entrainment and rhythmic behavior across species.

The first hypothesis deals with a gradual emergence of interval-timing and beat-timing mechanisms in primates and is known as the "gradual audiomotor evolution hypothesis" (Merchant and Honing, 2014; Honing et al., 2012). It entails that similar interval-based mechanisms are shared among primates, but that beat-based timing mechanisms gradually evolved and were completely developed in human lineage. This hypothesis is based on the stronger connections between primary auditory areas, the inferior parietal lobe and the medial premotor cortex found in humans but not in other primates. This hypothesis proposes the motor cortico-basal ganglia-thalamo-cortical circuit as the neural bases for sequential and temporal processing (Merchant, Harrington and Meck, 2013).

The second hypothesis directly tackles the synchronization to the beat and is known as "the vocal learning hypothesis" (Patel, 2006; Patel et al., 2009; Schachner et al., 2009). It establishes a link between beat perception and synchronization and vocal learning species (see Figure 5), which can learn to produce complex communication signals based on imitation (Patel, 2009). As listed in Ravignani et al. (2016), the non-human species capable of vocal production learning are bats, elephants, dolphins, seals, whales and many bird species. These species possess tight connections between motor and auditory brain regions that integrate auditory information with the production of complex vocal gestures creating and auditorimotor loop (Jarvis, 2006, 2007; Petkov and Jarvis, 2012). Comparative neuroanatomical research suggests that homolog brain circuits appear in vocal learner birds and mammals, which involve the thalamus, the striatum and the forebrain (Jarvis, 2007). Therefore, this second hypothesis relies on cross-species correspondences of auditory-motor links and other overlapping regions, such as basal ganglia (Petkov and Jarvis, 2012). However, beat perception and synchronization may also require non-vocal movement imitation and complex social group interactions (Patel, 2009).

The third hypothesis is based on social convergence (Fitch, 2009, 2012) and poses that rhythmic behavior could have emerged from a social coordination/cooperation instinct boosted by group synchronization. It seems that engaging in entrained social actions plays an important role in group-oriented behaviors (Fitch, 2009), from children social gameplays to parrots' vocal "badges" of group membership (Farabaugh, Linzenbold and Dooling, 1994). This rhythmic engagement is also found in the social imitation behavior of monkeys (Merchant and Honing, 2014). In primates, for instance, rhythmic social behaviors are found in the percussive drumming of gorillas and chimpanzees (Fitch, 2009).

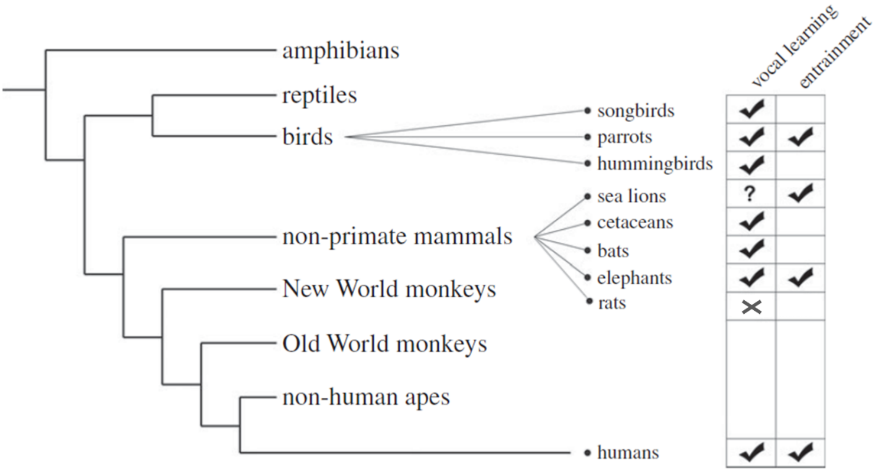

Figure 5 A schematic phylogenetic tree for the vocal learning ability. The table links vocal learning to beat entrainment abilities in distantly-related species (adapted from Hoeschele, Merchant, Kikuchi, Hattori, and ten Cate, 2015).

Departing from these three interesting hypotheses, one could link the gradual audiomotor evolution of beat-based timing mechanisms to the strengthening of auditory-motor connections necessary for the vocal learning ability found in humans. In this line, Patel and Iversen (2014) proposed a newer view on the evolution of beat perception, called the "action simulation for auditory prediction hypothesis". They propose that the ability to extract and predict a beat depends on the bidirectional communication between the auditory and motor planning regions of the cortex, which can simulate the neural activity of actions over time. According to them, humans' vocal learning ability may have strengthened the dorsal auditory pathway crossing the parietal cortex that connects these auditory and motor regions. In a similar way, Petkov and Jarvis (2012) also proposes that complex vocal learning evolved gradually, which fits the idea of a gradual development of auditory-motor skills in primates (Merchant and Honing, 2014).

Some aspects of these hypotheses have been challenged or discussed in detail the last years (see Wilson and Cook, 2016; Kotz, Ravignani and Fitch, 2018). For instance, the vocal learning hypothesis cannot explain why other vocal learner species do not overtly synchronize to the beat (e.g. dolphins, bats, songbirds); or why Ronan, the Californian sea lion, shows this ability adaptable to multiple tempi. Interestingly, Ronan is an otariid and the unique member of the pinniped family without the vocal learning ability and, as Wilson and Cook highlight, it could be that this species inherited the vocal learning neural substrates from a common ancestor with phocids and walruses. This motivated recent promising research on the rhythmic communication and percussive behavior of seals (Ravignani et al., 2016; Ravignani, 2019). In favor of a gradual development of beat-based mechanisms in humans, it is found that the sporadic sensorimotor synchronization of infant humans to the beat resembles the limited periods of synchronization found in other species (Patel, 2009). Regarding rhythmic behaviors in primates, it seems that the motor cortico-basal ganglia-thalamo-cortical circuit found in humans is less engaged in macaque monkeys, maybe because the direct connections between premotor areas, Broca's area and basal ganglia are reduced (Merchant and Honing, 2014). Together, the reported findings indicate that the neural structures necessary for rhythmic processing are found across species in different degrees, and that it is the presence and interaction of these multiple mechanisms that gives our brain the necessary circuitry to process temporal events and predict the beat in an accurate manner during social interactions.

1.3.3. *Discrimination of complex auditory signals*

In the previous section, we reviewed the main literature about the origins of isochrony and beat perception across species. We stated the main theories that are debated nowadays. One pointed to a link between vocal learning and beat perception and synchronization motivated by socio-affective rewarding properties, while another pointed to a more spread evolution of sensorimotor connections that allow prediction and coordination of rhythmic behaviors among individuals. In this section we will tackle a more abstract level of music. We will briefly go through relevant studies reporting the ability of distinct species to discriminate complex acoustic stimuli. First, we will review some non-human animal studies showing that certain species are able to distinguish between species-specific songs and vocalizations or between musical excerpts depending on their genre/style. Then, we will discuss how rodents deal with acoustic features of laboratory-designed tunes, mainly focusing on the rhythmic properties of the stimuli.

Discrimination of conspecific vocalizations and songs

A line of research has explored the discriminatory abilities of non-human animals using naturalistic vocalizations. Most of the studies focused on birds, to test whether they can discriminate conspecific calls or songs (see Watanabe and Nemoto, 1998). Successful discrimination was found in pigeons (Beer, 1971), great tits (Weary, 1990), budgerigars (Okanoya and Dooling, 1991), song sparrows (Stoddard et al., 1992) and Zebra finches (Cynx, 1993), among others. In mammals, spear-nosed bats were able to distinguish calls from conspecifics belonging to different caves (Boughman and Wilkinson, 1998). Some studies have not only tested animal discrimination, but also their preferences. For instance, preferences for conspecific songs were found in chaffinches (Stevenson, 1969), White crowned sparrows (Dobson and Petrinovich, 1973) and young Zebra finches (Ten Cate, 1991), which suggests that species-specific vocalizations may have a reinforcing property for these songbirds. In short, these studies highlight the sensitivity of distinct species to the complex vocalizations they produce.

Another line of research went beyond naturalistic vocalizations and tested whether non-human animals can discriminate between real musical excerpts. For instance, pigeons, rats and goldfish discriminated Bach from Stravinsky (Porter and Neuringer, 1984; Otsuka, Yanagi, and Watanabe, 2009; Shinozuka, Ono, and Watanabe, 2013; respectively), Java sparrows discriminated Bach from Schoenberg (Watanabe and Nemoto, 1998), and rats discriminated Mozart from the Beatles (Okaichi and Okaichi, 2001). Other animals, such as elephants (Reinhert, 1967), starlings (Hulse, Bernard, and Braaten, 1995), rhesus monkeys (Wright et al., 2000) and carps (Chase, 2001), were also found to discriminate real music stimuli. The findings of these studies point out that discriminating complex auditory stimuli may be a quite spread ability in the animal kingdom.

Discrimination of tunes and rhythmic features in rodents

A more concise line of research directly investigated which relevant properties of music animals use to discriminate among laboratory-designed tunes. D'Amato and Salmon (1982, 1084) studied the ability of rats (Rattus norvegicus) and monkeys (Cebus apella) to discriminate two tunes after applying changes in specific perceptual cues, such as intensity, timbre, octave transposition, pitch intervals and tempo. They found that both species were able to discriminate these tunes based on these structural properties of the stimuli, but that rats were unexpectedly faster than monkeys. They hypothesize that this finding could be due to the dominance of the auditory modality in rats. In another study, Poli and Previde (1991) found that rats only used timbre as the cue to discriminate between four versions of the "Frere Jacques" song that combined modulations of timbre and reversed pitch order.

Rats seem to be sensitive to rhythmic properties of the sounds, such as the expansion or compression of rhythms over time (d'Amato and Salmon, 1984) and the grouping of pairs of tones following the principles of the Iambi-Trochaic Law (de la Mora, Nespor and Toro, 2013; Toro and Nespor, 2015). Regarding its neural bases, Rybalko et al., (2010) found that the left auditory cortex of rats was involved in detecting the duration and repetition rate of gaps in a continuous sound stream. Beyond rats, sensitivity to rhythmic stimuli was also found in other rodents such as mice (Herry et al., 2007) and gerbils (Rajendran et al., 2017). These last studies suggest that rodents are sensitive to the temporal structure of auditory stimuli and that rats therefore are an interesting model to study rhythmic processing across species (Kotz, Ravignani, and Fitch, 2018).

1.4. Experimental settings and general scope

1.4.1. *Settings for non-human animal studies*

The animal laboratory is located in the Barcelona Biomedical Research Park. The female Long-Evans rats (*Rattus norvegicus*) were raised, trained and tested in an independent room of the Pathogen-free zone. The rodents were kept in boxes (two rats for box) and the room followed a 12-hour cycle of light and darkness. Rats always had access to water and food, as well as they received weekly veterinarian examinations and daily check controls. Our procedures followed the Catalan, Spanish and European guidelines on animal manipulation and received the ethical committee approval from the Universitat Pompeu Fabra and the Generalitat de Catalunya (protocol number 9068).

The laboratory setting

The training and the testing sessions occurred at the same room where the animals lived, within 8 independent soundproof boxes containing a speaker and a modular response box (reference LE1005; Panlab S. L., Barcelona, Spain), equipped with a pellet feeder. Attached to the feeder was a photoelectric sensor, that recorded the responses of the rats. Our group developed a software (RatboxCBC 1.0 and 2.0) that was implemented in two independent laptops. This custom-made program delivered the sounds to the speakers and recorded the nose-poking responses of the rats after the presentation of each stimulus. Every time that the rat introduced its nose into the feeder-hole (where the sensor was placed), a response was registered in the program output-file and a pellet was delivered to the rat when the stimulus was reinforced with reward. We presented the auditory stimuli using Electro Voice (s-40) speakers located next to the boxes, at an approximate intensity of 68 dB. Since each modular box was isolated within a bigger soundproof box, rats could not hear any external noise or stimuli giving them any cue for the responses.

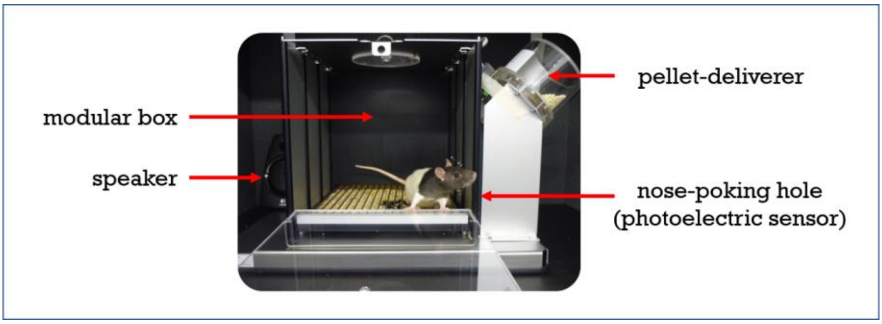

Figure 6 The animal setting. The position of the speaker and the modular box with the pellet-deliverer and the photoelectric sensor are depicted in the photo.

The experimental paradigms

Two distinct paradigms were implemented in our studies to obtain the responses of the animals:

a) go/no-go

The animals are trained with two kinds of stimuli (A and B) with a contrasting feature. One kind of stimulus (A+) is reinforced with food reward while the other kind of stimulus (B) is not reinforced. After several training sessions, animals are tested with new stimuli that belong to the two kinds of the training but that are not reinforced (A' and B'). The responses to these new stimuli are registered and compared. If the animals can detect the features that were reinforced during the training, the responses to the new stimuli should be different (A'≠B'). This discriminatory behavior may reflect the ability to identify a learned feature and generalize this identification into new stimuli.

b) familiarization

The animals are presented with several instances of one kind of stimulus (A). This stimulus is always reinforced (A+). After several familiarization sessions, the animals are presented again with the familiar stimulus (A) together with new stimuli (A' and B) that maintain or not a main feature of the familiar stimulus. During the test, neither the familiar nor the unfamiliar stimuli are reinforced. The responses between the familiar and the unfamiliar stimuli are compared. If the responses to familiar and unfamiliar stimuli are the same (A=A'=B), animals' behavior may reflect no discrimination of the stimuli. If the responses to the familiar and unfamiliar stimuli are different (A≠A'≠B or A≠A'=B), animals' behavior may reflect acoustic discrimination. However, if the responses to familiar and unfamiliar stimuli vary according to the presence or absence of the target feature (e.g. A=A'≠B), the discriminatory behavior may reflect the ability to identify a particular feature and generalize this identification into new stimuli.

1.4.2. *Settings for human studies*

The laboratory of the Center for Brain and Cognition is located at the Universitat Pompeu Fabra. Participants were contacted using the database of the Center for Brain and Cognition or through online advertisement in social media platforms, always following the data-protection regulations stipulated by the Universitat Pompeu Fabra. Participants always signed an informed consent form. The data obtained from them was stored and pseudo-anonymized, by giving to each participant a unique alphanumeric code. All the experimental procedures were carried out in accordance with Spanish and European guidelines and received the ethical committee approval from the European Research Council and the Universitat Pompeu Fabra (reference number: 2012/4852/I).

The EEG setting

The electrophysiological studies with humans were carried out in the isolated EEG rooms of the CBC lab. The EEG signal was recorded with the BrainAmp amplifier and the BrainVision Analyzer Software package (v.2.0; Brain Products), using 32 or 64 actiCAP-electrodes placed on the scalp of the participant following the International 10/10 system (Fp1, Fp2, AF7, AF3, AF4, AF8, F7, F3, F1, Fz, F2, F4, F8, FT9, FT7, FT8, FT10, FC5, FC3, FC1, FC2, FC4, FC6, C5, C3, C1, Cz, C2, C4, C6, T7, T8, TP9, TP7, TP8, TP10, CP5, CP3, CP1, CPz, CP2, CP4, CP6, P7, P5, P3, P1, Pz, P2, P4, P6, P8, PO9, PO3, POz, PO4, PO10, O1, Oz, O2). Two electrodes recorded the eye movements on the right eye outer canthus and its infra-orbital ridge. Two electrodes were also placed on the left and right mastoid. All the signals were referenced to the FCz online channel and their impedances were kept below 20 kΩ. The recorded sampling rate was 1000 Hz.

Participants sat in a comfortable armchair in the room while the electrodes were settled on their scalp and received the instructions of the experiment. The visual stimuli were presented on a screen located in front of the participant. The auditory stimuli were delivered either through headphones (Sennheiser HD 435) or through the speakers next to the screen. The stimuli were accurately sent using the Psychophysics Toolbox extensions (Brainard, 1997) of the software Matlab (v.2013, The MathWorks). When some behavioral answer was required, a keyboard was placed on the participant's lap. The experimenter controlled from outside the EEG recordings, the delivery of stimuli and the triggers, any issue with the EEG channels and the behavior of the participant through a webcam.

The behavioral setting

The behavioral studies with humans were carried out in the soundproof cabins of the CBC lab. Participants sat in front of a computer screen and gave responses pressing the keyboard. The auditory stimuli were presented through headphones Sennheiser PC 151 at a comfortable hearing level. The visual and auditory stimuli were presented with the Psychophysics Toolbox extensions (Brainard, 1997) in Matlab (v.2013, The MathWorks). The same software recorded the behavioral responses of the participants that pressed the keyboard. A microphone in the room allowed the experimenter to control that the participants were tapping during the study.

The experimental paradigms

For the EEG studies, the experiments were all structured following this design. The participants always started with a control condition. In the control condition, isochronous stimuli were presented to the participants to elicit neural entrainment to the frequency of the beat. The following conditions involved the metrical grouping of the beat, with the interaction of bottom-up sensory processes and top-down modulations of them. In these metrical conditions, the imagery of the meter, the involvement of attention and the properties of the stimuli across modalities were modulated to explore whether they can elicit neural entrainment to meter. The induction of meter was assumed when amplitude peaks appeared at the frequency of the meter (and its harmonics) in the metrical conditions, but they were absent in the control conditions. See Figure 7 for a graphical description of the method.

For the behavioral study, a go/no-go paradigm, as described in 1.4.1.1.a, was carried out in the lab. In contrast with the animal paradigm, participants followed less training sessions and the reward for each pressing response to reinforced stimuli consisted of "money". As the animals, participants did not receive any instructions.

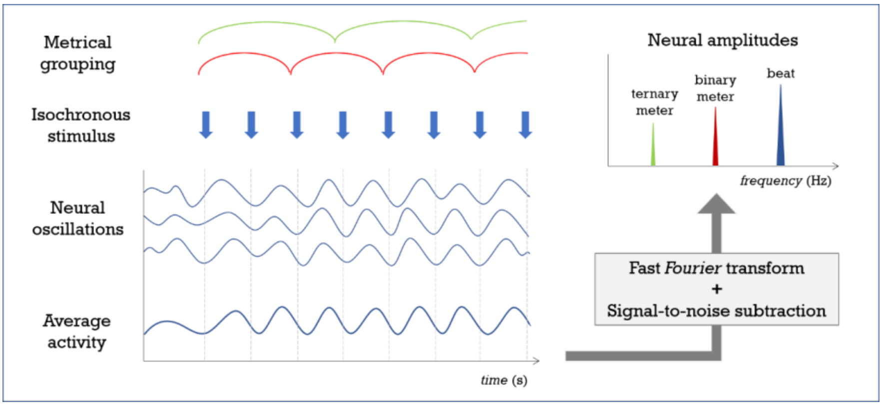

Figure 7 The Frequency-tagging approach. Several EEG responses to rhythmic stimuli (e.g. sequences of periodic sounds or flashes) are recorded and averaged in the time-domain to enhance event-related activities. The averaged activity is transformed into the frequency-domain, with the Fast Fourier transform, and a signal-to-noise subtraction enhances the peaks that are consistent and therefore related to the processing of the rhythmic stimuli.

1.4.3. *Scope and goals*

During the last decades, a great amount of research focused on the origins of our rhythmic cognition. The emergence of neuroscientific methodologies triggered most of the advances in understanding the neural substrates of our timing mechanisms, which underlie the processing of rhythmic signals, its beat and its metrical organization. A great research effort was put on understanding the bases of beat perception (and synchronization), normally comparing temporal processes between audition and other modalities. Similarly, rhythmic behaviors and temporal discriminatory abilities were compared between humans and non-human animals, to establish commonalities and differences among species that could explain the evolutionary origins of rhythm. In the present dissertation we will tackle both lines of research, to gain insight in the neural bases and evolutionary bases of rhythm. For this, two different methods have been put in practice. The first one is the comparative method, in which rhythmic discriminatory abilities were tested in a species distantly-related to humans. The second one is the neuroscientific method, in which electrophysiological techniques were used in humans to explore neural entrainment to beat and meter across modality features.

The experimental sections of the dissertation include four studies. The first study looks for the neural underpinnings of musicians projecting an imaginary meter in the visual modality. The second study tackles the auditory space as a musical feature to elicit neural entrainment to meter in musicians and non-musicians, with the presence or absence of attentional resources. The third study compares the discriminatory abilities of rats and humans when they have to detect isochrony in regular and irregular auditory sequences. And the fourth study explores whether rats can identify the rhythmic organization of a musical tune, or they rather focus on its melodic organization.

2. EXPERIMENTAL SECTION I

2.1. Neural processing of meter across modalities: frequency-tagging studies

This section includes two electroencephalographic studies on meter induction. This methodology allows us to record electro-voltaic changes on the scalp of the participants that reflect the neural activity of the brain. Both studies use the frequency-tagging approach (Nozaradan, 2014) to explore the neural activity synchronized to certain frequencies of interest, such as those of the beat (*f*), its metrical subharmonics (e.g. *f*/2 or *f*/3) or their harmonics (e.g. 2*f*, 2*f*/3, 4*f*/3 or 5*f*/3). The beat is a cognitive construct that organizes periodicities over time based on the regularities of the stimuli. In neural terms, the beat is assumed to be reflected by steady-state evoked-potentials that arise from these regularities and that reinforce a specific constant interval of time. The meter consists of the voluntarily or involuntarily perception of these events as groups of two (binary meter) or three (ternary meter), and is normally reflected in the brain by slower steady-state evoked potentials. The induction of metrical patterns can be externally-driven (exogenous/bottom-up), internally-projected (endogenous/top-down), or a mix of both mechanisms. The neural synchronization to beat and meter may be affected by a long experience with rhythmic processing, such as the extensive formal training in music.

In the first study we tackle beat perception and meter induction in two different modalities: audition and vision. This study is based on Nozaradan et al. (2011) and aims to prove the cross-modality of meter induction. We presented participants (musicians) with either isochronous pure tones or isochronous blinking circles and asked them to project binary or ternary meter on them, that is, to mentally group the regularly presented stimulus in patterns of two or three. In this first study we deal with top-down attentional mechanisms. All the stimuli presented in each trial were perceptually identical and no bottom-up cues can trigger any metrical grouping. To facilitate the implementation of the task we selected musicians, who are familiar to synchronize with each other even beyond the auditory modality (e.g. orchestra conducting).

In the second study we explore beat perception and meter induction in the spatial domain. Although space is very important in vision, here we focus on the spatial dimension of sound. This study aims to prove that listeners can extract metrical patterns over time from sounds that spatially alternate on the azimuth plane. We presented participants (musicians and non-musicians) with sounds that alternated from one side to the other following ternary meter. The sounds were approximately alternating at three distinct angles: ±30º, ±60º and ±90º. This study includes a control in which participants (musicians and non-musicians) were watching a muted movie. In this second study we disentangle the bottom-up and top-down mechanisms dealing with meter induction by spatially-located sounds. We also compare the effects of formal training in music, which may facilitate the synchronization to a beat and its metrical structure.

2.1.1. *Manuscript 1*

Celma-Miralles A, de Menezes RF, Toro JM. Look at the Beat, Feel the Meter: Top-Down Effects of Meter Induction on Auditory and Visual Modalities. Front Hum Neurosci. 2016 Mar 23;10:108. DOI: 10.3389/fnhum.2016.00108

2.1.2. ***Manuscript 2***

Celma-Miralles A, Toro JM. Ternary meter from spatial sounds: Differences in neural entrainment between musicians and non-musicians. Brain Cogn. 2019 Nov;136:103594. DOI: 10.1016/j.bandc.2019.103594

3.1.1. ***Manuscript 3***

Celma-Miralles A, Toro JM. Discrimination of temporal regularity in rats (Rattus norvegicus) and humans (Homo sapiens). J Comp Psychol. 2020 Feb;134(1):3-10. DOI: 10.1037/com0000202.

3.1.2. *Manuscript 4*

Non-human animals detect the rhythmic structure of a familiar tune[1]

Celma-Miralles A, Toro JM. Non-human animals detect the rhythmic structure of a familiar tune. Psychon Bull Rev. 2020 Aug;27(4):694-699. DOI: 10.3758/s13423-020-01739-2

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[1] This manuscript has been submitted in the Royal Society Open Science (2019).

4. GENERAL DISCUSSION

The goal of the present dissertation was to study the neural and evolutionary bases of our rhythmic cognition. On the one hand, we sought to identify the synchronization of neural populations to metrical structures in the visual and the spatial domains. This was to explore whether meter induction is a cross-modal mechanism that can go beyond canonical features of the auditory modality and may allow us to easily synchronize with each other in multimodal activities, such as dance or orchestra playing and conducting. On the other hand, we explored the presence of core rhythmic features of music in another species. This was to determine whether rats can discriminate the isochrony of the beat and the rhythmic organization of a tune, similarly to what humans do.

The first section of the dissertation aimed to discover meter induction beyond the typical features of the auditory modality. With the first EEG study we found that ternary meter can be voluntarily projected onto blinking flashes. With the second EEG study we demonstrated that ternary meter can be induced by the alternation of spatially-located sounds. In addition, the controls of this second study revealed that neural entrainment can be facilitated by attention to the stimuli and formal training in music.

The second part of the dissertation aimed to find common discriminatory abilities between humans and non-human animals regarding the temporal processing of music. Our two studies focused on the mechanisms that underlie rhythmic discrimination. With the first behavioral study we showed that rats and humans are able to generalize the detection of isochrony into two new tempi. With the second behavioral study we showed that most rats tend to focus on the rhythmic organization of a tune, rather than its melodic organization. We will summarize below the findings of these four studies and discuss the implications of these results with respect to the relevant literature. We will finish by listing the limitations and the future directions of our two lines of research.

4.1. Summary of results

4.1.1. Study 1. The projection of binary and ternary meter in vision and audition

The metrical organization of the isochronous beat has been studied in humans using multiple paradigms and methodological tools. In this work, our interest resides in the understanding of its neural bases. Our first study was devoted to extend to the visual modality a seminal study demonstrating voluntary neural entrainment to acoustic metrical structures (Nozaradan et al., 2011). In order to compare the meter across modalities, we created analogous auditory and visual stimuli that were presented to the participants at the same inter-onset interval, 2.4 Hz, in separated conditions. The auditory stimulus consisted of a pure tone gradually fading out to silence, while the visual stimulus consisted of a colored circle gradually fading out to the background color. This experiment recorded the electroencephalograms of musicians perceiving isochronous stimuli. The experiment started with the control condition, in which participants had to perceive an isochronous tone and a regular blinking circle presented at 2.4 Hz. Subsequently, they had to project either a binary (1.2 Hz) or ternary (0.8 Hz) metrical structure onto the same auditory and visual stimuli. The stimuli were presented separately across conditions and counterbalanced across participants.

Our EEG recordings reflected how participants mentally grouped the same isochronous sound either as a march (binary meter) or a waltz (ternary meter). Following the frequency-tagging approach, we found neural entrainment to beat and meter reflected by amplitude peaks at their frequencies in the frequency spectra. In the auditory modality, we found enhanced peaks for the imagined binary and ternary meter. In the visual modality we only found a peak for the imagined ternary meter, but not for the binary meter. This difference could reflect that distinct brain structures have been engaged in the processing of binary and ternary meter, as suggested by Fujioka et al. (2010), or that distinct degrees of neural activity underlies the processing of rhythms in each modality. Interestingly, we found that the peaks for the beat were higher in the auditory modality than in the visual modality, which could indicate a more accurate entrainment to sounds than to blinking circles in the brains of musicians. These findings were one of the first reporting top-down meter induction in the visual modality, which may be essential in processing the visual signs of an orchestra conductor, other players or a dancer. Importantly, we tested musicians, who may have been integrating visual rhythmic cues in their training and group rehearsals. It remains an open question whether the same findings will appear for non-musicians and even other rhythmically-trained populations (as in dance or synchronized sport activities).

4.1.2. Study 2. Musical training and attention on meter induction in the spatial domain

Vision is deeply connected to the spatial domain. In audition perceiving the space is fundamental to navigate in the environment and localize the sounds surrounding us. Space also has an important effect on music perception, either because of the acoustics of the place where music is played or due to the position where music sources are located in relation to the listener. In our second study we explored this last effect and focused on the rhythmic structure of music. We wanted to see whether spatially alternating sounds could elicit ternary meter. In a first, control condition, an isochronous beat was presented frontally at 2.4 Hz. We also had 3 experimental conditions; we started alternating the sounds from one side to the other following the ternary structure of a waltz: one sound placed on one side followed by two sounds placed on the other side. The sounds were located at ±30º, ±60º and ±90º on the azimuth plane. We carried out two experiments to take into account the role of attention and formal training in music.

In the first experiment we compared the EEG recordings of musicians and non-musicians listening to the spatially alternating sounds. As in the previous study, if the brain synchronizes with the spatially signaled meter, peaks should appear at 0.8 Hz and its harmonics. The results revealed that the spatial sounds elicited neural entrainment to ternary meter in both musically-naïve and musically-trained participants. There were no significant effects of the angular locations, which may mean that the processing of sounds alternating at ±30º, ±60º and ±90º was not different. Interestingly, the amplitudes of the peaks of the beat and the meter were higher for musicians compared to non-musicians. This suggests that experience modulates the processing of rhythm. The analyses of the EEG recordings separating the right and left electrodes did not reveal any lateralized bias for rhythmic processing (see Annex I). The comparison of the SSEPs related to the lateral in which the downbeat of the stimuli occurred did not reveal any lateralization effect in the brain. Therefore, the main findings of this experiment are that the spatial dimension of a sound may be an acoustic cue as relevant as timbre, pitch or amplitude, to process the temporal information of music (i.e. the meter), and that formal musical training modulates the processing of spatial rhythms enhancing the amplitude of the frequency peaks related to the neural entrainment to beat and meter.

In the second experiment we followed the same procedure as before, with the exception that we asked participants to watch a silent video while they were listening to the sounds. To be sure that they were paying attention to the movies, participants had to answer a questionnaire about the Pink Panther episodes after the experiment. The results showed that neural entrainment to meter clearly appeared when the sounds alternated at ±90º and did not differ between groups. Thus, it seems that the visual distractor prevented to locate top-down attentional resources to process the meter in the spatial conditions alternating at ±30º and ±60º. Interestingly, the frequency peaks related to meter were more consistent across conditions in musicians than in non-musicians. In contrast, the peaks related to the first and fourth harmonics of the meter were more consistent in non-musicians. This suggests that, although non-significant in our data, musical training may lead to some differences in the processing of unattended metronomic rhythms. In sum, attention to the binaural properties of the sounds may be important to reliably elicit a metrical structure on them, and only the complete alternation at ±90º overcomes the attentional deficits.

Beyond these results, the comparison of these two experiments demonstrated solid differences between musicians and non-musicians regarding the processing of beat and meter. When the increases of the amplitudes with respect to the control were compared between the two experiments, a significant effect for both attention and musicianship appeared. This effect consisted of a clear enhancement of the neural entrainment to meter in the spatial conditions. It seems therefore that attention and formal training in music modulate the way the brain processes rhythms. These differences may reflect an improved accuracy of the neural populations that synchronize with the frequencies of the beat and meter. In a nutshell, these two experiments reveal that the spatial dimension of sound can alter our perception of the structural rhythms of music, as it happens with other features (e.g. amplitude, pitch or timbre), and that formal training in music facilitates the neural entrainment to beat and meter, especially when top-down attentional mechanisms are devoted to predict the alternating sounds.

4.1.3. Study 3. A comparative approach to regularity detection in two mammals

One of the clearest characteristics of the musical rhythm across cultures is that it normally has an underlying isochronous beat that organizes the temporal events and allows individuals to synchronize with each other (Savage et al., 2015). In study 3, we explored the discrimination of isochrony in two phylogenetically distant mammals. We carried out two experiments to compare the ability of rats and humans to discriminate fixed inter-onset intervals in sequences of sounds. In order to prevent them from focusing on any other characteristic of the sound, we introduced variability in the training and the test items using five different pitches. Likewise, we presented each pitch at four tempi in the training and two new tempi in the test. To control that animals were not focusing on absolute durations, the length of every sound was designed relative to the tempo (i.e. 25% of the duration). To make the comparison between the two species as fair as possible, we ran analogous go/no-go paradigms in which the subjects had to learn by themselves the target discriminatory trait. They had to base their answers to the rhythmic sequences on the presence or absence of reward.

The first experiment investigated whether rats, a non-vocal learning species, could tell apart regular sequences of sounds from irregular ones. Importantly, to reinforce "regularity" as a feature, we created for each regular sequence a unique irregular counterpart that pseudo-randomly jittered the onset of the sounds of the sequence. During the training sessions, rats received food reward every time that they poked the feeder-hole with the nose after the presentation of a regular sequence. After several training sessions, we ran three tests with sequences at two new tempi that were never rewarded: neither the regular nor the irregular ones. The idea behind this paradigm is that, if rats learned the discrimination, they would give more responses to the regular test items than to the irregular ones, despite not receiving any reward. Indeed, the results showed that, although rats always gave nose-poking responses, they insisted significantly more for the regular test items than for the irregular ones. This may mean that rats succeeded in generalizing the discrimination of regularity. In addition, the higher number of responses to the regular sequences compared to the irregular ones did not vary across the two new tempi. In contrast to some findings in bird species (ten Cate et al., 2016), rats seem to have generalized the detection of temporal regularity regardless of the absolute duration of the sounds. Finally, the comparison of the three tests pointed out that rats gave more responses to the faster auditory sequences in the first test (regardless of whether they were temporally regular or irregular), but not in the second and third tests. This could reflect a bias towards fast auditory rhythms that could be related to the fast vocalizations these animals produce. In summary, the main finding of this experiment is that rats possess the timing mechanisms necessary to discriminate events that are equally-spaced over time, which may be relevant for beat perception.

The second experiment aimed to confirm that humans, a vocal learning species, can easily learn to discriminate isochrony in sequences of sounds presented at distinct tempi. No research has reported any issues regarding isochrony detection nor beat perception in humans, except for cases of individuals with amusia or beat deafness (Phillips-Silver et al., 2011) or patients with Parkinson's disease (Grahn and Brett, 2009). In this experiment, the participants were tested with the same stimuli described before, and the procedure tried to emulate the self-learning paradigm the rats went through. This means that the participants received no instructions regarding the task and had to learn by themselves to tap on the keyboard to receive reward and score some "money" after the rhythmic sequences. After a pair of training sections, one test was delivered to the participants. The results showed that humans pressed more times after the presentation of regular test items than irregular test items. As it was found in rats, there was no difference in the number of responses humans gave to the two new tempi. Thus, our experiment confirmed that a training procedure with no explicit instructions is enough for humans to succeed in the discrimination of isochronous from non-isochronous auditory sequences.

The general finding of Study 3 is that two distantly-related mammal species can generalize the detection of isochrony in auditory sequences that are presented at new tempi. In addition, this generalization occurs regardless of the distinct absolute duration of the sounds in the test. This finding suggests that the vocal learning ability is not a pre-requisite to process and identify isochrony. Detecting a regularly-paced event could be a helpful first step for beat perception, although this latter ability may involve more complex mechanisms (reviewed in the Introduction). Importantly, both species could have used interval-timing mechanisms, rather than beat-based mechanisms (A.S.A.P., in Patel and Iversen, 2014), to solve this discriminatory task. All in all, the present results show that detecting regularity is an ancient ability that is present in these two distantly-related mammals. This ability may appear in other species, because it entails some evolutionary advantages regarding the processing of temporal information: it may facilitate the prediction of events that occur in a regular manner in the environment.

4.1.4. Study 4. The rhythmic structure of a tune may facilitate its recognition

Apart from the isochronous beat, worldwide music has other rhythmic traits that constantly appear across cultures (Savage et al., 2015). One trait is that musical rhythms are made of few durational values that are related by small integer ratios (e.g. 1:2; 1:3 or 1:4). Another trait is that these durational values are metrically organized over time. In Study 4 we explored the processing of the rhythmic dimension of a tune by focusing on these two statistical universals. We tested rats to study if they could identify the rhythmic structure underlying a familiar tune. To familiarize the rats with a musical tune, an excerpt of the happy birthday song was presented to the rats during several weeks. Rats received food reward when they poked the feeder-hole with their nose. During the test, rats were presented with (i) the same familiar excerpt, (ii) an isotonic version of the tune that preserved the rhythmic structure but reduced the melody to a single tone, and (iii) a rhythmic-scrambled version of the tune that preserved the melodic intervals but scrambled the rhythms. No one of these three test items gave food reward to the rats.

The idea behind the familiarization paradigm is that rats would give the same number of responses to the familiar and unfamiliar items that were perceived as similar, while they would give a different number of responses to items that were perceived as different. The results showed that most of the rats discriminated the rhythmically-scrambled version from the familiar tune and its isotonic version. Importantly, they did not discriminate the isotonic version from the familiar tune. This means that the animals based their responses on how the sounds were organized over time and used rhythmic structure as a reliable identifying feature of the tune. Interestingly, a fifth of the animals focused on the melodic intervals instead, and they discriminated the isotonic version of the tune from the familiar tune and its rhythmically-scrambled version. Again, these animals did not discriminate the rhythmically-scrambled version from the familiar tune. This indicates that they based their responses on the maintenance of the melodic intervals of the tune. In sum, these two findings reveal that distinct strategies are available to this rodent model to process the relevant information of a tune. However, most rats focused on its underlying rhythmic structure. The fact that rats were able to discriminate between two unfamiliar excerpts in bases of their rhythmic organizations suggests that these animals possess the necessary cognitive structures to identify the metrical organization of few durational values over time. Thus, the ability to identify temporally structured auditory information may be ancient in the phylogenetic tree, and it could even be present in other species beyond rats.

4.2. Implications of cross-modal rhythmic abilities

Sensorimotor synchronization is not restricted to the auditory modality in the animal kingdom. Some species entrain in rhythmic displays in the visual modality (Ravigani, Bowling and Fitch, 2014), such as the Indomalayan fireflies that couple their firing displays in phase and frequency (Buck, 1938) and the male fiddler crabs that produce synchronized courtship waves to attract females while competing to lead the waving (Reaney et al., 2008). Visual sensorimotor synchronization can be also found in the pecking behavior of budgerigars (Hasegawa et al., 2011) and monkeys performing rhythmic tasks (Merchant et al., 2013; Zarco et al., 2009; Merchant and Honing, 2014; Takeya et al., 2017, 2018). Since humans engage in music, dance and other group activities that require visual synchronization, it seems plausible that our brain may integrate information from several modalities. Visual metronomic cues are found to facilitate rhythmic synchronization in primates (Zarco et al., 2009) as well as visuospatial cues help the internal maintenance of rhythms at distinct paces (García-Garibay et al., 2016). While non-human primates seem to be biased towards visual rhythms, humans seem to be more proficient in the auditory modality. However, we should be careful in assuming an auditory superiority for the processing of rhythms: we are better in tapping when the visual rhythms involve moving objects instead of static flashes (Hove and Keller, 2005; Repp, 2005; Repp and Su, 2013). Thus, our timing mechanisms may have evolved to afford an accurate temporal processing of perceptual events beyond audition, integrating visual, proprioceptive and vestibular information in the fully accomplished beat-based mechanisms found in our hominid lineage (Merchant and Honing, 2014).

In the first study reported in the dissertation (Celma-Miralles, de Menezes and Toro, 2016), we brought evidence that, beyond bottom-up beat synchronization, the brain is able to voluntarily modulate the internal oscillations and create neural entrainment to the frequency of an imagined ternary meter in both the auditory and the visual modality. This finding indicates that metrical organization, an abstract aspect of our rhythmic cognition, should not be considered restricted to the auditory domain. A similar EEG study exploring imaginary rhythms seems to support our findings (Okawa, Suefusa and Tanaka, 2017). As in our first study, Okawa and colleagues recorded the neural entrainment to imagined binary and ternary meter but using moving visual cues instead. In their study, the peaks for both the imagined binary and ternary meter were significantly different from zero. This finding is very interesting because it could mean that dynamic visual stimuli (which help in sensorimotor synchronization tasks) may facilitate the entrainment to binary structures. An open question is if this movement facilitation to process a binary grouping emerges due to a bias towards binary-organized movements, such as those of the human walking.

Beyond vision, in the second study of this dissertation (Celma-Miralles and Toro, 2019), we reported the emergence of meter in the spatial domain of sound. Space is not a modality per se but could be considered a cross-modal feature in cognition, because several senses are recruited to process spatial information. As we discussed in the study, the spatial location of the sounds (i.e. the positions of the musicians or the speakers) may affect the way in which the listeners (i.e. the general audience) perceive and group the musical objects, its rhythms and its melodies. In the study, we found that the modulation of interaural cues to locate the sounds on the azimuth space elicited neural entrainment to a ternary grouping. This metrical grouping was dependent on attentional resources, because when participants were watching a silent movie, most of the meter-related peaks decreased. Together with Study 1, the findings from both articles suggest that top-down predicting mechanisms are necessary to reliably establish the metrical ternary structure. In Study 1, these top-down mechanisms were endogenously imposed by the task demands. In Study 2, these top-down mechanisms were rather constructed from recurrent bottom-up information. Presumably, after noticing a constant alternating pattern, top-down predictions may have arisen to anticipate the location of the events at every side. However, when attention was placed onto the silent movie, the recurrence of these alternations was masked and not always obvious to the participants (mainly in those that were non-musicians). Finally, it is interesting to notice that space was used as an imagery feature by some musicians to metrically organize the blinking circles in Study 1, which establishes a bridge between both studies and the type of sensory information that each modality tends to use.

4.3. Implications of formal training in music and the processing of the rhythm

As discussed in the Introduction, functional and structural differences appear when musicians are compared to musically-naïve populations (Schlaug, 2012); and even between musicians from distinct musical fields or instrumental areas. In Study 1 we found that musicians can extend the processing of ternary meter in the visual modality. It is unknown whether this finding is also applicable to non-musicians, although this could be the case in Okawa, Suefusa and Tanaka (2017), because no distinction between musicians and non-musicians is reported, which suggests that their participants were recruited regardless of their formal training in music. If this is true, then the hierarchical meter found in music would be a more general structuring mechanism available to all humans independently of music training and applicable to distinct modalities. The idea of a general syntactic mechanism across domains would be in line with the view of meter proposed by Fitch (2013). While Study 1 does not bear on possible differences in neural entrainment between musicians and non-musicians, Study 2 directly tackled this point.

Study 2 shows some differences in neural entrainment to ternary meter when musicians and non-musicians are compared. We found that musicians had higher amplitudes than non-musicians reflecting the entrainment to meter, but essentially when both groups were paying attention to the sounds. As discussed in Study 2, musical training can enhance pre-attentive skills in audition (Tervianemi et al., 2019), and spatial cues are relevant to jazz and rock musicians (Vuust et al., 2012; Tervianemi et al., 2006). Less differences between the populations were found in our experiment when attention was directed to the silent movie, although musicians showed a peak at the frequency of the meter more consistently across conditions. Only when the sounds were monaurally delivered at each ear, the neural entrainment to meter was observed in both groups, perhaps because this monaural alternation overcame the attentional needs to build up meter. When the amplitudes were compared to the control condition in both experiments, we found that musicians always had higher increases than non-musicians regardless of attention, which reflects a better processing of the metrical schema. These differences between populations may be found in simple rhythmic schemas, but they could be absent in more complex rhythms (Stupacher, Wood and Witte, 2017). Importantly, our study looked for meter induction in the auditory spatial domain, which is an unusual way to metrically structure the sounds.

Space is not an attribute usually considered in music theory, but it is fundamental in the fields of acoustics and sonology, and of course dancing. Although music playing may not require so much attention to space at the individual level, it may be much more important at the group level, because the melodies and sounds of each instrument come from different spatial positions and must be integrated into a polyphonic multitimbral unit. Therefore, the training in music may have impacted the processing of auditory spatial sounds. This idea is in line with previous studies (Tervianemi, 2009; Vuust et al., 2012). Furthermore, since space is a structural property of dancing, it would be interesting to explore if there are differences arising from formal training in dance as well. Regarding sensorimotor synchronization, for instance, Karpati et al. (2016) found that, although similar skills are trained in dancers and musicians, dancers normally involve greater whole-body movements, with better proprioception, stability, posture and interlimb control (see Nguyen, 2017). They found that while musicians are better in sensorimotor tasks requiring finger-tapping, dancers are better in tasks requiring body movements (Karpati et al., 2016). These differences due to training could also be reflected in the neural entrainment to auditory and visual rhythms, so future studies may carefully study them.

In Study 3, we compared the discrimination of regular and irregular sequences of sounds in two species: rats and humans. Since rats were never exposed to the rhythms of music, we recruited participants who never followed formal training in music nor dance. We acknowledge that it is impossible to ascertain that they had no knowledge about rhythmic structure, because mere exposure to any culture or society (even before birth) involves music: from the rhythmic vibration of an adjacent nightclub to the pervasive tune of a commercial. Therefore, we must accept that human participants had an obvious advantage compared to the rats in the learning and discrimination of the rhythmic stimuli. To compensate this, the self-learning training pursued by human participants was reduced in time and consisted of just two rounds, with the test immediately after. Even with this initial disadvantage, rats learned the discrimination of isochrony across tempi. Since they were never exposed to rhythmic stimuli before our training sessions, their discrimination success may imply that the cognitive mechanisms underlying the detection of temporal regularities have deep biological roots and could have been selected across species to process and organize events in the environment.

4.4. Implications of rhythmic abilities across species

Comparative studies allow us to place in a phylogenetic tree those traits that emerge or disappear in closely- and distantly-related species (Hoeschele et al., 2014). We found that rats, which were never classified as vocal learners, possess the ability and the neural mechanisms to process important aspects of rhythmic perception. These musicality traits are related to some musical universals that account for the isochronous beat and the temporal organization of few durational values, and that are related to multiples or subdivisions of the beat. The fact that rats can discriminate these universal features of music perception suggests that these characteristics of the auditory sequence processing are very ancient in the evolutionary tree.

The findings of Study 3 extend the discriminatory abilities attested in birds (ten Cate et al., 2016; van der Aa, Honing and ten Cate, 2015) to a mammal species which is not a vocal learner. We say "extend" because, although some birds were able to discriminate regular temporal sequences from irregular ones, and few of them generalized this discrimination to new tempi, some bird species may have focused on absolute durations, while rats could have only focused on relative durations. However, we have to be cautious because rats could have solved the discriminatory task by comparing either the temporal intervals of the full sequence of sounds or the temporal intervals of the last three events in each sequence. Regardless of this limitation, these findings are in line with the neural activations related to the beat found in rats (Jongsma, Coenen and van Rijn, 2002) and gerbils (Rajendran et al., 2017). Beyond perceptual discrimination, some non-human animals are able to "feel" isochrony and synchronize with it (Honing et al., 2018; Merchant and Honing, 2014), while others can extract an isochronous beat from complex rhythms and entrain to it (Cook et al., 2013; Patel et al., 2009). Together, these findings suggest that the ability to detect and sometimes produce temporal regularities may be a common trait shared across species.

Our studies tackle rhythmic perception: isochrony across tempi and the organization of metrical rhythms. The findings of our two studies are in line with d'Amato and Salmon (1984), who found that rats and monkeys were able to generalize the discrimination of a learned tune to versions in which the tempo was compressed or expanded. Concretely, their transformations of the durations expanded a tune lasting 1.3 s to 2.1 s or compressed it to 0.75, 0.4 and 0.3 s. Only the compression to 0.3 s affected the animal responses. In our experiments, we found that rats succeeded in generalizing temporal regularities in other tempi and that most of them consistently identified the rhythmic structure of a tune. While d'Amato and Salmon

(1984) found that rats based their identification in local features (i.e. the presence of a particular tone in the stimuli that every rat preferred), we controlled this by training and testing rats with 5 distinct pitches in Study 3 and by presenting the rats with the rhythm of the tune in a constant pitch (C6) in Study 4. Both studies suggest that rats were focusing on more global features. In Study, 4, it is possible that the few rats that focused on the melodic organization of the tune actually based their responses only on the presence of a particular pitch (distinct to C6) at some ordinal position in the tune. However, most of the rats discriminated the rhythmic-scrambled version of the tune, which maintained the tones in the same order, from the familiar tune and its isotonic rhythm (see Annex II). This leaves the rhythmic organization of the tune as the abstract trait that rats could have used to discriminate the new stimuli. These findings reveal that, beyond local features, rats can extract and process global features, such as the regular organization of durations relative to a tempo and the organization of the metrical rhythms underlying a tune.

4.5. Future directions

The studies we report in this dissertation shed some light on the processing of musical rhythms in rats and humans. We studied the discrimination of isochrony and rhythmic grouping in animals, as well as the entrainment of neural populations to beat and meter in humans. Our experiments however raised some issues that could be addressed in future work, such as the interplay of other modalities and domains, the effects of different degrees of musical training, the limitations of attentional distractors, the role of syncopation in meter prediction, the metricality of rhythms and the importance of rhythmic production in animal behavior. Here we will comment some of them.

Meter induction in other domains

As we reviewed in the introduction, the hierarchical meter seems to be absent in non-human species but present in other human cognitive domains, such as in language phonology or dance (Fitch, 2013). In language, stress-patterns signal the syllabic prominence of words in sentences, creating the rhythms of prosody. These prosodic rhythms may be important in sign languages as well, because the visual modality underlies the processing of linguistic gestures. In dance, salient visual cues may guide precise actions in choreographies, integrating the auditory information of music and the visual information of individual and group movements. We explored musicians in Study 1 and Study 2, but one could consider extending this exploration to dancers, to see if their ability to synchronize with audiovisual cues in space is reflected on the rhythmic oscillations elicited in the brain. Similarly, one could also test the perception of visual rhythms in deaf people, who master the processing of visual linguistic signs over time. It could be that the visual modality may recycle and engage some auditory areas related to the rhythm. Beyond vision per se, we should keep in mind that music, dance and sign language involve movements, and that the vestibular system seems to interact in our processing of the beat and its slower and faster periodicities (Chemin, Mouraux and Nozaradan, 2014), even since birth (Phillips-Silver and Trainor, 2005). Therefore, future studies tackling the perception of beat and meter should include rhythmic production and explore how synchronized movements modulate the perception of rhythms across modalities.

Distinct degrees of training in music and dance

In this dissertation, we tested and compared two human populations: musicians and non-musicians. Assuming that the training in music is linear, we compared people that either never studied music or that had at least 10 years of training. However, the training in music may vary a lot depending on the style/genre of music, the practiced instrument and the educational institutions. In addition, formal training in music may extend far beyond 10 years and this would be reflected in stronger functional and structural changes in the brain. Therefore, one should consider studying the effects of training in music in a more gradual way and compare population groups at distinct points/years of training. Beyond training in music, people practicing dance or synchronized sports should also be studied to see how these activities modify the processing of rhythms in the brain. Some studies that we reviewed showed that dancers, for instance, have an improved motor synchronization of the whole body and the limbs.

Attention to the same/distinct modality

The effect of attention on meter induction was directly explored in the second experiment of Study 2. In order to prevent top-down mechanisms processing the spatially alternating sounds, we asked participants to watch a silent movie, that is, to place their attention onto the visual modality. The distractor was demanding in the sense that it required the processing of narrative content (i.e. the Pink Panther episodes). We found that the involvement of top-down mechanisms in the visual modality was detrimental to the peaks that may have appeared at the frequency of the meter and its harmonics. These few small peaks may indicate that some neural entrainment to meter, likely driven by bottom-up processes, was still present, and perhaps mixed, with some involuntarily top-down responses in the auditory modality. We do not know, however, what would have happened if attention was driven to an auditory distractor instead of a visual distractor. Perhaps, all these small remaining peaks may disappear because the attentional mechanisms would be fully in use to process the auditory features of the distractor. The effects of modal-specific distractors should therefore be taken into account in future research.

Other ways to study metrical predictions

In the present thesis, we analyzed the EEG recording in the frequency domain. Using the same stimuli, one could have also compared the beats occupying the downbeat and upbeat positions in the stimuli and look for differences in either their event-related potentials or in the increases and decreases of beta- and gamma-band activity preceding them. Another way to support the metrical processing of visual or spatial auditory beats could have consisted of using mismatch negativity paradigms, in which omissions of the beats produce distinct neural responses depending on the metrical position they occupy. The use of paradigms studying faster frequencies or mismatch negativities could bring more support to our findings of meter induction in vision and the spatial auditory domain.

A promising line of research would be to move from metronomic stimuli to more complex rhythmic patterns, as those found in real music. Syncopation, which anticipates a strong beat by placing it in a weak metrical position, is very usual in music and can help to explore metrical predictions. In a Predictive-Coding approach (Vuust et al., 2009, 2014, 2018), syncopated events elicit mismatches and prediction errors when metrical expectations do not match the sensory information. These mismatches could be used to study sounds that occur in strong, weak or unexpectedly-invalid temporal positions. Besides, one could apply this paradigm to both the slower metrical level of the beat and its faster subdivision level. Thus, one could study, for instance, whether distinct prediction errors reflect binary and ternary metrical groupings of the beat or binary and non-binary subdivisions of the beat.

Metrical versus non-metrical rhythms

Some future studies should also take into account the difference between metrical and non-metrical stimuli. This means that the studies should differentiate those rhythmic patterns whose temporal intervals are related by simple integer ratios from those whose temporal intervals are not related by integer ratios and therefore are irregularly distributed over time. If we found an advantage of processing metrical over non-metrical rhythms in, for instance, animal discrimination, we could say that this musicality trait is evolutionary ancient, and that its underlying neural mechanisms may be present in a common ancestor shared by the studied species and humans. If this integer-ratio rhythmic advantage was not found in other species, then this musicality trait would be unique to humans. In this line, we started an experiment on metrical subdivision to see if rats could discriminate duplets, triplets and quadruplets, but they apparently failed. Similarly, if this metrical advantage was reflected in the EEG of humans, we could hypothesize that this trait may depend on biological constraints underlying all music cultures. In this line, we started a project to explore if there is a bias towards binary subdivisions in humans, a trait that is present in most cultures and that improves the accuracy and precision of finger-tapping. In this ongoing project, we study the metrical subdivision of the beat in both perception and production, using EEG and finger-tapping. Future work will tell if there is a neural bias towards the processing of binary subdivisions correlated with motor actions.

From perception to production

Our studies with rodents tackled their perception of musical tones. We tested rats' discriminatory abilities, without relating them to their behavior or their fast ultrasonic vocalizations produced in contexts of pleasure and stress. In an interesting study, Slabbekoorn and ten Cate (1999) found that collared doves were sensitive to the rhythmic structure of their own vocalizations: their responses decreased when the coos were shifted over time. This means that the animals detected the abstract rhythmic structure underlying their natural species-specific vocalizations. In Study 4, we found that rats detected changes on the rhythmic organization of musical tones. A way to facilitate the test of rhythmic stimuli in rats could consist of recording and manipulating rats' own vocalizations over time, instead of musical tones, to see whether the animals are more sensitive to their species-specific sounds. Beyond that, another way to see the effect of perceptual training on production could consist of recording rats' vocalizations before and after several sessions of rhythmic auditory stimulation to see if there is any effect to the exposure of auditory rhythms.

Finally, one could also explore rhythmic behavior in the rats' responses by changing the nose-poking mechanism for a level-pressing mechanism, and timing the intervals between pressings. These analyses could reveal if any rhythmic structure is present in the behavioral responses of the animals. In addition, it could also show whether production can be modulated by the presence of a rhythmic stimulus, as it was found in budgerigars (Hasegawa et al., 2011). If metronomic or beat-based auditory stimuli could modify the pressing behavior of the rats, this would mean that their responses are not limited to perception but that they are also integrated in actions.

5. CONCLUSIONS

The main conclusions of the present dissertation are listed below.

Regarding the neural roots of rhythmic processing, we found that:

- Neural entrainment to the beat can be elicited in the visual modality by periodically presenting a blinking circle.
- Musicians can project a ternary meter on isochronous visual stimuli. Their steady-state event potentials endogenously changed to synchronize with the grouping of a blinking circle as if it followed the metrical pattern of a waltz.
- Ternary meter can be induced when participants pay attention to sounds that cyclically alternate in the auditory space.
- No lateralization effect was found for the processing of beat and meter in the brain, neither for the onset lateralization of the stimuli nor for the ipsilateral and contralateral electrodes.
- Formal training in music enhances the neural synchronization to beat and meter. Although both musicians and non-musicians are exposed to the rhythms of music, formal training in music may have enhanced the processing of rhythmic structures.
- Top-down attention may be a crucial factor to reliably build up metrical structures.

Regarding the evolutionary roots of rhythmic processing, we found that:

- The cognitive structures required to discriminate isochrony in the auditory modality might be shared by two mammal species, regardless of their vocal learning abilities. Differently from beat perception, isochrony detection can be solved with interval-based timing mechanisms, which does not need to be linked to vocal learning abilities.

- Both rats and humans learned to detect auditory temporal regularity focusing on the relative durations of the sounds that depended on the tempo of the beat. The generalization task could not be solved by focusing on the absolute durations of the sounds, as found in some species of birds.
- Rats could have an innate preference for fast rhythms, probably related to the tempo of the ultrasonic vocalizations they produce in relaxing and stressing situations.
- Non-human animals can discriminate new versions of a familiar tune depending on the rhythmic organization of the tones. Thus, rats were able to identify how distinct durations of the tones were metrically organized.
- Several strategies to identify a tune are available to rats, either focusing on the underlying rhythm or the melodic organization of the song. However, most rats focused on its temporal information, that is, how distinct rhythms were grouped.

In sum, the findings presented in this dissertation suggest that core aspects of our rhythmic cognition are already present in rats, a phylogenetically distant species, and factors such as attention or training in music modulate the way the brain synchronizes with beat and meter beyond the auditory modality and its typical features.

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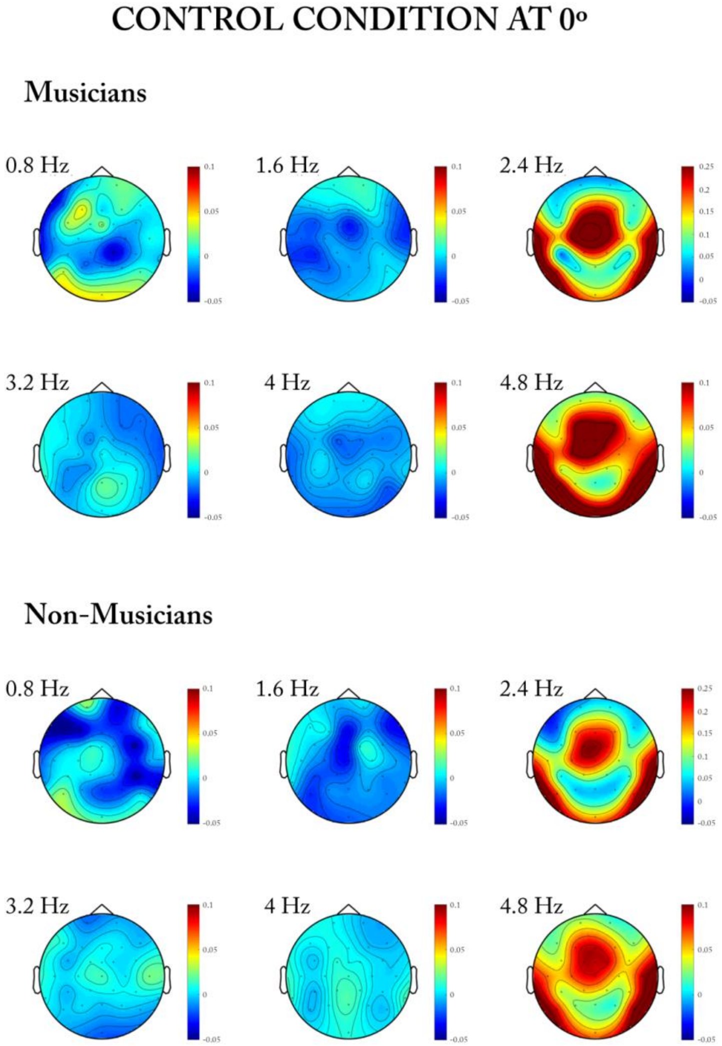
7. ANNEX I

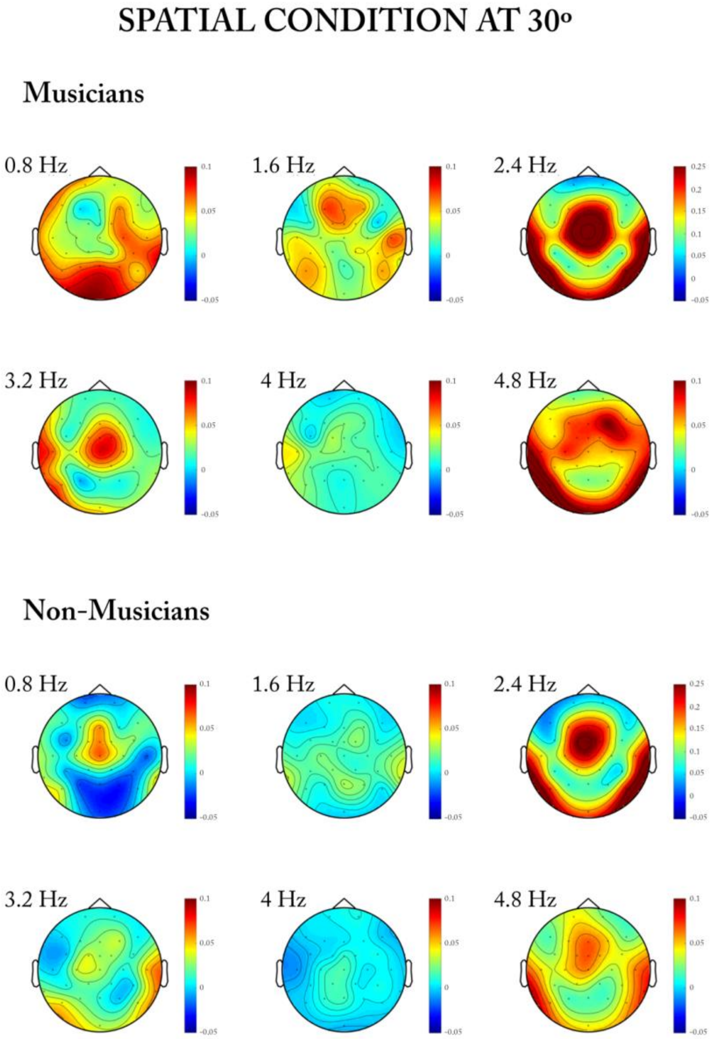
SUPPLEMENTARY MATERIAL OF STUDY 2

Supplementary Figure 1



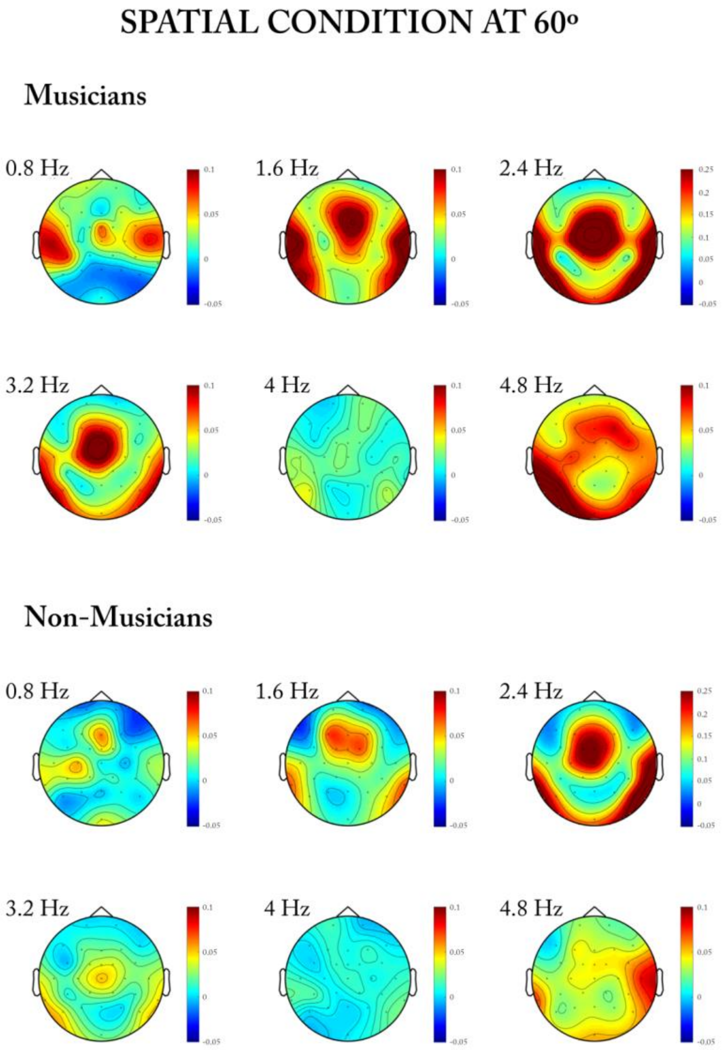
Suppl. Fig 1. Topographies of the amplitudes for the Control condition at 0º. *The topographies show the amplitudes of musicians (above) and non-musicians (below) at the six frequencies of interest during the Control condition at 0º. The color bar indicates the magnitude range, from -0.05 to 0.1 µV, for the frequencies 0.8, 1.6, 3.2, 4 and 4.8 Hz, and from -0.05 to 0.25 µV, for the frequency of the beat, 2.4 Hz.*

Supplementary Figure 2



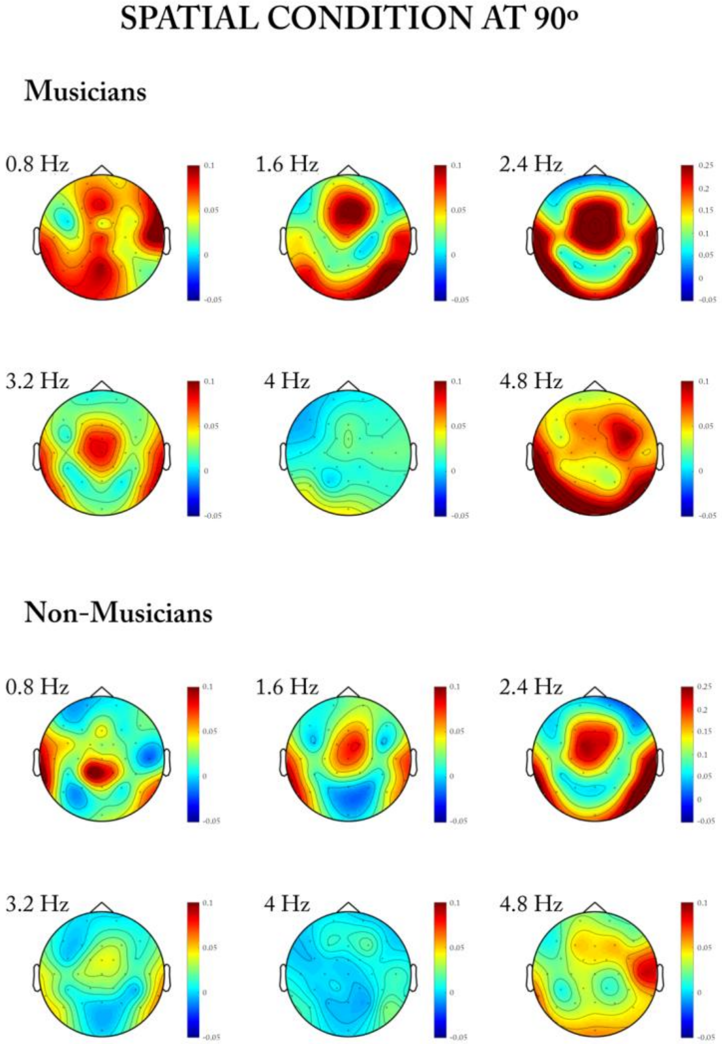
Suppl. Fig 2. Topographies of the amplitudes for the Spatial condition at 30º. *The topographies show the amplitudes of musicians (above) and non-musicians (below) at the six frequencies of interest during the Spatial condition at 30º. The color bar indicates the magnitude range, from -0.05 to 0.1 µV, for the frequencies 0.8, 1.6, 3.2, 4 and 4.8 Hz, and from -0.05 to 0.25 µV, for the frequency of the beat, 2.4 Hz.*

Supplementary Figure 3



Suppl. Fig 3. Topographies of the amplitudes for the Spatial condition at 60º. *The topographies show the amplitudes of musicians (above) and non-musicians (below) at the six frequencies of interest during the Spatial condition at 60º. The color bar indicates the magnitude range, from -0.05 to 0.1 µV, for the frequencies 0.8, 1.6, 3.2, 4 and 4.8 Hz, and from -0.05 to 0.25 µV, for the frequency of the beat, 2.4 Hz.*

Supplementary Figure 4



Suppl. Fig 4. Topographies of the amplitudes for the Spatial condition at 90º. *The topographies show the amplitudes of musicians (above) and non-musicians (below) at the six frequencies of interest during the Spatial condition at 90º. The color bar indicates the magnitude range, from -0.05 to 0.1 µV, for the frequencies 0.8, 1.6, 3.2, 4 and 4.8 Hz, and from -0.05 to 0.25 µV, for the frequency of the beat, 2.4 Hz.*

8. ANNEX II

In this annex we attach the musical scores of all the stimuli used in the test session of Study 4. We also include an additional statistical analysis that reinforces the main findings reported in the manuscript.

STIMULI FOR THE TEST SESSION:

a) 21 reinforced familiar items

Happy Birthday song excerpt on piano: eight tones (G4, A4, B4, C5, D5, E5, F5, G5)

b) 7 non-reinforced familiar items

Identical Happy Birthday song excerpt on piano:

c) 7 non-reinforced new items

Identical rhythm on piano: same tone (C5) with the rhythm from Happy Birthday

d) 7 non-reinforced new items

Scrambled rhythm on piano: same melody with scrambled rhythms from Happy Birthday

The Supplementary Figure 5 shows the music scores of the 8 unfamiliar test items presented to the rats to discern whether they discriminated the familiar song from versions in which the rhythmic organization of the same durational values was altered or preserved in a constant pitch.

a) Isotonic rhythm version

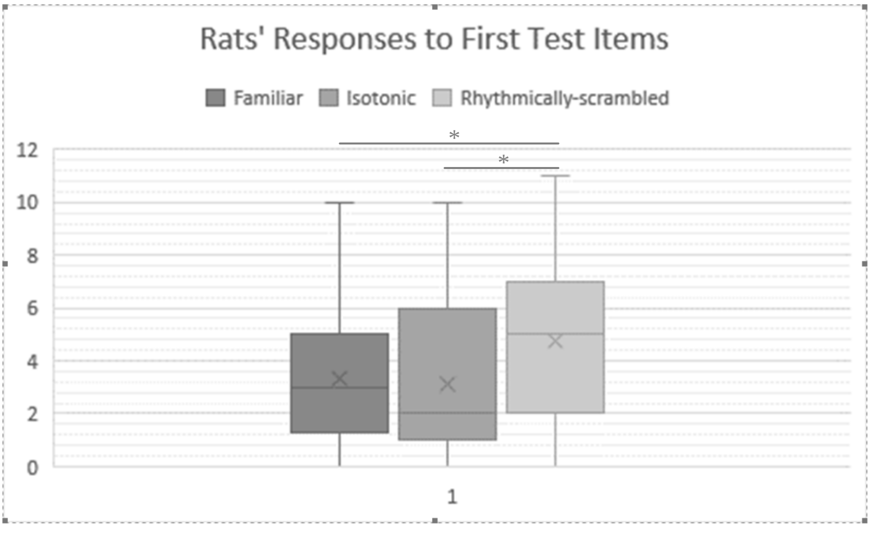
b) Rhythmically-Scrambled versions

Suppl. Fig 5. Music scores of the unfamiliar test items of Study 4: one version of the constant-pitch rhythm (a) and seven versions of the rhythmically-scrambled song (b).

EXTRA STATISTICS

One could complaint that the different number of unfamiliar test stimuli influenced rats' responses. To explore this, we compared the number of responses that rats gave to the first presentation of each kind of test item using a Repeated Measures ANOVA with the within factor Test Stimuli (familiar song, isotonic rhythm, rhythmically-scrambled song). As in Study 3, the animals responded differently to the 3 types of test stimuli ($F_{(2,78)}$=5.448, *p* < .006, $ŋ^2$ = .123).

Post hoc pairwise comparisons with the Bonferroni alpha correction revealed that rats gave more nose-poking responses for the rhythmically-scrambled excerpts (M=4.78, SD=0.45) compared to the familiar song (M=3.33, SD=0.40; MD=1.45, *p* < .016, 95% CI [0.22, 2.68]) and to the isotonic rhythm excerpts (M=3.15, SD=0.44; MD=1.63, *p*=.016, 95% CI [0.25, 3.00]). The number of responses after the isotonic rhythm excerpts and the familiar song did not differ (MD=-0.18, *p*=1.000, 95% CI [-1.62, 1.27]).



Suppl. Figure 6 Rats' responses to each first test item. The mean of the responses to the first item of each stimulus (the familiar, isotonic and rhythmically-scrambled versions of the Happy Birthday song) is marked by the x-symbol within every boxplot.

Thus, the animals discriminated the rhythmically-scrambled rhythm from the two excerpts that maintained the rhythmic organization of the song, even when the first item was presented and both unfamiliar stimuli were completely new. Again, rats did not discriminate between the 2 excerpts that differed in their melodic intervals but that kept the same rhythmic structure (see additional Figure 11).