UNIVERSITAT DE BARCELONA

Theta synchronization correlates of musical pleasure

Alberto Ara Romero

ADVERTIMENT. La consulta d'aquesta tesi queda condicionada a l'acceptació de les següents condicions d'ús: La difusió d'aquesta tesi per mitjà del servei TDX (**www.tdx.cat**) i a través del Dipòsit Digital de la UB (**diposit.ub.edu**) ha estat autoritzada pels titulars dels drets de propietat intel·lectual únicament per a usos privats emmarcats en activitats d'investigació i docència. No s'autoritza la seva reproducció amb finalitats de lucre ni la seva difusió i posada a disposició des d'un lloc aliè al servei TDX ni al Dipòsit Digital de la UB. No s'autoritza la presentació del seu contingut en una finestra o marc aliè a TDX o al Dipòsit Digital de la UB (framing). Aquesta reserva de drets afecta tant al resum de presentació de la tesi com als seus continguts. En la utilització o cita de parts de la tesi és obligat indicar el nom de la persona autora.

ADVERTENCIA. La consulta de esta tesis queda condicionada a la aceptación de las siguientes condiciones de uso: La difusión de esta tesis por medio del servicio TDR (**www.tdx.cat**) y a través del Repositorio Digital de la UB (**diposit.ub.edu**) ha sido autorizada por los titulares de los derechos de propiedad intelectual únicamente para usos privados enmarcados en actividades de investigación y docencia. No se autoriza su reproducción con finalidades de lucro ni su difusión y puesta a disposición desde un sitio ajeno al servicio TDR o al Repositorio Digital de la UB. No se autoriza la presentación de su contenido en una ventana o marco ajeno a TDR o al Repositorio Digital de la UB (framing). Esta reserva de derechos afecta tanto al resumen de presentación de la tesis como a sus contenidos. En la utilización o cita de partes de la tesis es obligado indicar el nombre de la persona autora.

WARNING. On having consulted this thesis you're accepting the following use conditions: Spreading this thesis by the TDX (**www.tdx.cat**) service and by the UB Digital Repository (**diposit.ub.edu**) has been authorized by the titular of the intellectual property rights only for private uses placed in investigation and teaching activities. Reproduction with lucrative aims is not authorized nor its spreading and availability from a site foreign to the TDX service or to the UB Digital Repository. Introducing its content in a window or frame foreign to the TDX service or to the UB Digital Repository is not authorized (framing). Those rights affect to the presentation summary of the thesis as well as to its contents. In the using or citation of parts of the thesis it's obliged to indicate the name of the author.

Theta synchronization correlates of musical pleasure

Alberto Ara Romero

Supervisor: Josep Marco Pallarés

Department of Cognition, Development and Educational Psychology
University of Barcelona

PhD program in
Brain, Cognition and Behavior
Barcelona, April 2021

Acknowledgements

[ESP] Ha sido un largo camino, y no exento de dificultades ni desafíos. Por suerte no he caminado solo. En todo momento he tenido a buenas personas cerca, ayudándome con la carga y animándome a seguir adelante. A estas personas quisiera dedicarles las siguientes palabras, desde la más profunda sinceridad. Espero que así queden para la posteridad y que nos den energías para seguir acompañándonos mientras transitamos caminos futuros.

Mis primeros agradecimientos quisiera dedicárseos a mis padres, María y Alberto. Esta tesis consigue culminar gracias a vuestra inagotable paciencia, determinación y esfuerzo para que primero un niño, luego un adolescente y finalmente un adulto pudiera canalizar una curiosidad errática y desmedida en un proyecto útil. Sin vosotros y sin la educación que me habeis prestado un documento como el que tenemos delante nunca hubiera podido gestarse. Por eso, de todo corazón, gracias.

Como el lector ya habrá intuido por su título, esta tesis trata, entre otras cosas, de música. Este interés intrínseco viene de una etapa donde conocí a una persona muy especial. Loren, quiero agradecerte que en aquellos años tan importantes me introdujeras al noble arte de expresar lo que pensamos y sentimos a través de un instrumento. También agradecerte todos los años que hemos pasado de proyecto en proyecto. A nuestras espaldas discos, giras y sudor. Si no hubieras aparecido en mi vida esta tesis trataría sobre cualquier otra cosa. Por ello, gracias.

En esta misma línea quisiera agradecer a mis últimos compañeros de viaje musical -Sergio, Alex y Chus- por estos tres últimos años. Durante este tiempo nuestro proyecto ha sido la válvula de escape que me recargaba las pilas para poder seguir adelante. El resultado ha sido tres trabajos de estudio de los que me siento orgulloso, y varios conciertos que me han recordado el valor de la amistad. Muchas gracias por devolverme la ilusión en un aspecto de mi vida que daba por perdido, y por enseñarme que merece la pena continuar pese a desafíos y fatigas. Mi más sincera gratitud.

Cuando empecé mi vida académica no fue fácil. Enfrentarse solo a la tarea de aprender una disciplina compleja puede ser aterrador. Por suerte no tardé demasiado en encontrar mi bandada, mis “Tosicos Mocsados”. Los agradecimientos que quiero dedicar a estas personas son muy importantes, ya que nuestras interminables conversaciones han definido tanto mi identidad como la motivación para dedicarme a esto. Junto a vosotros y a través de vosotros he descubierto esta apasionante disciplina, además de otros aspectos de la vida igual de importantes. Muchas gracias por estar siempre disponibles para hacer piña.

De forma similar, mi primera experiencia académica en Barcelona fue tremendamente enriquicedera. Fue durante el curso de mi máster que tuve la suerte de conocer a cuatro compañeros formidables, los cuales supusieron una fuente inagotable de estimulación. Muchas gracias Oscar, Joan, Victor y Patri. Sin vosotros nada de esto hubiese sido igual. Aprendimos mucho juntos, pero sobre todo encontramos una amistad que todavía hoy perdura. Por muchos más años de conversaciones intrincadas y proyectos locos. Nos volveremos a encontrar de mil maneras distintas.

También quiero hacer una mención muy especial a las personas con las que he convivido durante toda mi estancia en Barcelona. En particular agradezco de todo corazón a Francis, Sergi, Laura y Carmen por haber estado a mi lado todo este tiempo. No solo os habeis convertido en mejores amigos, también me habeis brindado un apoyo tremendo en esta gigantesca aventura. Hasta tal punto de que el éxito de esta tesis ha dependido en gran medida de vosotros. Estoy en deuda, y espero poder devolveros en el futuro aunque sea una pequeña parte del amor que me habeis otorgado.

[VAL] També volia agrair de bona gana a tot l’equip de la unitat de cognició i plasticitat cerebral -passat, present i futur. Tot aquest temps de doctorat ha sigut una exper-

iència molt intensa i enriquidora. He tingut la sort de desenvolupar la meua carrera acadèmica en un grup de recerca únic en el món. No només per la seua qualitat científica sinó també per la seua qualitat humana. Aquesta manera de treballar ha sigut sense cap mena de dubte un aprenentatge en si mateix. Gràcies a aquesta experiència improbable el meu futur serà un poc més brillant, n'estic segur.

Aquesta secció d'agraïments no tindria sentit sense dedicar unes paraules a Josep, el tutor d'aquesta tesi doctoral. No exagere quan dic que no només has sigut un tutor, sinó un mentor. Vull expressar l'agraït que estic d'haver tingut un cap com tu al meu costat. He aprés moltíssim. A més, el teu suport incondicional ha sigut incommensurable. Vull que sàpies l'admiració que tinc per tu, encara que no ho haja expressat molt sovint. Espere que hages gaudit d'aquesta experiència tant com ho he fet jo, i que continuem treballant en el futur. Moltíssimes gràcies de bon cor.

[ENG] I would also like to dedicate a few words to my fellow Quebecker research hosts. It was a couple of years ago that I arrived in Montreal to start a collaboration with Robert Zatorre's team, where I found a whole new world of discovery. It was only three months but the knowledge and experience I acquired during this period was vast and certainly contributed to this thesis. For all this, thank you very much to all the team, and specially to Robert and Neomi for their disposition, great ideas, and mentoring. I hope we can transit many future endeavors together.

Last but not least, I would like to acknowledge with great pride the unconditional support I got from a very important person in my life. Thank you so much Floriane for standing by my side along the whole way, relentlessly. You have been a constant source of inspiration and motivation, which has taken me to where I am today, this thesis as proof. I could not have finished this journey if you had not been here for me in both the good and in the bad moments, and for that I will be ever grateful. I have learnt so much from you in so many ways, and be certain that I will always carry this experience with me. For all this and much more I admire you and I sincerely wish you the best in life. *Merci beaucoup pour tout. Tout.*

Index

Abstract

Arguably, one of the stimuli that move human the most is music. What physically consists in an array of sounds organized in time and frequency, is capable of evoking a rich palette of emotions, thoughts and behaviors in the listener. Despite the complexity of these psychological phenomena, however, music is also capable of evoking one of the most basic psychophysiological reactions to stimuli in humans: pleasure. Thus, a relevant question is how music, an arbitrary concatenation of sounds, ends up translated into this unique affective experience. As with many other aspects of human behavior, studying the brain function underlying this psychological phenomenon offers an insightful view on this intriguing inquiry.

As of today, decades of research have been devoted to elucidate the neuropsychological mechanisms through which music-evoked pleasantness takes place. From psychological models of emotion and affect to evidence-based neuroscientific theories, the question of how music becomes pleasurable has been addressed from many different disciplines, approaches and methodologies. As a result, the brain architecture and mechanics underlying music evoked pleasantness have begun to be understood to great detail. Perhaps the most important breakthrough has been to verify that music engages the brain reward system, validating the idea that musical stimuli are indeed a source of hedonic impact. Nevertheless, along the brain reward system work a number of cortical areas responsible for the perceptual processing of musical stimuli. Altogether, this anatomical and functional interplay conforms an extensive network that actively contributes to the pleasurable experience of listening to music. Furthermore, other brain areas have been observed to be involved in these networks depending on

the level of familiarity with the music stimuli, a factor that has been replicated to be intimately associated with music reward processing.

As such, these networks utilize precise neural dynamics in order to transfer the information back and forth between the areas involved. A candidate mechanism for this information transfer are neural oscillations. By synchronizing to the same inputs, neuronal populations can pass information and process it efficiently to fulfill a task or demand. The neural oscillations associated with music-evoked pleasantness are just beginning to be understood. However, a common oscillatory signature of musical pleasure does appear consistently in the literature: theta oscillations. Nonetheless, whether the different areas engaged in music reward processing are indeed synchronized by these rhythms is yet to be determined. One goal of this thesis is to study whether theta rhythms indeed synchronize relevant brain nodes during pleasant music listening. In order to answer this question, in study 1 we acquired EEG signals from a cohort of participants while they listened and rated a number of musical excerpts. After analysis of the EEG data jointly with the self-reports, we observed that right frontal and temporal signals were more synchronized by theta rhythms the more pleasant music was found. These results converge with previous literature pinpointing right fronto-temporal connectivity to be actively involved in the process of assigning value to music, as well as with literature identifying theta rhythms as a correlate of music-evoked pleasantness and related constructs.

Following this line of research, another goal of this thesis is to test whether the nodes synchronized by theta rhythms during pleasant music listening are indeed related to the music processing brain networks consistently replicated in the neuroimaging literature. For this purpose, in study 2 we acquired simultaneous fMRI-EEG recordings with a similar paradigm to that of study 1. After replicating previous results identifying a fronto-temporal music-related brain network in our fMRI data, we studied the activity of this network in relation to theta synchronization as measured with EEG and reported pleasantness. We observed that theta synchronization between frontal and temporal signals was positively related to music-related brain function when music was reported to be liked the most, providing empirical evidence for the link between the two phenomena.

Yet another intriguing question is whether liking for familiar music synchronizes similar or different brain nodes by theta rhythms. Familiar music has been observed to be liked more than unfamiliar music, suggesting qualitative and/or quantitative differences in its processing. Indeed, previous research has revealed that in addition to music processing areas, familiar music engages the parietal cortex. In study 3 we familiarized a cohort of participants with some music stimuli and had them rate the excerpts 24h later along a new set of stimuli while their EEG was recorded. We found that the right fronto-temporal theta connectivity profile found in the previous studies was only associated with liking for novel music. Instead, temporo-parietal theta connectivity was more engaged when liking familiar music. These results go in line with previous research and pose the first attempt to our knowledge to study the familiarity effect on musical liking from an oscillatory dynamics perspective.

Therefore, the research conducted in this thesis adds up to the state of the art in the neuroscience of music-evoked pleasantness. We provide novel evidence for the role of theta oscillations in synchronizing relevant brain nodes during pleasant music listening, as well as the different cortical nodes these rhythms synchronize depending on the familiarity level with music. Particularly, fronto-temporal theta rhythms were identified to be associated with music-evoked pleasantness overall, and with liking for novel music specifically. We also provide evidence that in the particular case of familiar music, liking is supported by theta temporo-parietal synchronization. Last but not least, our results also link empirically the fronto-temporal brain networks underlying music perception as measured with fMRI with theta oscillations associated with music-evoked pleasantness as measured with EEG. Altogether, the results presented in this thesis contribute to the understanding of the brain networks involved in pleasant and familiar music listening, insofar they corroborate theta rhythms as a means of synchronization dynamics, opening up new windows for future research.

Resumen

Podría decirse que uno de los estímulos que más conmueven al ser humano es la música. Lo que físicamente consiste en una serie de sonidos organizados en tiempo y frecuencia, es capaz de evocar una rica amalgama de emociones, pensamientos y comportamientos en el oyente. Sin embargo, a pesar de la complejidad de estos fenómenos psicológicos, la música también es capaz de evocar una de las reacciones psicofisiológicas más básicas que los estímulos pueden despertar en los seres humanos: placer. Por tanto, una cuestión relevante es cómo la música, una concatenación arbitraria de sonidos, acaba traduciéndose en esta experiencia afectiva única. Como ocurre con muchos otros aspectos del comportamiento humano, estudiar la función cerebral asociada a este fenómeno psicológico ofrece un punto de vista esclarecedor sobre esta intrigante cuestión.

A día de hoy, se han dedicado décadas de investigación para dilucidar los mecanismos neuropsicológicos a través de los cuales se produce el placer evocado por la música. Desde modelos psicológicos de emoción y afecto hasta teorías neurocientíficas basadas en evidencia empírica, la cuestión de cómo la música se vuelve placentera se ha abordado desde muchas disciplinas, enfoques y metodologías diferentes. Como resultado, la arquitectura del cerebro y la mecánica subyacente a el placer a la música han comenzado a entenderse con gran detalle. Quizás el avance más importante ha sido verificar que la música activa el sistema de recompensa del cerebro, validando la idea de que los estímulos musicales son en efecto una fuente de impacto hedónico. Sin embargo, junto al sistema de recompensa cerebral funcionan una serie de áreas corticales responsables del procesamiento perceptual de los estímulos musicales. En

conjunto, esta interacción anatómica y funcional conforma una red extensa que contribuye activamente a la experiencia de escuchar música placentera. Además, se ha observado que otras áreas del cerebro están involucradas en estas redes dependiendo del nivel de familiaridad con los estímulos musicales, un factor íntimamente asociado con el procesamiento de la recompensa musical, como así se ha replicado en la literatura.

Como tal, estas redes utilizan dinámicas neuronales concretas para transferir la información entre las áreas involucradas. Un mecanismo candidato para explicar esta transferencia de información son las oscilaciones neuronales. Al sincronizarse con los mismos *inputs*, las poblaciones neuronales pueden comunicar información y procesarla de manera eficiente para cumplir con una tarea o demanda. Las oscilaciones neuronales asociadas al placer musical apenas han comenzado a entenderse. No obstante, hay un correlato oscilatorio del placer musical que aparece consistentemente en la literatura: las oscilaciones theta. Sin embargo, aún no se ha determinado si las diferentes áreas involucradas en el procesamiento de recompensas musicales están realmente sincronizadas a través de estos ritmos. Uno de los objetivos de esta tesis es estudiar si los ritmos theta realmente sincronizan los nodos cerebrales relevantes durante la escucha de música placentera. Para contestar esta pregunta, en el primer estudio adquirimos señales de EEG en un grupo de participantes mientras escuchaban y evaluaban una serie de fragmentos musicales. Después del análisis de los datos de EEG junto a las evaluaciones de placer, observamos que las señales frontales y temporales derechas estaban más sincronizadas a través de ritmos theta cuanto más placentera resultaba la música. Estos resultados convergen con literatura previa que señala que las redes fronto-temporales derechas participan activamente en el proceso de valoración musical, así como con literatura que identifica los ritmos theta como un correlato del placer evocado por la música y constructos relacionados.

Siguiendo esta línea de investigación, otro objetivo de esta tesis es probar si los nodos sincronizados por ritmos theta durante la escucha de música placentera están realmente relacionados con las redes cerebrales de procesamiento musical normalmente hayadas en la literatura de neuroimagen. Para ello, en el estudio 2 adquirimos registros simultáneos de fMRI-EEG en un paradigma similar. Después de replicar resultados anteriores identificando una red cerebral fronto-temporal relacionada con la música en nuestros datos de resonancia magnética funcional, estudiamos la actividad de esta red en relación con la sincronización theta medida con EEG, y el placer evocado. Observamos que la sincronización theta entre las señales frontales y temporales se relaciona positivamente con la función cerebral relacionada con la música cuando se reporta que ésta gusta más, proporcionando evidencia empírica del vínculo entre estos dos fenómenos.

Otra cuestión importante es si el placer evocado por la música familiar sincroniza los mismos o diferentes nodos cerebrales por ritmos theta. Se ha observado que la música familiar gusta más que la música desconocida, lo que sugiere diferencias cualitativas y/o cuantitativas en su procesamiento. De hecho, investigaciones anteriores han revelado que, además de las áreas de procesamiento musical, la música familiar activa la corteza parietal. En el estudio 3 familiarizamos a un grupo participantes con algunos estímulos musicales y les pedimos que evaluaran los mismos fragmentos 24 horas después junto a un nuevo conjunto de estímulos mientras se registraba su EEG. Encontramos que la connectividad theta fronto-temporal derecha encontrada en los estudios anteriores solo se encontró asociada al placer evocado por música novel. En cambio, un perfil de conectividad theta temporo-parietal se encontró más asociado al placer cuando éste fue evocado por música familiar. Estos resultados estan en línea con investigaciones previas y suponen el primer intento, a nuestro entender, en estudiar el efecto de familiaridad en el placer musical desde una perspectiva de dinámicas oscilatorias.

Por todo esto, la investigación realizada en esta tesis contribuye a la vanguardia en la neurociencia del placer musical. Proporcionamos evidencia novedosa sobre el papel de las oscilaciones theta en la sincronización de los nodos cerebrales relevantes durante la escucha de música agradable, así como los diferentes nodos corticales que estos ritmos sincronizan según el nivel de familiaridad con la música. Particularmente, se identificó que los ritmos theta fronto-temporales están asociados con el placer evocado por la música en general, y específicamente con el placer evocado por la música nueva. También proporcionamos evidencia de que en el caso particular de la música familiar, el placer está asociado con sincronización theta temporo-parietal. Por último, aunque no menos importante, nuestros resultados también vinculan empíricamente las redes cerebrales fronto-temporales relacionadas que subyacen a la percepción de la música (medidas con fMRI) con oscilaciones theta asociadas al placer musical (medidas con EEG). En conjunto, los resultados presentados en esta tesis contribuyen a la comprensión de las redes cerebrales involucradas en la escucha de música placentera y familiar, en la medida en que corroboran los ritmos theta como medio de comunicación neuronal, abriendo nuevas oportunidades para futuras investigaciones.

1. Introduction

1.1 Music-evoked pleasantness, a multidimensional phenomenon

Pleasantness is evoked in human beings by a variety of stimuli, including basic needs such as food and water; and the resources that give access to these basic needs, such as currency or credit. The former are referred to as primary reinforcers, defined as biologically determined and unconditioned, whereas the latter are referred to as secondary reinforcers, defined as conditioned through association (Sescousse et al., 2013). Reward processing of these stimuli has an evolutionary *raison d'être*, as it guarantees the perpetuity of conducts that maximize survival.

The psychological mechanisms underlying this function are complex. The influential theoretical account of Berridge et al., 2009 poses that the construct of reward can be broken down into three different, though interlaced components: *wanting, learning and liking*. While wanting and learning refer to the motivational and cognitive aspects of reward, respectively, it is the liking component that explains the hedonic impact of rewarding instances, hereby referred to as pleasantness.

Nonetheless, primary and secondary reinforcers are not the only stimuli associated with hedonic experiences in humans. It is widely recognized that the arts are capable of evoking pleasantness, as well as other activities that are social in nature (Vessel et al., 2012). Importantly, such hedonic experiences, however aesthetic, are not dissociated from motivation and learning. Experimental studies in psychology and neuroscience have shown that aesthetically evoked pleasantness can be accompanied by incentive salience and cognition, similarly to basic reward processing (Gold et al., 2013). This has led to the theorization of an additional, humanly unique, type of reinforcer: abstract stimuli. Reward-processing of abstract stimuli is characterized by displaying no evident contingencies between stimulus/action and outcome (Salimpoor et al., 2011). Despite this apparent lack of utility, abstract reinforcers have been hypothesized to be evolutionary advantageous for our species, as they would facilitate social processes such as emotional expression and comprehension, and ultimately group cohesion (Koelsch, 2014).

The most studied abstract reinforcer to date has been music. Regarded as the most abstract of aesthetic stimuli, music is capable of evoking powerful pleasurable and emotional reactions in the listener despite its level of abstraction (Salimpoor et al., 2011). The interest in music in the cognitive sciences is not limited to its rewarding and emotional qualia, however. From perception to action, cognition to affect, and personality to social behavior, music intrigues a variety of research topics due to its complex multimodal nature (Hallam et al., 2014). The complexity of music begins at the perception of its acoustic features. The spectrum of single auditory events layers frequencies down to intensity, beat, pitch and timbre percepts. When perceived as a stream, these basic features form patterns through repetition and segmentation, resulting in rhythmic, melodic, timbric and dynamic content (Roeder, 2008). Organized over time, these higher-level features can generate predictions and associations in the listener, as well as become a source of surprise and salience (Tillmann et al., 2014).

These properties, along a system that comprehends them, are necessary to translate acoustic percepts into reward. Nevertheless, the enjoyment of music cannot be reduced to mere acoustics and behavioral reactivity. The concepts previously explained describe the necessary -rather than sufficient- processes that enable a much more complex psychological phenomenon. Music-evoked pleasantness may emerge from statistical contingencies, but also from positive associations with contexts or memories, as well as from aesthetic evaluation (Juslin, 2013).

It is this multifaceted nature that has motivated extensive research in music cognition and emotion. As we will see, the human brain is capable of integrating all these psychological phenomena through complex information processing via key functional structures and mechanisms. Therefore, the hedonic experience associated with music listening can be rich and multifaceted while efficiently integrated through the encoding and decoding of information carried out by the human brain.

1.2 Psychological aspects of music-evoked pleasantness

Different constructs can be explored in the study of music-evoked pleasantness, depending on the level of analysis and dimensions of interest. While the concept of pleasantness clearly resonates with the notions of emotion, feelings and affect, it also extends to other neuropsychological phenomena. Particularly, reward processing and its components are pivotal to explaining musical liking. Likewise, several other factors that contribute to this experience can be investigated. Perception, predictive processes, memory function and familiarity are all relevant determinants or moderators in finding music pleasurable. Furthermore, all the involved mechanisms contribute and interact to different extents depending on the context, individual and stimuli.

In the following sections the most relevant psychological processes and dimensions in the literature of music-evoked pleasantness will be reviewed. First, the main models of musical emotions and how these relate to the hedonic experience of listening to music will be introduced. Second, the role of implicit knowledge in the cognitive processes that precede music reward processing will be discussed. Third, the predictive coding framework will be presented as a novel theoretical account that aims at explaining how the perception of acoustic features can lead to rewarding instances through predictive processes and memory mechanisms. It will be argued that this framework explains to a great extent the affective nature of music as well as the importance of implicit knowledge in music-evoked pleasantness in an integrated information processing system of evolutionary relevance.

1.2.1 Music and emotion

Music can arouse a complex palette of emotions in the listener. Importantly, these are not limited to sentiments of attachment or detachment, but can also include expressions such as sadness, joy or awe. Researchers and academics have tried to understand and assort musical emotions over decades, if not centuries (Juslin and Sloboda, 2001). A historical distinction in the literature is the difference between *everyday emotions* and *aesthetic emotions* in musical contexts. The former range from basic emotions (e.g. fear, anger, joy) to more complex ones (e.g. delight, pessimism, hope) and are not specific to music or the arts in general, insofar they can be found in other life situations. The latter, on the other hand, are thought to be unique to musical or artistic contexts given their appreciative nature (e.g. awe, wonder, admiration; Juslin, 2013). This distinction, however, is controversial and its foundations have been called into question (Skov and Nadal, 2020).

Another distinction, more relevant still, is that made between *perceived emotions* and *evoked emotions*. Such dichotomy has been motivated by the attempt of explaining conflicting emotional states, such as feeling positive emotions from music conveying negative emotions (e.g. finding joy in listening to sad music). According to this view, perceived musical emotions would be those emotions identified by the listener *as conveyed by* music, whereas evoked musical emotions would be those experienced by the listener *in response to* music (Kawakami et al., 2014). It would thus be possible that an emotion is identified and transmitted (e.g. feeling happy by resonating with a song conveying happiness), but also that music arouses feelings in the listener different to the identified emotion as a product of associations and idiosyncrasies.

Therefore, the perceived emotions' locus is external since its function is to understand the emotions expressed by the emitter. In turn, the evoked emotion's locus is internal and refers to the emotional reactions aroused by music in the receiver (Schubert, 2013). Music-evoked pleasantness would lie in the latter category. However, this now classic distinction does not completely account for the possibility of liking music regardless of its emotional content, since it assumes a positive emotional state that would be incompatible with “contagion” when negative emotions are perceived. On the contrary, one could argue that there are situations in which one does feel, and not only perceive, negative emotions, and that these emotions coexist with feelings of pleasantness, nonetheless. This conundrum has been often described in the literature as “mixed” emotions.

Models of emotion where evoked emotions are functionally dissociated from approach/avoidance behavior have tried to resolve this conceptual confound. Schubert, 2013 proposes that musical emotions, both perceived and evoked, can be operationalized in a bidimensional space composed by *valence* (the sign of the emotional instance, ranging from negative to positive valuation) and *arousal* (the activation related to the emotional instance, ranging from calm to exciting; Russell, 1980; Figure 4.1A). Perceived emotional information can then be naturally mirrored into evoked emotions with the listener feeling the same emotion as perceived, or on the contrary evoke different emotions than those conveyed by the music through personal associations or idiosyncrasies (Juslin and Västfjäll, 2008; Figure 4.1B).

While in most situations the evoked valence dimension would naturally account for pleasant and unpleasant reactions to stimuli, the case of music potentially dissociates the two constructs. In order to resolve this discrepancy, Schubert, 2013 states that evoked valence can be further broken down into *emotional valence* (sign of the emotions felt by the listener) and *affect valence* (approach/avoidance toward music and its associated emotional and cognitive states; Figure 4.1C). This validates the idea that while it is natural to approach positive emotions and avoid negative ones in a wide range of situations, it is also adaptive to approach negative emotional states in some contexts (Garrido and Schubert, 2015). Furthermore, this resolution resonates well with considering emotional and reward processing to be carried out by related, but independent systems, the latter more related to the construct of affect valence (Murray, 2007). All this is relevant because most of the EEG literature concerned with music-evoked pleasantness has been conducted without disentangling liking from emotional valence. As we will see in further sections, this is an important aspect in this thesis.

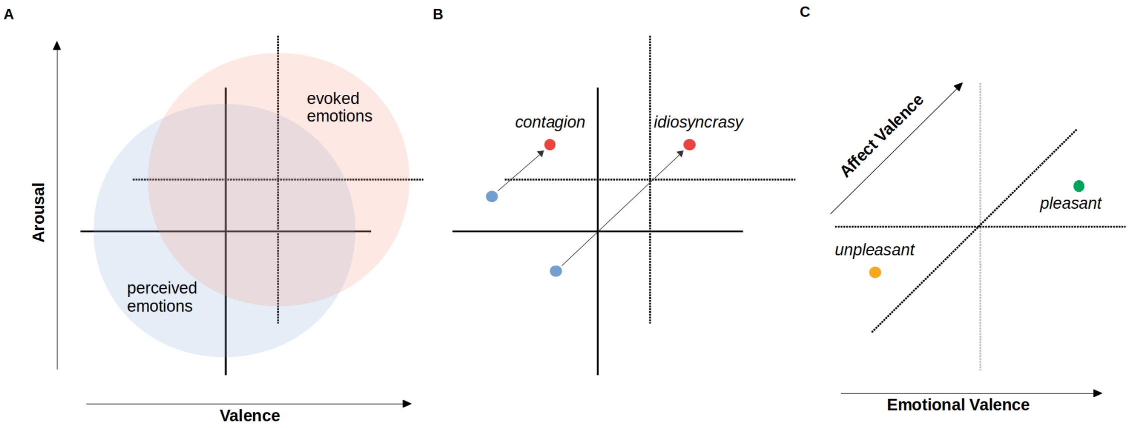


Figure 1.1 **A)** Bidimensional circumflex model of emotion mirroring perceived and evoked emotions. **B)** Perceived emotional events are mapped onto evoked emotional events through contagion (mirroring) or idiosyncratic associations (dissociation). **C)** Evoked valence can be further broken down into emotional valence (sign of the felt emotion) and affect valence (approach/avoidance).

Discrete and dimensional models of emotion are useful insofar they make affective phenomena explicit and operative. However, these models explain very little about the mechanics behind these psychological phenomena. On the other hand, meticulous research has been devoted to dissecting the candidate mechanisms that might explain music-evoked emotions and pleasantness from sensation to affect. Juslin and his colleagues have proposed a framework to analyze and contextualize emotions evoked by music: the BRECVEMA framework (Juslin, 2013). The acronym stands for its eight proposed psychological mechanisms underlying music-evoked emotions: *Brainstem reflexes, Rhythmic entrainment, Evaluative conditioning, Emotional contagion, Visual imagery, Episodic memory, Musical expectancy and Aesthetic judgment.* Each one of them would contribute differently to emotional and affective reactions to music.

From the BRECVEMA model stems that different mechanisms contribute independently to evoking emotions over different timescales, in reaction to musical events (defined as music-listener-context compounds). By the assumption that affect valence must be supported by reward processing, evaluative conditioning and musical expectancy are plausible candidates to explaining music's hedonic impact, given their potential to assign value to percepts, memories and/or emotional reactions. On the one hand, evaluative conditioning is defined as a mechanism from which idiosyncratic reactions can emerge through associations between music stimuli and other emotionally signed events, internal or external (e.g. finding a music genre unpleasant because it is associated with a context arousing negative feelings that one prefers to avoid). On the other hand, musical expectancy is defined as a system that works over predictive processes: it allows the generation of predictions based on prior learning of perceptual contingencies and online monitoring of the accuracy of such predictions. As a consequence, this online monitoring system results in surprise and realization dynamics.

These two mechanisms exhibit the predictive, salience, and realization/surprisal dynamics necessary to potentially trigger reward signals. Aesthetic judgment is also interesting in these regards, insofar it can direct attention toward stimuli in order to evaluate their significance. For instance, one could find pleasure in the realization of salient predictions, or in moderate surprisal emanating from discrepancies between top-down predictions and bottom-up percepts. On the other hand, one could also enjoy listening to music that is paired with an episodic memory, whose positive emotional content is salient and conditioned to pleasure. Yet another example would be an individual that finds the emotional instances encoded into angry music relevant because he/she seeks feeling that emotion at a moment in which it might be adaptive to do so, rewarding the activation of such feelings. Finally, one could actively evaluate music seeking for musical instances that meet certain subjective criteria and make online predictions accordingly, arousing interest and evoking pleasantness when these conditions are met. For all these dynamics to take place, however, there must be a representational system that supports them, operating over both long-term and short-term information and subject to learning. In the next sections we will see how the acquisition and reactivation of implicit knowledge about music's attributes and contingencies as well as the active capacity of buffering over several sources of auditory representations are key for music to become rewarding.

1.2.2 The role of implicit knowledge

As we saw in the previous section, musical expectancy has been hypothesized as a key mechanism in evoking pleasantness. This mechanism must thus rely on the listener's past experience with music. In other words, the degree of pleasantness evoked by music depends on the implicit knowledge that an individual posses about music schemata and concrete pieces of music. This has been demonstrated in experiments showing that familiarity with music is indeed intertwined with the degree of pleasure it evokes. Most notably, this phenomenon has been observed in now classic experiments studying what is known as the *mere exposure effect*. The mere exposure effect refers to the observed increase in reported pleasantness in response to a stimulus after repeated exposure (Zajonc, 1968). This phenomenon has been replicated over the years and has motivated theories and research about the role of implicit knowledge and predictive processing in music's hedonic impact. Importantly, this effect has not only been observed behaviorally, but also at the physiological level in certain biological correlates of pleasure.

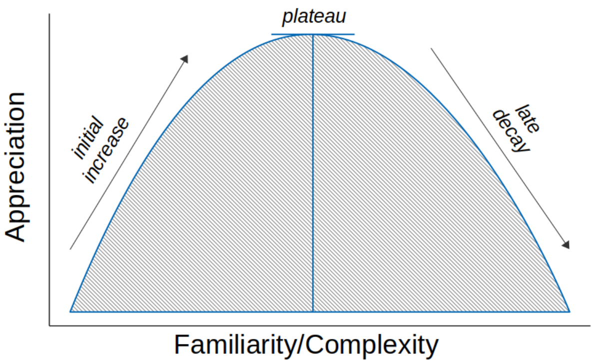


Figure 1.2 The inverted U shape of musical appreciation. Appreciation increases as a function of familiarity and/or complexity up to a *plateau*, whereby appreciation starts decaying with higher levels of familiarity and/or complexity.

The mere exposure effect does not take place exclusively in musical contexts. It is a phenomenon longtime observed in psychology and has been replicated with a variety of stimuli, aesthetic and non-aesthetic, such as paintings, faces, words or sounds (Zajonc, 2001). Such preference can take place even in the absence of conscious cognition about the stimuli's familiarity (Kunst-Wilson and Zajonc, 1980). The strength and maximal preference vary between stimuli classes, but it is generally agreed that in the case of music one repetition is enough to observe the effect, and that it reaches its peak after several repetitions (Peretz et al., 1998). It has also been observed that after many repetitions have taken place the effect can reverse and induce a decrease in preference, characterizing the exposure history by an *inverted U shape* (Chmiel and Schubert, 2017; Figure 1.2).

This inverted U shape in preference behavior had already been observed in empirical musicology as a function of exposure, originality and complexity (Chmiel and Schubert, 2017). This includes many studies reporting the mere exposure effect to take place after several repetitions of various music excerpts belonging to various music styles (Peretz et al., 1998). Johnson et al. (1985) established that this effect was present even in the absence of conscious evaluation or recall in a study with amnesic patients, which set out future research interested in the relation between affect and implicit memory. Further developments were realized by Peretz et al. (1998), who in a series of experiments systematically studied the mere exposure effect framed as an implicit memory phenomenon by diverting attention toward other tasks during exposure. They also studied the scope of the effect over time and feature space.

In their first experiment they demonstrated how this mere exposure effect resembles the properties of implicit memory by showing an increase in preference for unfamiliar melodies after one repetition, but not for already familiar melodies (which already displayed high preference and showed no increase headroom whatsoever); and contrary to explicit recognition, which displayed clear discrimination between exposed and non-exposed materials, both familiar and unfamiliar (with familiar melodies recognized better overall than unfamiliar ones). Importantly, this differences in affect persisted after several months after two repeats, contrary to the effect on recognition. In other words, exposure exerted different effects on affect and recognition, proving that one mechanism cannot be explained by the other, and confirming that the two are indeed dissociated.

In a second experiment, they established that the effect after one repetition could be observed after 24 hours after exposure, but not after one month, for which a second repeat would be needed. Contrary to this, recognition after one repetition, although attenuated, survived temporal decline over a period of a month. This added up to pre-existing evidence about the two phenomena following different dynamics and defined some of the temporal properties of the effect. In the last experiment they found that the effect of exposure on liking was not affected by changing surface characteristics such as timbre, contrary to recognition. This established that the processing of the implicit realizations take place at the abstract level, rather than the perceptual level, as had been previously thought (Peretz et al., 1998).

The series of experiments by Johnson et al. (1985) and Peretz et al. (1998) are important insofar they set out that the mere exposure effect on musical liking happens at the implicit, albeit abstract level of processing, contrary to what had been classically hypothesized. This opened a whole new arena to explaining and studying the inverted U shape profile of music-evoked pleasantness that classic authors had already established (Peretz et al., 1998). In the following years similar studies where extended to include more repetitions to characterize the scope of the effect and whether it decreases after reaching a *plateau*; to consider other modalities of implicit retrieval such as musical complexity; and to utilize artificially constructed musical grammars to study the extent to which such effects are truly explained by learning and are not inherent to certain musical attributes (Peretz et al., 1998; Loui et al., 2010; Loui, 2012).

Many studies since have supported the hypothesis that liking increases as a function of familiarity (Chmiel and Schubert, 2017). The literature on whether the effect is indeed characterized as an inverted U shape has been more controversial, with mixed results, but with more support than rejection overall (Chmiel and Schubert, 2017). Importantly, many studies have reported similar results as a function of complexity in addition to familiarity (Chmiel and Schubert, 2017), suggesting that both variables could be one and the same at different levels of predictability. This would mean that complexity is also subjective to the implicit knowledge an individual (or culture) has acquired about music, rather than objective to music's physical attributes. Thus, the inverted U shape of musical liking as a function of both familiarity and complexity could be explained by common underlying mechanisms. However, both phenomena have been shown to take place simultaneously or independently (Madison and Schiölde, 2017). This has led to the theorization that the implicit knowledge re-activated during music listening comes in the form of top-down predictions from two different, albeit intertwined sources: *schematic expectations* (i.e. generic knowledge about encultured rules of music) and *veridical expectations* (i.e. concrete knowledge about pieces of music; Schubert and Pearce, 2016). Schematic expectations would thus underlie subjective complexity through generalization, whereas veridical expectations would underlie familiarity through recognition (Schubert and Pearce, 2016).

Furthermore, psychophysiological studies have since attempted to provide objective biological markers of the mere exposure effect. It has been shown that physiological arousal increases contingently with reports of evoked pleasantness, as reflected in several variables (Salimpoor et al., 2009), with event-related skin conductance as the milestone measure in this type of studies due to its ease of use and clear and reproducible response. Accordingly, evidence shows that listening to familiar music induces an increase in electrodermal activity (EDA) as compared to listening to unfamiliar music; that repeated exposure to a piece of music increases its associated evoked EDA; and that these emotional dynamics can happen even without conscious recall of the experimental materials (van den Bosch et al., 2013). The effect of familiarity on musical liking, however, must be the result of particular information processing dynamics. In the next section we will see how the brain's ability to generate predictions and compare them to the environment could explain how implicit knowledge can be at the basis of music-evoked pleasantness, accounting for the previously explained mechanisms of expectancy and evaluative conditioning.

1.2.3 Predictive coding and reward processing

So far we have reviewed concepts such as familiarity, complexity, the inverted U shape, implicit knowledge and schematic and veridical expectations. All these constructs can be integrated in an information processing account of reward processing under the *predictive coding* framework. This theoretical account states that reward function can be explained as a predictive process: a stimulus or action raises expectations about a desirable outcome, which triggers reward signals if present. The hedonic impact of these reward signals would be subject to salience and learning: non-salient predictions and predictions that result in little learning are less likely to evoke pleasure, while salient predictions and predictions that result in learning are more likely to become a source of pleasantness (Schultz, 2016).

The above description matches nicely with the inverted U shape of music-evoked pleasantness as a function of familiarity or complexity, which can be redefined as musical expectancy based on past implicit learning in the form of schematic expectations (i.e. rules of music) and veridical expectations (i.e. concrete music). Tentatively, music-evoked pleasantness by evaluative conditioning (i.e. subject to associations between the stimuli and other rewarding outcomes) can be redefined as psychological events displaying similar predictive dynamics. In combination with aesthetic judgement, which can act as an attentional funnel, this framework covers the previously proposed psychological mechanisms behind affect valence toward music, each one of these contributing independently and in parallel to the final experience of experiencing pleasure from music (Juslin, 2013).

Particularly, the link between musical expectancy and reward processing within the predictive coding framework has drawn a lot of attention. From this theoretical standpoint, it is assumed that humans acquire statistical relationships between acoustic features through exposure, and that these associations crystallize at different levels of concretion, from broad generalizations (e.g. frequent musical structures) to specific contingencies (e.g. precise knowledge about pieces of music). When listening to music -and based on this manifold musical knowledge- the agent would make online predictions about how music will unfold. These top-down predictions will eventually be compared to incoming bottom-up percepts to update the existing knowledge and motivate learning (Gold, Pearce, et al., 2019).

From these assumption stems that musical predictions carry a given *certainty* level, and that the magnitude of the resulting surprises is computed as the difference between predicted instances and the actual incoming instances, or *prediction error* (PE).

Predictive certainty about musical events thus depends on the strength of the statistical regularities and associations that the agent has captured to be present in music through his/her learning history, while musical PE depends on how close these predictions are to the actual incoming stimuli. The more exposure to a piece of music or to a musical style, the greater the certainty of the predictions and the smaller the associated PEs, since accuracy is maximized (Salimpoor et al., 2015). Importantly, this process happens at different scales both in time and feature space: pitch, harmony, timbre, rhythm, intensity, etc.

However, while certainty and PE tend to change jointly over time, they are different phenomena happening at different processing stages: certainty is a property of predictions, while PE is the result of comparing these predictions to the actual musical events. The fact that certainty tends to increase while PE tends to decrease as a function of exposure can be explained by learning function: exposure strengthens musical contingencies while increasing the chances of predictive success in future iterations. Nevertheless, not every predictive instance falls along this trend: one can think of musical contexts where strong predictions are not met (e.g. a change in tonal mode that breaks up with assimilated musical conventions); or conversely, where weak predictions are met (e.g. the beginning of a passage after an undetermined interlude that is correctly predicted). In fact, research has shown that these musical contexts can also arouse pleasantness in addition to compromising certainty-PE instances, at least when studying schematic expectations (Cheung et al., 2019).

Perhaps this is better understood under the parsimonious reformulation of Koelsch et al., 2019. Predictions are made about some *content* within some *context*. Contexts carry precision about the “what” and “when” of future iterations. Subsequently, surprise emerges from comparing this predicted content to the actual content. Thus, the precision of the context matters in considering the relevance of surprisal events. In other words, context precision filters out surprise such as that small PEs resulting from uncertain predictions, great PEs from certain predictions, or moderate PEs from moderately certain predictions are perceived as salient and motivate further exposure. In turn, small PEs from certain predictions and great PEs from uncertain predictions are considered non-salient and thus disregarded, resulting in loss of motivation to keep on listening.

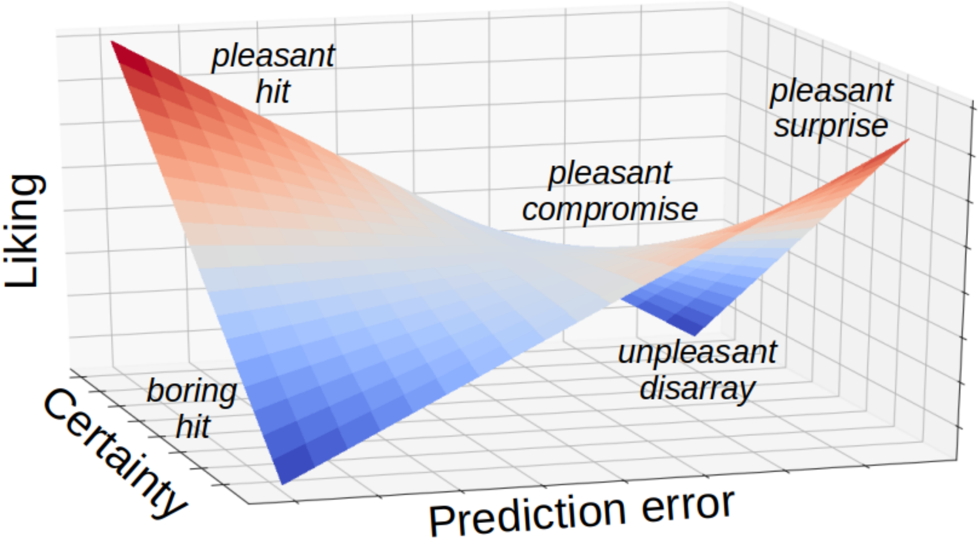


Figure 1.3 Music evoked pleasantness as the product between predictive certainty and prediction error. Both the inverted U shape and pleasantness evoked by correct predictions in imprecise contexts and surprises in precise contexts are accounted for by this mathematical expression in the case of schematic expectations.

This has led to the realization that evoked pleasantness is better operationalized as an interaction between certainty and PE (Hansen et al., 2017; Cheung et al., 2019), as this would account for the inverted U-shape as a function of familiarity or complexity, on the one hand, and all three contexts where hedonic impact is maximized, on the other hand (i.e. low certainty-low PE, high certainty-high PE and intermediate certainty-intermediate PE). It is worth noticing that all three contexts have something in common: room for learning. In the first case, an uncertain prediction is rewarded when it is confirmed, motivating further concretion; in the second case, a certain (schematic) prediction is unconfirmed and rewarded to readjust prior knowledge; and in the third case, put simply, both mechanisms come into play to some extent, since learning has not yet been completed (Figure 1.3). It must be noted, however, that pleasantness outcomes based on veridical expectations are expected to slightly differ from this model's predictions (for instance, it is unclear whether a radical change in the elements of a very familiar melody should evoke pleasantness). Nonetheless, the mere exposure effect and the inverted U-shape as a function of familiarity could still be explained by concrete cases in this model, with exposure resulting in an increase in context certainty and a decrease in factual PE as veridical expectations gradually take over schematic expectations. Peak pleasantness would be evoked in the intersection between certainty and PE in the listener's history for a particular music piece (Hansen et al., 2017; Figure 1.4).

Importantly, this model is not tautological: there are combinations of certainty and PE that have little to no hedonic impact. Particularly, the least evoked pleasantness emerges in contexts with low certainty and PE -where information is incomprehensible- or in contexts with high certainty and low PE -where learning is no longer possible. This taps onto an interesting idea about the evolutionary *raison d'être* of music-evoked pleasantness: in addition to its social and emotional utility, music might be rewarding because it keeps learning function active in the auditory system. It follows from this hypothesis that it is adaptive to maintain the auditory system in a dynamic influx of stimulation that guarantees flexibility and reconfiguration (Gold, Pearce, et al., 2019). While this statement is only tentative, it is a sound argument in favor of information processing accounts on the phenomenon.

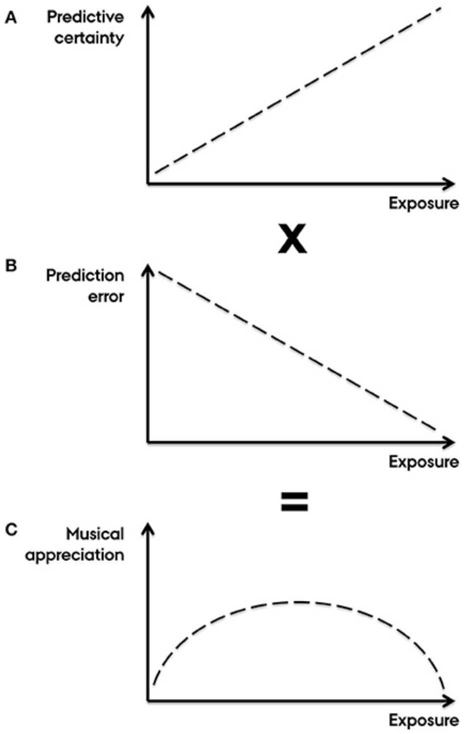


Figure 1.4 The inverted U shape is accounted for in the case of veridical expectations as a function of exposure. Adapted from Hansen et al. (2017).

1.3 Music-related brain function and anatomy

The functional amalgam underlying music's hedonic impact presented above must naturally involve different brain mechanisms, each one supporting different information processing operations at different processing stages. From sensation to affect, through perception and representation, and along evaluation and action, music-evoked pleasantness relies on very diverse neural populations to take place. Despite this apparent functional segregation, the distinct neural areas involved in this complex phenomenon happen to be well integrated and coordinated in response to the object stimulus. Not only this is relevant to understanding how music perception and emotion are implemented in the brain, but also offers an excellent example of how brain function is better understood as emerging from well-orchestrated networks rather than localized activations.

In this section the brain anatomy and function underlying music-evoked pleasantness will be reviewed. First, a brief explanation of the theoretical accounts that view the brain as a network and brain function as the interactive dynamics between its components will be introduced. Second, the most influential literature about the key brain areas, pathways and networks supporting the cognitive processes behind music perception, comprehension and reward will be reviewed. Finally, the limitations of the neuroimaging techniques that have been traditionally used to study music perception and reward in the brain will be discussed. Regarding this last point it will be argued that despite the strengths of these methods to study the brain spatial distribution of the phenomena of interest, other techniques must be considered to characterize how these brain interactions take place.

1.3.1 The brain as a network and brain function as network dynamics

Since functional neuroimaging techniques became widely accessible to researchers in the cognitive sciences, knowledge about the brain patterns underlying the cognitive processes long studied by psychologist has grown rapidly. What had been formerly inferred by studying lesions in neurological patients, comparing static brain images from different individuals or guessing the sources of scalp brain electrodes, was now possible to study by capturing intra-individual processes over time during performance of a task thanks to techniques such as *positron emission tomography* (PET) or *functional magnetic resonance imaging* (fMRI). This technical breakthrough has since provided new insights into many theories in cognitive psychology and neuroscience. Consequently, fMRI designs have become the quintessential method in cognitive neuroscience research as of today.

Until recently, however, functional neuroimaging research had dragged a modularity bias from previous schools of thought in the brain sciences. Much research has been devoted to identifying the different brain areas underlying the different cognitive functions. This way of approaching cognitive function and its underlying brain activity feeds both from classic theories stressing that human cognition is better understood as a collection of clearly distinguishable modules and from attempts to map the human brain into divisions based on anatomical features and/or cognitive function in isolation (Sutterer and Tranel, 2017). While this approach has been valuable insofar it has helped identify the fundamental anatomic units of the functional organization of the brain, it falls short of explaining more complex brain function beyond simple dissociable operations (Mišić and Sporns, 2016).

A different approach to interpreting task-related neuroimaging data has become more popular in recent years. This new framework considers the whole brain, and not only the different areas that compose it, as a multilayered network. According to this view, cognitive function emerges from the different connectivity dynamics taking place between the nodes composing a given network that temporally ensembles in response to a stimulus, operation or action demand (Bassett and Sporns, 2017). This way of understanding brain function has been influenced by the fact that few cognitive processes can be successfully attributed to a single brain area and that few single brain areas appear to be exclusively devoted to a single cognitive process. Furthermore, brain function has been observed to be shaped by the connectivity maps present in the cortex, (Honey et al., 2007), providing tangible evidence of the brain as an intraconnected organ that forms networks in response to external and internal demands.

Importantly, while this approach challenges previous ontologies of brain function, it does not completely override them. Instead, it broadens the extent to which we can interpret cognition to emerge from brain activity. Considering a cognitive process to be supported by a network rather than an area does not rule out specialization, insofar highly specialized brain areas also constitute networks of neurons. Moreover, it is undeniable that some brain areas are better suited to carry on concrete information more than others, given their biochemical features or topological organization (Sutterer and Tranel, 2017). Likewise, the different communities composing a large-scale network supporting a complex cognitive process can in turn perform suboperations, therefore exhibiting some degree of specialization within a larger system (Sporns, 2007). Therefore, while specialization does take place to different extents with certain brain areas accounting for some fundamental operations, some higher-order processes emerge from the connectivity dynamics of a given network. In some cases, these network dynamics consist in putting together suboperations carried out by fundamental communities. In some other cases, however, these operations emerge from widespread interactions (Bassett and Sporns, 2017).

This theoretical framework has motivated broader interpretative efforts of whole-brain neuroimaging data, as well as it has posed the inception of novel analysis techniques that quantify connectivity between different brain areas and network dynamics as associated with tasks or states. These range from *structural connectivity* measures (i.e. whether physical connections exist between areas and the strength and directionality of such connections), *functional connectivity* measures (i.e. the extent to which two or more areas co-activate during a task or state) to *effective connectivity measures* (i.e. the causal influences and timing of an area on other areas during a task or state; Park and Friston, 2013). In addition, network science has offered a new window to study not only the links and the nodes of composing brain networks, but also their behavior and topology (Rubinov and Sporns, 2010).

To date, functional connectivity has been the most studied brain network phenomenon in fMRI designs. Functional connectivity is usually operationalized as statistical relationships between activity in different brain areas during a task or state (Park and Friston, 2013). While this type of connectivity does not convey information about the physical pathways that connect different nodes nor about the influence nodes exert on each other, it conveys important information about what nodes are jointly involved during a cognitive process of interest and how this network behaves. Furthermore, effective connectivity has proved to be challenging to elucidate from fMRI data given the difficulty of inferring causality in data with strong temporal smoothing (Park and Friston, 2013).

Popular procedures to study functional connectivity include covariance metrics where the co-dependency between two different brain areas is computed over the time and/or trials of a task or state (e.g. correlation, K. J. Friston, 1994); and mass-univariate psychophysiological interactions (PPI), where the relationship between two different brain areas is modeled as being moderated by a task condition, stimulus or behavioral variable (K. J. Friston et al., 1997). More recently, multivariate techniques have been developed in order to capture dependencies between brain areas that go beyond the bivariate case, resulting in estimations of overall network activity. This is the case of blind source separation methods, such as independent components analysis (ICA), which find the underlying spatial-temporal patterns that characterize the engagement of the different networks present in an fMRI dataset (Mckeown et al., 1998). Functional connectivity measures, however, are not exempt of limitations. Given their mere correlational nature, causal inferences drawn from functional connectivity results alone can only be tentative (Sporns, 2007). However, as we will see in the following section, these methodologies have contributed enormously to the understanding of the neural substrates underlying music perception and liking.

1.3.2 From perception to pleasure in music: a network approach

Music perception and music evoked pleasantness are very good examples of how a complex psychological phenomenon emerges from the coordination between different brain areas and circuits. Auditory sensation begins in the outer ear, where sound waves are funneled toward the *eardrum*, a sensitive membrane that shapes the amplitude of the incoming frequencies. These filtered waves are amplified by three bones in the middle ear (*malleus, incus and stapes*) and transmitted to the inner ear's *cochlea* (Koelsch, 2013). In the cochlea, inner fluids oscillate in response to pressure changes caused by the vibration of these bones. The changes in fluid dynamics are ultimately captured by the *hair cells* located in the *organ of Corti*, a structure that traverses the cochlea. When stimulated, these cells excite the *auditory nerve* causing action potentials (Koelsch, 2013).

The frequency, duration and intensity (i.e. number of contributing neurons) of this firing results in the encoding of sound waves into information. This information is carried through the auditory nerve into the *brainstem*, where information from both ears is integrated. This integration is not only important for the ulterior information processing carried by the brain, but also to encode information about the localization of the sound. This is achieved by sending connections both contralaterally and ipsilaterally, which meet in the *olivary nuclei*, where phase and intensity differences are computed (Koelsch, 2013). This information is carried through the *inferior colliculus* to the *medial geniculate body* of the *thalamus* (both integrative hubs for multimodal perception and fast-responding behavior), which in turn project to the ipsilateral *primary auditory cortex* (Koelsch, 2013).

In turn, the primary auditory cortex is part of the *superior temporal gyrus* (STG) and is surrounded by *belt* and *parabelt* areas, which compose the *auditory associative cortex*. It is in these two interlaced structures where the fundamental auditory information is decoded into acoustic features and percepts. In addition, basic cognitive processing of this information already takes place within this anatomic formation. Auditory short-term memory, multimodal perception integration and fundamental sound-to-sound associations engage the auditory cortex. While no absolute hemispheric specialization takes place, there is evidence for some functional dominances. The left auditory cortex has been observed to be better at processing temporal information, while the right auditory cortex seems to be better in the processing of frequency information and chunking percepts (Koelsch, 2013).

These auditory processing areas project ventral and dorsal streams toward frontal areas through the temporal and parietal lobes, respectively. This target areas, in turn, project back to the seed auditory regions, constituting functional loops (Zatorre and Salimpoor, 2013). Through the dorsal loop, the auditory cortex interacts with *premotor* and *dorsolateral frontal cortices*, while the ventral loop connects the auditory cortex with the *inferior frontal cortex* (Figure 1.5). These loops are particularly important for supporting auditory working memory. Auditory working memory allows the maintenance and association of auditory information for longer periods than those possible in auditory short-term memory (Zatorre and Salimpoor, 2013). Evidence suggest that the ventral loop represents feature information, while the dorsal loop represents timing information, in other words, the “what” and “when” of long auditory sequences (Zatorre and Salimpoor, 2013).

Thanks to this network, auditory patterns that go beyond single percepts can be identified. Another function enabled by these loops is that auditory long-term memory can be retrieved and coexist along incoming information (Barton and Brewer, 2019). These are the reasons music can be perceived as such: a coherent palette of sounds where both detected and learned relations between different frequencies and intensities are organized over time and frequency space resulting in melodies, harmony, groove, textures and dynamics (Zatorre and Salimpoor, 2013). This buffer also facilitates future percepts to be processed and integrated. Through feedback connections, frontal nodes also exert top-down influence on the auditory cortex by transferring the worked-up information, constituting the neural basis for auditory expectancy (Zatorre and Salimpoor, 2013).

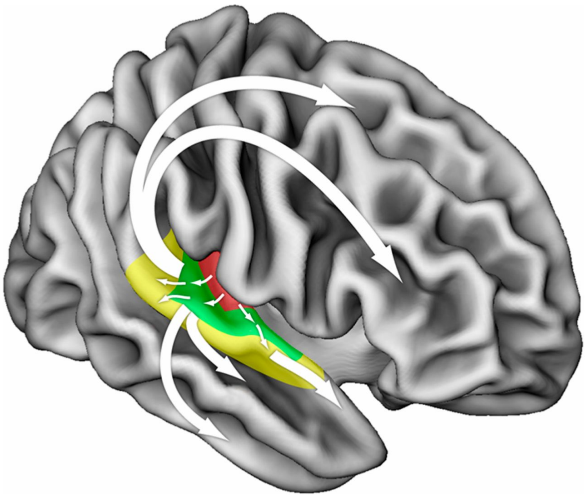


Figure 1.5 Fronto-temporal auditory streams. These loops are important in supporting auditory working memory, with the ventral loop representing “what” information and the dorsal loop representing “when” information. Adapted from Zatorre and Salimpoor (2013).

This ability to form expectancy within the auditory system generates a constant flow of top-down predictions about upcoming acoustic stimuli. These predictions have the belt and parabelt areas of the auditory cortex as target, which in turn receive feedforward inputs from the primary auditory cortex through the ventral pathway (Zatorre and Salimpoor, 2013). On the other hand, mismatches between top-down predictions and bottom-up percepts are believed to be encoded in the same pathway following similar dynamics in the opposite direction. This bottom-up PE signals would inform the frontal nodes of the loop about violations in order to update the online, more abstract representations being held in working memory (Schönwiesner et al., 2007; Zatorre and Salimpoor, 2013).

All these computations must be ultimately exchanged with the *mesolimbic reward system* in order to become a source of pleasure. The temporal cortex, however, does not share direct connections with the subcortical *basal ganglia*. It is through the frontal cortices belonging to the music perception network depicted above that auditory percepts and musical computations reach the reward system, possibly via the *orbitofrontal cortex* (OFC) and the *dorsolateral prefrontal cortex* (dlPFC), structures thought to integrate cortical and subcortical information (Haber., 2011; Jarbo and Verstynen, 2015). An important part of this network is the *striatum*, a nucleus located in the basal ganglia. This structure also receives dopaminergic inputs from the *substantia nigra/ventral tagmental area* (SN/VTA; Bolam et al., 2009) and has consistently been shown to respond to musical rewards (Salimpoor et al., 2015). When musical information transmitted from the *prefrontal cortex* (PFC) constitutes the anticipation or realization of a reward, dopamine is released in the striatum (dorsally and ventrally, respectively), correlating with responses constitutive of liking, wanting and learning (Salimpoor et al., 2011; Gold et al., 2013; Salimpoor et al., 2015; Hansen et al., 2017; Figure 1.6).

Indeed, several studies have shown that the auditory cortex, the PFC and the striatum form a functional complex during pleasant music listening. In a now seminal study, Blood and Zatorre (2001) showed that when participants reported experiencing pleasure while listening to music, not only activity in the striatum emerged, but was also accompanied by activity in the OFC and the *medial prefrontal cortex* (mPFC). Since,

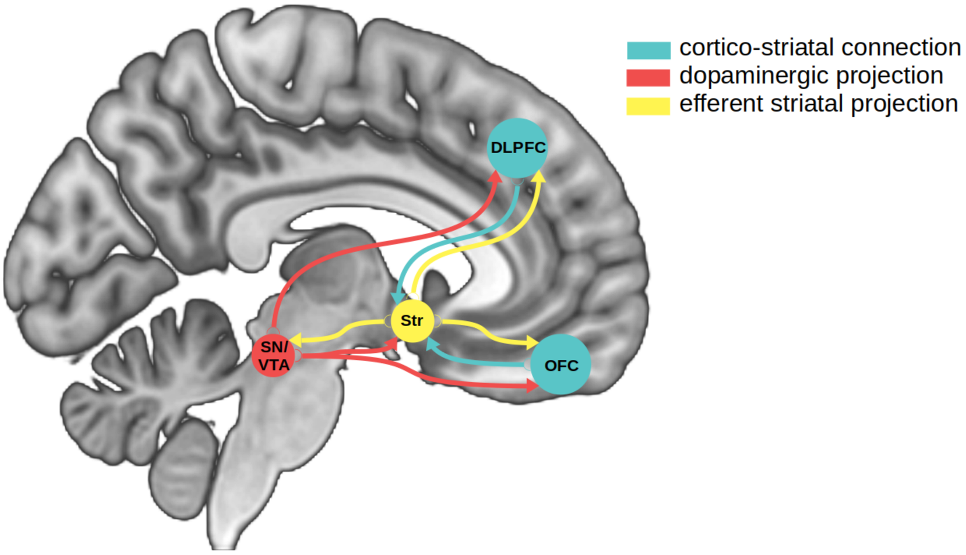


Figure 1.6 The meso-limbic reward network. The prefrontal cortex shares connections with the striatum (Str) via the orbitofrontal cortex (OFC) and the dorsolateral prefrontal cortex (dlPFC). Reward signals are encoded through dopamine release in the Str from substantia nigra/ventral tagmental area (SN/VTA) projections.

other studies have extended this music-reward network to include superior temporal and inferior frontal cortices, indicating that music perception areas are functionally intertwined with those related to reward processing (e.g. in Brown et al., 2004; Menon and Levitin, 2005; Koelsch et al., 2006). Functional connectivity between these structures has also been demonstrated in relation to music-evoked pleasantness. Salimpoor et al. (2013) showed that prefrontal and temporal cortices exhibit greater functional connectivity with the *nucleus accumbens* (NAcc; a key structure of the striatum) as a function of musical value, operationalized as monetary utility. Ultimately, music-related activity in the striatum and its associated hedonic value have been attributed to the expectancy dynamics happening within auditory working memory (Zatorre and Salimpoor, 2013). The dorsal and ventral striatum have been shown to engage during the anticipation and realization of rewards, respectively (Salimpoor et al., 2011), with these signals being intimately related to predictive certainty, PE and the interaction between the two (Gold, Mas-Herrero, et al., 2019; Cheung et al., 2019; Shany et al., 2019). Finally, individual differences in music-reward sensitivity have been linked to the strength of both functional and structural connectivity (via OFC) between auditory processing areas and the NAcc (Martínez-Molina et al., 2016; Martínez-Molina et al., 2019), providing ground evidence for the idea that the auditory and associative cortices constitute a dedicated network along the brain reward system in response to pleasurable music.

Note, however, that most of the evidence explained above comes from studies that did not tackle familiarity directly. As stated above, in addition to schematic knowledge, music evoked pleasantness as a function of expectancy has also been hypothesized to emerge from veridical knowledge. The neural correlates of this phenomenon have not been extensively investigated, but some evidence exists supporting the idea that liking for familiar music involves overlapping nodes with the music-network depicted above, while other structures appear to be uniquely involved. It has been shown that frontal nodes are also involved during familiar music listening (Freitas et al., 2018). In addition, the left *inferior parietal cortex* (IPC) appears to be engaged as a function of familiarity with music (Green et al., 2012; Figure 1.7), a network attributed to recollection and memory retrieval of veridical knowledge (Vilberg and Rugg, 2008; Ciaramelli et al., 2008). Another topic that has not been extensively explored is what neural mechanisms might be underlying the functional networks found in these imaging studies. Brain connectivity must take place by neural binding mechanisms, most likely neural oscillations -a topic to which we shall return later. However, the physiological processes captured by functional imaging are limited in inferring fine grained neural activity, as we will see in the next section.

1.3.3 Caveats of neuroimaging to study network dynamics in music cognition

Functional neuroimaging has contributed to understanding the complex network depicted above to a great extent of detail. Whole brain analyses as well as functional and structural connectivity studies have revealed the network patterns underlying music perception and music-evoked pleasantness. This has been demonstrated using a variety of behavioral methods and designs, such as self-reported pleasantness ratings, expressed value or individual differences in music reward sensitivity (e.g. Salimpoor

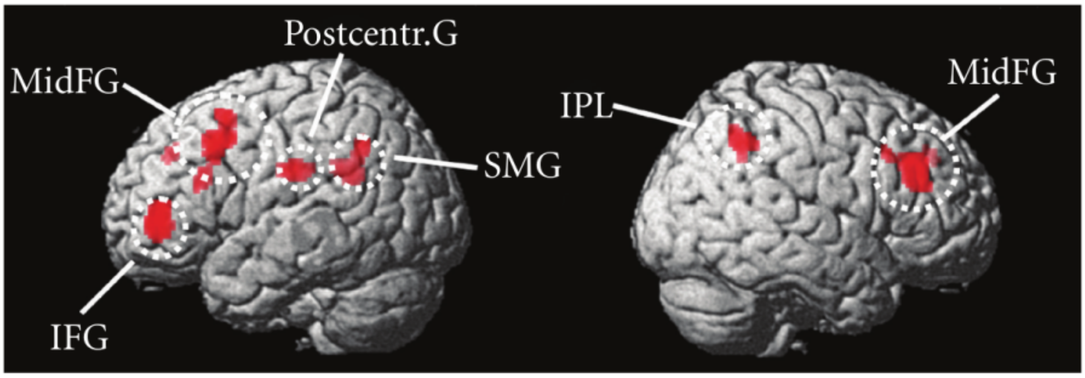


Figure 1.7 Familiar music-listening network. In addition to frontal areas, the left inferior parietal cortex is involved. Adapted from Green et al. (2012). IFG: inferior frontal gyrus; IPL: inferior parietal lobe; MidFG: middle frontal gyrus; Postcentr. G: postcentral gyrus; SMG: supramarginal gyrus.

et al., 2011; Salimpoor et al., 2013; Martínez-Molina et al., 2019). In addition, computational modeling of musical expectancy has been used to elucidate whether music reward encoded in this brain network is indeed related to predictive processes (Gold, Mas-Herrero, et al., 2019; Cheung et al., 2019; Shany et al., 2019). Furthermore, and from a different optic, the neuroimaging study of music cognition has contributed to understanding brain function because of the ideal window it offers to study complex cognition, insofar it constitutes the integration of different cognitive phenomena (Koelsch et al., 2013).

However, while fMRI offers great spatial resolution to identify areas and networks, its temporal resolution is rather poor. It can be argued that this is due to fMRI's low sampling rate. Indeed, in order to provide high-resolution imaging, scanners must be set to acquire samples at a rather slow acquisition time. On the other hand, lowering the acquisition time closer to the scanner's limit comes at the expense of undermining its spatial resolution (Bandettini, 2002). In theory, higher sampling rates are possible when focusing on regions of interest rather than whole brain imaging (Posse et al., 2012). Using stronger magnetic fields (e.g. 7-tesla) also helps ameliorating the compromise between spatial and temporal resolution at higher sampling rates (Thanh Vu et al., 2017). However, none of this solves the fact that the acquired brain signal in fMRI studies is also of rather slow response. As opposed to neurophysiological techniques, fMRI does not measure the brain electric activity directly. Instead, it measures the *blood oxygenation level dependent* (BOLD) response that precedes neural activity. In other words, fMRI uses the blood that neurons need to draw upon firing as a proxy of neural activity. Since oxygenated blood has a different magnetic behavior than deoxygenated blood, the scanner can detect changes in the oxygen carried by blood. From this proxy we can infer brain activity by the assumption that the presence of more oxygenated blood in a particular brain area or network means that those neural populations are firing more. Since fMRI measures blood dependent activity, however, the signals it captures follow a *hemodynamic response function* (HRF), which is characterized by a rather long fluctuation, in the order of seconds (Bandettini, 2002).

This slow hemodynamic response makes it difficult to discern faster brain activity fluctuations. This problem would persist even with high sampling rates, since only more samples defining the HRF would be acquired. As a result, not only faster fluctuations cannot be studied, but neither the neural mechanisms underlying brain connectivity, since it can only be inferred statistically. This limitation, therefore, prevents the study of finer-grained temporal dynamics in fMRI studies. This is particularly critical for the study of music cognition and its neural correlates for two reasons. First, the complex brain network engaged during music perception and music reward processing must pose a rich functional interplay characterized by equally rich timing and oscillatory dynamics. Second, any attempt to relate musical features to brain activity must be able to follow music's timing and frequency information, when pertinent.

In constrast to fMRI, non-invasive neurophysiological techniques such as *electroencephalography* (EEG) are adequate to study neural signals at a high temporal resolution, at the expense of a poor spatial resolution. Thus, in order to understand not only what networks underlie cognition, but also how brain activity takes place, multimodal approaches that combine multiple data sources must be addressed. One promising multimodal approach is simultaneous EEG-fMRI recordings. This technique allows researchers to acquire both fMRI and EEG signals simultaneously while human subjects perform a task. Subsequently, a variety of signal processing routines and statistical analysis can be carried out in order to combine all data sources to elucidate both the spatial distribution and its temporal dynamics underlying a cognitive phenomenon of interest.

1.4 Oscillatory dynamics of music-evoked pleasantness and related constructs

The rich functional interplay underlying music perception and its hedonic impact explained in previous sections must take on different mechanics to take place. It is now clear that brain function is not reduced to activity in a single area. Likewise, brain activity is not reduced to mere co-activations. Rather, the brain utilizes different mechanisms so that neurons, or neural populations in a broader sense, can communicate a diverse corpus of information. This information transfer can be unimodal or multimodal, sequential or in parallel, and unidirectional or multidirectional. In short, brain connectivity needs a means of communication that enables all these dynamics efficiently over time and space. The brain achieves this endeavor by exploiting the electrical nature of neural activity, encoding and decoding information via multiband oscillations.

In this last section the oscillatory markers of music evoked pleasantness and related constructs and processes will be reviewed. First, a summary of what neural oscillations consist in and what brain mechanics they have been hypothesized to support will be addressed. Second, the neurophysiological literature studying music-evoked pleasantness and related concepts such as consonance and emotional valence will be reviewed. Finally, it will be discussed how evidence about the oscillatory dynamics underlying familiarity and expectancy might elucidate the precise mechanics behind the neurophysiological markers of music evoked pleasantness. This last point will be put in perspective along evidence from fMRI studies as well.

1.4.1 Brain oscillations as means of information transfer

Neurons respond to stimuli and other neurons, on the one hand, and exert influence on other neurons, physiological processes and behavior, on the other hand. In a simple description, they can be considered as active nodes that receive input from other nodes and send output to other ones. When a target neuron receives input from an *excitatory neuron*, the target neuron *depolarizes*, making it more likely to reach the threshold above which neurons fire. When this threshold is reached, a burst of electrical activity called *action potential* happens within the neuron and is propagated through its output connections. Conversely, when a target neuron receives input from an *inhibitory neuron*, the target neuron *hyperpolarizes*, making it less likely to reach the threshold that the neuron needs to cross in order to fire (Cohen, 2014).

Regardless of the influence that neurons exert on each other, their activity is expressed as electric signals. Single cells ensemble into neural populations, which are characterized by proximal neurons behaving synchronously in response to the same inputs. The summation of the activity in a neural population, be it excitatory or inhibitory, can be observed as an overall *field potential*. The alternating interactions between excitatory and inhibitory neural populations results in rhythmic electrical fluctuations that are sustained over some period of time. These rhythms are what we call brain oscillations. Neural oscillations can be observed as locked to a stimulus, action or operation. They can also be observed as related to a stimulus, action or operation, though not locked to it, or simply during resting state (Cohen, 2014).

In human neuroscience, brain oscillations have been classically associated with cognition. Using EEG or *magnetoencephalography* (MEG), researchers have revealed meaningful neural markers and dynamics of a variety of cognitive processes, otherwise hidden to observation. Whether these markers are what cause cognition, or whether these are epiphenomena contingent to the true underlying causes of cognition is still a matter of debate (Cohen, 2014). However, many authors advocate for understanding brain oscillations as a means of information transfer between neurons. From this theoretical standpoint, neurons from the same or different neural populations would synchronize through the same rhythms in order to establish efficient communication channels (Singer, 1993; Buzsáki and Draguhn, 2004; Fries, 2005; Akam and Kullmann, 2012).

Neural oscillations accomplish several functions. One function this mechanism supports is *input responsivity*. Different neural populations respond differently to different frequency inputs. Thanks to this frequency specialization, both sensory and other neural events can be processed selectively with high resolution. Two other important functions of neural oscillations, crucial for network dynamics to take place, are *neural binding* and *representation*. By synchronizing through the same frequencies, different neural populations bind together forming functional ensembles. In turn, neural ensembles encode and decode sensory and cognitive information using rhythms as representational code. Finally, neural oscillations also serve the purpose of "rehearsing" learned neural contingencies during resting states (Buzsáki and Draguhn, 2004).

Brain oscillations exhibit particular properties due to the physical, biological and chemical constrains of neurons. For example, neighboring frequencies (i.e. close in frequency space) and harmonic frequencies (i.e. integer multiples) are more likely to resonate with each other than far-apart frequencies (Buzsáki and Draguhn, 2004). This property organizes rhythms into *frequency bands* that capture different brain states. The canonical frequency bands are *delta* (1-3 Hz), *theta* (4-8 Hz), *alpha* (8-12 Hz), *beta* (13-25 Hz) and *gamma* (26-80 Hz), although frequency ranges and sub-bands slightly differ depending on the consulted classification work (Cohen, 2014; Buzsáki and Draguhn, 2004). This frequency organization facilitates alternation between states, with adjacent bands being functionally at odds; as well as multiband coding, with non-adjacent bands interacting together for multimodal, parallel information processing (Buzsáki and Draguhn, 2004).

Another property of neural oscillation is that their amplitude follows a *1/f* law, this is, that slower rhythms are more prominent than faster rhythms (Buzsáki and Draguhn, 2004). This property allows a hierarchical organization of neural activity, with slower rhythms orchestrating faster rhythms. Moreover, slower rhythms are characteristic of more distant connectivity patterns, while the opposite is true for faster rhythms. This is a result of the physical constrains posed by the brain circuitry. Far-off connections are characterized by longer paths, resulting in longer transmission times. Consequently, oscillatory cycles take longer to complete. Therefore, global and distal connectivity is more likely characterized by slow oscillations, while local connectivity between close areas or between neurons of the same population is more likely to take place via faster rhythms (Buzsáki and Draguhn, 2004).

Signal processing of EEG or MEG signals, among other neurophysiological techniques, offers a vast window to study brain oscillations and their relationship with cognition. Three main approaches have been taken to study neural rhythms in cognitive neuroscience: *time-domain analysis*, *frequency-domain analysis* and *time-frequency domain analysis*. Time-domain analysis focuses on the amplitude fluctuations of a signal in relation to a stimuli or operation and is concerned about the precise timing of brain processes. Frequency-domain analysis, on the other hand, focuses on how rhythmic information in the brain is characterized in a particular period. Finally, time-frequency analysis compromises the two approaches to approximate the timing of frequency information fluctuations in the brain (Cohen, 2014).

Furthermore, the last two approaches (frequency and time-frequency analysis) can focus on two different aspects of rhythms: *Power* amplitude and *phase* information. Power amplitude quantifies the presence of rhythmicity in a particular frequency present in a signal. In turn, phase information is important to understand the state of the oscillatory cycles of a rhythm present in a signal. Knowing the oscillatory cycles of different frequencies is crucial to infer how different brain areas synchronize: if the relationship between cycles of a rhythm in two different brain signals is kept coherent over time and/or over trials, it can be assumed that the source areas of those signals are synchronized (Cohen, 2014). This makes the study of *phase synchronization* a powerful tool to investigate the functional connectivity underlying cognition and its oscillatory dynamics.

1.4.2 Oscillatory dynamics of expectancy in the auditory domain

Before reviewing the existing literature tackling the oscillatory correlates of musical liking it is worth reviewing those underlying the cognitive processes hypothesized to precede it. This includes working memory and expectancy dynamics in the auditory domain. Discussing these processes will help us understand candidate dynamics that could explain how the different brain areas involved in music perception communicate. Moreover, understanding these correlates will be useful for interpreting results from experiments directly investigating the relationship between neural oscillations and music-evoked pleasantness in further sections.

The functional interplay between temporal and frontal nodes that encodes and maintains working memory in the auditory domain has been revealed to work most efficiently by synchronizing these loops through theta rhythms (Kaiser, 2015). This is also true in the musical domain. In a simultaneous EEG, MEG and *transcranial magnetic stimulation* (TMS), Albouy et al. (2017) demonstrated that theta power in the fronto-temporal auditory stream predicts performance in active working memory manipulation. Furthermore, they directly stimulated this pathway and found causal evidence for more efficient rhythmicity in theta supporting better performance during a melodic working memory task, as reflected in both power and phase synchronization between its nodes. As previously mentioned, working memory's ability to buffer information beyond mere storage is what makes musical expectancy and pleasantness possible (Zatorre and Salimpoor, 2013).

Indeed, predictive dynamics have also been associated with fronto-temporal theta connectivity. Recasens et al. (2018) have proved in a MEG study that PEs following violations of acoustic patterns are computed within functional loops involving prefrontal and auditory cortices and the hippocampus through theta rhythms. Furthermore, they inferred directed theta and alpha connectivity from the auditory cortex toward the prefrontal cortex to underlie PE computation, while they also found evidence of directed alpha connectivity from the hippocampus toward the auditory cortex underlying the predictability of sounds (Figure 1.8). Indeed, the hippocampus has been found to help encode regularities and respond to violations in previous research (Barascud et al., 2016). Interestingly, in the reward processing literature frontal theta power has been related to reward PE, this is, to violations of predicted reward outcomes (Mas-Herrero and Marco-Pallarés, 2014; Mas-Herrero and Marco-Pallarés, 2016).

In the musical domain, Omigie et al. (2019) found that computational simulations of unexpectedness (i.e. PE) predicted slow oscillatory activity in the STG and *medial temporal gyrus* (theta, alpha and beta oscillatory bands) in a study using intracranial recordings. Moreover, they found these activations to be accompanied by similar effects in the *anterior cingulate cortex* (ACC) and *insula*, areas classically associated with arousal control, PE computation and reward processing (Critchley et al., 2001). Finally, while they did not find evidence of similar effects in the *inferior frontal gyrus* (IFG), they did report a non-significant trend in these regards. All in all, these results converge with previous and recent evidence from *event-related fields* (ERFs) demonstrating that interactions between the STG, the IFG and the *hippocampus* underlie predictive coding in the auditory and musical domains (Barascud et al., 2016).

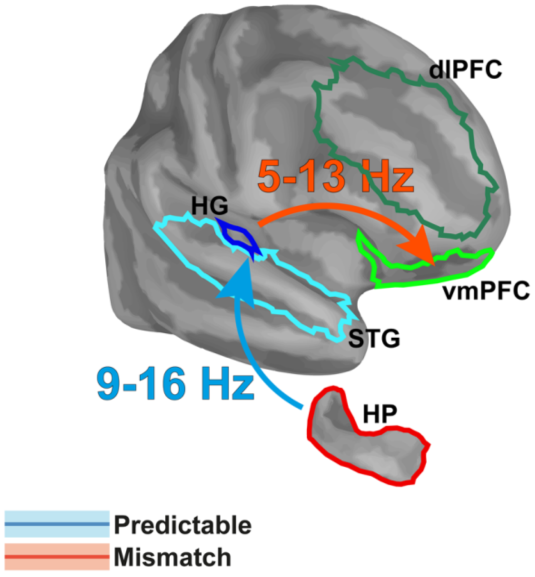


Figure 1.8 Oscillatory dynamics associated with auditory expectancy. Slow (theta-alpha) rhythms originating in the auditory cortex (Heschl's gyrus) toward the prefrontal cortex (ventromedial prefrontal cortex) underlies prediction error computation in the auditory domain. In turn, alpha rhythms originating in the hippocampus toward the auditory cortex correlates with predictability. Adapted from Recasens et al. (2018).

All of the aforementioned literature focuses on expectancy dynamics converging from different sources. However, little is known about potential differences in the oscillatory and anatomic signatures between schematic and veridical expectations, neither it is clear how these differences might relate to the processing of music-evoked pleasantness. As we had seen, familiarity with music seems to engage a slightly different brain network during music listening. It is thus expected that the oscillatory dynamics related to pleasantness bind different nodes when music is familiar as compared to when expectations are predominantly schematic. Nevertheless, no study so far has tasked the oscillatory binding mechanisms of musical familiarity or their relation to those of music reward processing.

1.4.3 Oscillatory dynamics of musical valence, consonance and liking

Despite the great corpus of fMRI research devoted to understanding the brain anatomy and function underlying music-evoked pleasantness, little research has been carried out to understand the brain oscillatory dynamics associated with music's hedonic impact. In fact, most related research has been conducted operationalizing related, but conflated concepts with music reward. The most used dimension has been evoked valence in a circumflex model of emotion. However, this dimension has often been measured without specifying whether it tasked emotional valence (i.e. sign of the emotions felt by the listener) or affect valence (i.e. approach toward music and/or the content it evokes). This makes it difficult to discern or speculate about the precise cognitive and affective processes behind the studied phenomenon.

However, this kind of research is valuable insofar it set out the methododology to study EEG correlates of music-evoked pleasantness, as well as because it provided insightful results that guide future research in the topic. One of the classic oscillatory markers used in the study of evoked emotions is *alpha asymmetry*. This is computed by taking the difference between alpha power from symmetric electrodes, often frontal. Frontal alpha asymmetry has been related to both evoked positive valence and arousal during music listening in several studies (Chabin et al., 2020), as well as in other emotional contexts (Sammler et al., 2007). Some studies suggest that this phenomenon takes place because of a left-hemisphere predominance in the positive valuation of music (Davidson, 1995), as well as a right-hemispheric predominance in alpha suppression, which correlates negatively with arousal (Craig, 2005).

An oscillatory marker that consistently appears associated with evoked valence in the literature is frontal theta power. Several studies have found that the greater evoked valence reported by participants, the greater theta power is expressed over frontal areas of the brain. Lin et al. (2010) found theta power to increase with positive valuation of music over fronto-central areas. This effect was accompanied by a decrease in delta power with reported evoked valence and an increase in both delta and theta with evoked arousal. The positive relationship between frontal theta power and valence, on the one hand, and arousal, on the other hand, has also been observed by Mikutta et al. (2014) and Rogenmoser et al., 2016. It has been proposed that the source of frontal theta power could be reward-related activity in the ACC, a functional node in reward processing and emotional integration (Sammler et al., 2007; Marco-Pallarés et al., 2015).

On the other hand, a handful of studies has determined a priori what music was most likely pleasant or unpleasant based either on validated norms (e.g. Flores-Gutiérrez et al., 2007; Flores-Gutiérrez et al., 2009) or using consonant and dissonant music as proxies for pleasant and unpleasant music as proxies, respectively. In doing so, Sammler et al. (2007) found frontal theta power to correlate with consonant music in an EEG study. In another experiment with epileptic patients where direct intracranial recordings from areas of interest could be acquired, Omigie et al. (2015) found theta, alpha and beta power to increase in the OFC and the auditory cortex with consonant chords as opposed to dissonant chords. Furthermore, they found partial evidence of functional connectivity in all three bands between OFC, the auditory cortex and the amygdala to increase during processing of consonant chords.

The advantage of using predefined pleasant and unpleasant stimuli is that different liking conditions can be predefined experimentally and controlled. The drawback, however, is that individual idiosyncrasies that are difficult to control might arise. After all, music that is pleasant/unpleasant for most people does not necessarily have to be pleasant/unpleasant for all people. Likewise, considering that consonant music must be pleasant and dissonant music unpleasant for every individual regardless of the piece of music is a bold assumption. The concept of consonance and its relation to agreeability has been proven to be highly dependent on culture (McDermott et al., 2016). Even within western culture, many modern music genres with millions of listeners thrive on musical attributes long considered dissonant or discordant to more traditional folk or classical music (e.g. metal music).

For all these reasons, pleasantness self-reports that are dissociated from emotional valence and that are comparable across individuals with different musical preferences should be preferred. Few studies have done so in the EEG literature. Among the few, Nemati et al. (2019) observed that fronto-central theta activity was associated with reported pleasantness (operationalized as affect valance), while parieto-occipital alpha activity was also associated with pleasant music listening in comparison to neutral music listening. In a high-density EEG study, Chabin et al. (2020), found that intense pleasurable events (i.e. *chills*) positively correlated with source-localized OFC theta activity as well as negatively with right central and temporal theta activity.

It is important to note that most of these studies are correlational, that is, offer very little insight regarding the cognitive mechanisms that could explain the relationship between the neural marker and the self-reported data. Nevertheless, the fMRI and EEG literature reviewed in previous sections offer a window for interpretation. Especially noteworthy is the fact that the frontal and temporal neural networks and oscillatory dynamics of working memory and reward processes that explain expectancy dynamics show a great degree of overlap with those identified during pleasant music listening. This theoretical overlap tentatively converges with the previously exposed idea that reward signals elicited by music ultimately emerge from expectancy dynamics generated within auditory working memory loops.

All in all, frequency domain analysis has proved to be adequate to elucidate the neurophysiological correlates of musical liking, since it is well suited to study oscillatory dynamics sustained over long periods of time, as opposed to *event-related potentials* (ERPs) or time-frequency domain analysis, which are more suited to study time-locked or event-locked responses. Most of the reviewed literature has focused on the power amplitude dimension of brain oscillations, perhaps obeying the interest of identifying what oscillatory rhythms characterize the phenomenon and their spatial distribution. However, in order to study whether the rhythms associated with music-evoked pleasantness are indeed a binding mechanism between the different brain areas involved, synchronization between their different signals must be investigated. Likewise, multimodal studies are needed in order to empirically link these rhythms to the brain networks typically identified in fMRI studies underlying music perception and reward. Nevertheless, no phase synchronization study has been conducted in recent years regarding evoked pleasantness nor its underlying anatomic network. Finally, and as already stated in the previous section, the oscillatory dynamics underlying liking for familiar music have not been investigated to date, despite proving to be an important variable directly interacting with music's hedonic impact.

2. Research Objectives

In the previous pages the known-to-date psychological and neural aspects underlying music evoked pleasantness have been introduced. From models of emotion, reward processing and predictive coding to anatomical, functional and network brain science, the most influential theoretical accounts and neuroscientific evidence explaining how music's hedonic impact is processed in the brain have been reviewed, as well as the role of familiarity in modulating these neuropsychological phenomena. Nevertheless, it has also been conveyed how little we know about the oscillatory dynamics underlying this functional interplay, with a few exceptions pinpointing theta oscillations as rhythmic correlates of musical liking and related constructs. Therefore, the aim of this thesis is to study the role of theta rhythms in the synchronization of the brain areas underlying musical pleasure and how familiarity might modulate this phenomenon. This main goal can be subdivided in three subgoals:

2.1 Identifying what functional nodes theta rhythms synchronize during pleasant music listening

Most previous research tackling the neural correlates of music-evoked pleasantness has been conducted with functional neuroimaging methods. Thanks to this literature we know that frontal and temporal areas involved in music perception also play an active role in music reward processing in addition to the reward system (Zatorre and Salimpoor, 2013). Nonetheless, while this corpus of evidence has revealed the anatomical characteristics underlying this network with great spatial resolution, the temporal dynamics operating over these brain interactions are just beginning to be understood. Frontal theta power has been observed to increase while listening to positively valenced music (Lin et al., 2010; Mikutta et al., 2014; Rogenmoser et al., 2016), pleasant music (Nemati et al., 2019; Chabin et al., 2020) and consonant music (Sammler et al., 2007; Omigie et al., 2015). It is unclear, however, whether theta rhythms serve the purpose of binding the nodes relevant for musical liking to take place.

The aim of study 1 was to identify the functional nodes that theta rhythms synchronize during pleasant music listening. To this end, we exposed a cohort of participants to a series of musical stimuli and required them to evaluate the degree of evoked pleasantness experienced while listening to the music. During the task, EEG signals were acquired. We hypothesized that there would be a relation between theta synchronization and liking, supporting the critical role of this mechanism in the process of assigning value to music. For each musical excerpt we computed the average pleasantness rating and an index of phase synchronization between all theta signal pairs over the corresponding time window. We then regressed theta synchronization in every connection on reported pleasantness in order to pinpoint what functional pairs significantly changed their degree of theta synchronization as a function of liking.

2.2 Understanding the neural networks underlying theta synchronization during pleasant music listening

Functional neuroimaging has revealed that music perception is characterized by a brain network involving portions of the temporal lobe, such as the STF, and of the PFC, such as the IFG. This network, in turn, interacts with the brain reward system when music is found pleasurable (Salimpoor et al., 2015). On the other hand, theta rhythms have been associated with the cognitive processes thought necessary for music-evoked pleasantness to take place, such as auditory predictive coding and working memory (Kaiser, 2015; Recasens et al., 2018; Albouy et al., 2017; Zatorre and Salimpoor, 2013). It can thus be hypothesized that the fronto-temporal loops in this music network bind via theta rhythms in order to process the information that is utterly relevant in finding music pleasurable. Nevertheless, whether the anatomic interactions and the theta rhythms that have been associated with musical liking are indeed intertwined has not been tested empirically to date.

The aim of study 2 was to understand how theta rhythms are related to music-related functional anatomy during pleasant music listening. The procedure was nearly identical to that of study 1, only this time both fMRI and EEG signals were acquired simultaneously. We hypothesized that the self-reported pleasantness ratings would moderate the relationship between music-related fMRI activity and fronto-temporal theta synchronization, providing evidence for the idea that all three phenomena are indeed intertwined. In order to test this hypothesis we extracted the activity of a music network engaged during the experiment as well as EEG theta synchronization signals. We then studied whether the pleasantness ratings significantly modulated the relationship between music-related fMRI activity and theta synchronization between the EEG nodes.

2.3 Studying how familiarity modulates theta synchronization during pleasant music listening

Familiarity and expectancy have been some of the most researched factors moderating music-evoked pleasantness. In its simple experimental form, it has been observed that the mere exposure effect results in an increase in evoked pleasantness by familiar music as compared to unfamiliar one. This suggests that when veridical knowledge comes into play, in addition to schematic knowledge, the processes that link music perception with pleasantness are enhanced. Evidence revealing the network mechanics behind this phenomenon, however, is scarce. In addition to prefrontal areas, parietal activity has been observed to underlie pleasantness evoked by familiar music (Green et al., 2012). Nevertheless, whether theta rhythms also play a part in assembling this network is unclear.

The aim of study 3 was to study the relationship between theta synchronization and the mere exposure effect on music-evoked pleasantness. In this study we exposed a cohort of participants to a series of musical stimuli and registered their self-reported pleasantness and EEG activity 24 hours later while listening to this same music plus a new set of unfamiliar stimuli. We hypothesized that familiarity with music would moderate the relationship between liking and theta synchronization, with different connections synchronizing differently depending on whether music was familiar or unfamiliar. In order to test this hypothesis, we computed the average liking rating for each music stimulus as well as theta synchronization between EEG signals. We then run moderation analyses in order to explore what theta connections significantly exhibited different dynamics as a function of pleasantness in the two familiarity conditions.

3. Results

Fronto-temporal theta phase-synchronization underlies music-evoked pleasantness

3.1 Study 1[1]

3.1.1 Abstract

Listening to pleasant music engages a complex distributed network including pivotal areas for auditory, reward, emotional and memory processing. On the other hand, frontal theta rhythms appear to be relevant in the process of giving value to music. However, it is not clear to which extent this oscillatory mechanism underlies the brain interactions that characterize music-evoked pleasantness and its related processes. The goal of the present experiment was to study brain synchronization in this oscillatory band as a function of music-evoked pleasantness. EEG was recorded from 25 healthy subjects while they were listening to music and rating the experienced degree of induced pleasantness. By using a multilevel Bayesian approach we found that phase synchronization in the theta band between right temporal and frontal signals increased with the degree of pleasure experienced by participants. These results show that theta fronto-temporal synchronization plays a key role in music-evoked pleasantness.

3.1.2 Introduction

Listening to music is a powerful source of pleasure for most human beings. This pleasurable experience is often associated with the activation of areas of the brain reward network (Blood and Zatorre, 2001), via dopaminergic activation of the dorsal and ventral striatum in the anticipation and realization of peak pleasurable musical events, respectively (Salimpoor et al., 2011). However, music-evoked pleasantness is not only explained by reward-related striatal activation, but engages a broader neural network,

---

[1] This study has been published in Ara, A., & Marco-Pallarés, J. (2020). Fronto-temporal theta phase-synchronization underlies music-evoked pleasantness. *NeuroImage*, 212. Text, tables and figures are a reproduction of the article.

including perceptual, associative and emotional areas. Indeed, the temporal lobe is crucial in the processing of auditory inputs (Koelsch, 2014) and previous studies have found that the functional interaction of this area and the ventral striatum is pivotal in giving value to musical stimuli (Salimpoor et al., 2013) and in the pleasurable experience of listening to music (Martínez-Molina et al., 2016). In addition, the PFC also plays a role in this mechanism. The *ventromedial prefrontal cortex* (vmPFC), OFC and IFG have all been related to the processing of pleasant music listening (Blood and Zatorre, 2001; Brown et al., 2004; Menon and Levitin, 2005; Koelsch et al., 2006). It has also been found that people experiencing frissons with music present higher structural connectivity between the posterior portion of the *supratemporal gyrus* (suTG) and mPFC than those people that do not experience them (Sachs et al., 2016). Furthermore, a recent study has linked the structural connectivity between the *supratemporal cortex* and the OFC, as well as between the OFC and the ventral striatum, with individual differences in music-evoked pleasantness sensitivity and the activation of the NAcc in response to pleasant music (Martínez-Molina et al., 2016). Limbic structures such as the amygdala, the hippocampus and the insula also appear to be involved in the processing of music-evoked pleasantness (Blood and Zatorre, 2001; Koelsch et al., 2006).

Within the broader topic of music-evoked emotions, it has been revealed that more complex psychological states and their associated brain correlates underlie pleasurable reactions to music. Familiarity, high emotional valence, as well as domain-specific emotions such as wonder and joy all appear to be related to activity in the striatum, although each construct relates to slightly different cortical and limbic structures, such as the OFC, the insula or the amygdala (Trost et al., 2012). The specific acoustic features and time-courses of music appear to be important in music-evoked emotions as well. Tightly related constructs to pleasantness, such as evoked valence or dissonance, correlate with the activity of the amygdala and the NAcc (Trost et al., 2014). Noteworthy is the proposal by Trost and Frühholz (2015) on the role of the temporal-limbic system, which includes the amygdala and the hippocampus, in orchestrating affective responses to music along personal preferences, memory associations and aesthetic evaluations.

The coordination of such distant brain areas involves a complex interplay of brain interactions. In order to coordinate all these distant structures the brain needs a mechanism to couple their respective activities efficiently. Neural oscillations have been proposed to fulfill such task (Buzsáki and Draguhn, 2004). By synchronizing to the same inputs, different brain areas are able to oscillate in one or several frequency ranges, thus facilitating coordination among those areas supporting a particular function. Allegedly, it has been proposed that slow rhythms would be a neural marker of more distant brain interactions, whilst faster rhythms would imply more local synchronization due to the natural constrains posed by structural connections (Buzsáki and Draguhn, 2004).

Despite the growing body of literature unraveling the anatomic interactions supporting music-evoked pleasantness, little is known about the oscillatory dynamics underlying these functional networks, and the consistence among the different results is limited. Among the few, Sammler et al. (2007) observed an increase in frontal theta power during consonant music listening as opposed to dissonant music in an EEG study. Other studies have consistently reported a positive relationship between theta power and positive valence (Lin et al., 2010; Mikutta et al., 2014; Rogenmoser et al., 2016). In addition, Omigie et al. (2015) found consonant chords to be related to greater power in the theta-alpha-low beta range in intracranial electrodes placed over the OFC. Both consonance and evoked valence were considered to be related to pleasantness by the respective authors.

In the present experiment we sought to study the oscillatory dynamics of the brain interactions underlying music-evoked pleasantness using EEG. To this purpose, we measured phase-synchronization between EEG signals. Many different indexes are available to study phase-synchronization in EEG research, all presenting advantages and disadvantages (Bastos and Schoffelen, 2016). We chose the inter-site phase clustering (also known as phase locking value in the literature) for being easily computed over time and maximally sensitive to phase synchronization (Cohen, 2014). We focused on the theta oscillatory band since it has previously been associated with music-evoked pleasantness in the power domain (Sammler et al., 2007; Rogenmoser et al., 2016; Lin et al., 2010; Omigie et al., 2015), and because given the far-off anatomic landmarks of music-evoked pleasantness, we assume that slow rhythms would be the ideal communication mechanism of such segregated network (Buzsáki and Draguhn, 2004). Previous studies have addressed the oscillatory dynamics of EEG when listening to music by computing the oscillatory power of different frequency bands over time in relation to musical and emotion attributes (Jäncke et al., 2015). Nevertheless, we consider the study of phase-synchronization appropriate in the context of the current experiment given our assumptions regarding neural rhythms and anatomic interactions.

In order to analyze the data, we propose a multilevel Bayesian approach to overcome the statistical challenges of the study of the brain synchronization using EEG, in particular dealing with non-normal multilevel-structured data and multiple testing. In experimental paradigms where each participant is exposed to and responds to different stimuli there are usually two levels of inference, at the individual and the group level. Doing the analysis separately or computing summary statistics for each participant may result in information loss (Bryk and Raudenbush, 1988). Multilevel modeling tackles this by estimating effects at all levels of inference, where individual effects inform group level effects and vice-versa (Baayen et al., 2008). In addition, different response distributions can easily be implemented in this modeling framework, which allows for more appropriate analyses when the data are not normally distributed (Stroup, 2012). Finally, Bayesian inference has gained popularity in this modeling framework, as it allows to quantify epistemic uncertainty and incorporate prior beliefs to the statistical problem at hand (Kruschke, 2015).

Particularly, Bayesian inference is useful in contexts where mass-univariate models must be run, such as in EEG research, because multiple testing does not inherently pose a problem in terms of type-I error inflation. This is the case because the same null hypothesis is not tested several times under the same theoretical distribution, thus inflating the probability of rejecting it by chance. Instead, the likelihood that a parameter of interest is relevant for explaining each data set is explored, with the prior believe that the contrary is more probable, and a decision is made on whether a null effect is excluded from the resulting posterior distributions (Han and Park, 2018). Hypothesis testing thus consists in deciding whether the parameter of interest has an effect in predicting each data set after Bayes' rule is applied, rather than checking several times whether a test statistic is extreme enough under the same theoretical null distribution (Kruschke, 2015). This procedure typically results in more conservative decisions as compared to using uncorrected frequentist thresholds, but less than those yielded by standard p-value corrections (Han and Park, 2018).

Therefore, the goal of the present study was to determine the oscillatory neuronal connectivity underlying the pleasurable experience associated with listening to music. Based on previous literature, we hypothesized that oscillatory activity in the theta band would play a role in this process. In addition, we also introduce a modeling framework to deal with the problems associated with multilevel responses, non-normally distributed data and multiple testing in the study of EEG synchronization.

3.1.3 Materials and methods

Participants

Twenty-five right-handed individuals (M = 22.32 years old, SD = 2.66, 19 women) participated in the experiment. All participants were chosen to roughly have similar music preferences toward indie, pop, electronic and folk music genres as assessed with the Short Test of Music Preferences revised (STOMP-R, Rentfrow and Gosling, 2003; cut-off ≥ 4) as well as similar profiles of music reward and physical anhedonia as assessed with the Barcelona Music Reward Questionnaire (BRMQ, Mas-Herrero et al., 2013, cut-off > 64) and the Physical Anhedonia Scale (PAS, Chapman et al., 1976, males cut-off < 28, females cut-off < 20), respectively. None of the participant had received formal training in music for more than three years. All participants gave written informed consent and were paid 10€ per hour. All procedures were approved by the local ethical committee.

Stimuli

Sixty musical fragments formed a pool of stimuli from which the experimental excerpts were taken. The stimuli consisted in fragments of 45s from commercially available songs of several music genres including indie, pop, electronic, folk and experimental music (see Table 3.1 in the appendix for the complete list of songs). These stimuli were selected to be likely unfamiliar and to elicit variable degrees of pleasantness based on the results of a pilot study with a separate sample of individuals. The 45-s fragments were chosen to be representative of the whole musical pieces (e.g. that they included more than one theme, that variations took place and/or that several instruments were present).

Experimental procedure

Participants listened to 30 music excerpts randomly drawn from the pool of stimuli to avoid effects to be explained by common musical attributes of a fixed set of stimuli across subjects. Participants were asked to rate the degree of evoked pleasantness on a continuous basis while listening to each excerpt with as many responses as they wanted. Responses were given via the numeric keys of a computer keyboard with the following equivalences: 1: 'I don't like it'; 2: 'I like it a little'; 3: 'I like it moderately'; 4: 'I like it a lot'; and 5: 'I experience frissons'. Response keys had to be held for as long as a particular rating applied for the individual. Participants had to look to a fixation cross during the course of the excerpts. If no response was given after half the stimulus was presented, that trial was halted and automatically rejected. After each excerpt had finished participants responded to a series of 7-point Likert scales: the overall liking for the musical fragment, its evoked valence and arousal, its perceived familiarity and the number and intensity of frissons, if experienced. Only the overall liking item is used in this study, where 1 meant 'I despise this song' and 7 'I love this song'. Exceptionally, one participant listened to all 60 excerpts. In order to make data from this participant comparable to the rest of the sample, only the first 30 excerpts were considered for this participants.

Self-reported data

In order to have a metric index of online evoked pleasantness we computed the average of every response given for each excerpt weighted by the amount of time each response was held. This index was compared to the overall liking Likert scale in order to be validated.

EEG data acquisition

EEG was recorded from the scalp (0.01 Hz high-pass filter with a notch filter at 50 Hz; 250 Hz sampling rate) using a BrainAmp amplifier with tin electrodes mounted on an Easycap (Brain Products©), at 61 standard positions (Fp1/2, AF3/4, Fz, F7/8, F5/6 F3/4, F1/2, FCz, FT9/10, FT7/8, FC5/6, FC3/4, FC1/2, Cz, T7/8, C5/C6, C3/4, C1/2, CPz, TP9/10, TP7/8, CP5/6, CP3/4, CP1/2, Pz, P7/8, P5/6, P3/4, P2/1, POz, PO7/8, PO3/4, Oz, O1/2) and left and right mastoids. An electrode placed at the lateral outer canthus of the right eye served as an on-line reference and an electrode at the infraorbital ridge of the right eye was used to monitor vertical eye movements. Electrodes impedance were kept below 10 kΩ during the whole session.

EEG signal processing

EEG was re-referenced off-line to the linked mastoids and band-pass filtered from 0.1 to 45 Hz. Subsequent processing steps are depicted in Figure 3.1. Epochs consisted in the whole time frame of each listening and were baseline-corrected using the average of the whole time window. Artifacts in these epochs were identified and corrected using ICA. Epochs with absolute mean amplitude higher than 100 µV after ICA correction were rejected. Three subjects were excluded from the analysis because of poor physiological data quality. The surface Laplacian transform was applied to these data in order to reduce volume conduction and make the data reference-free (Perrin et al., 1989). To avoid effects of surprise at the beginning and end of the song, the first and last 2s were removed from the epochs for subsequent analysis. Time-frequency decomposition was computed on each epoch using 5-cycle complex Morlet wavelets in the frequency band of interest (theta: 4–8 Hz). Phase values for each electrode and frequency were obtained over time from this decomposition.

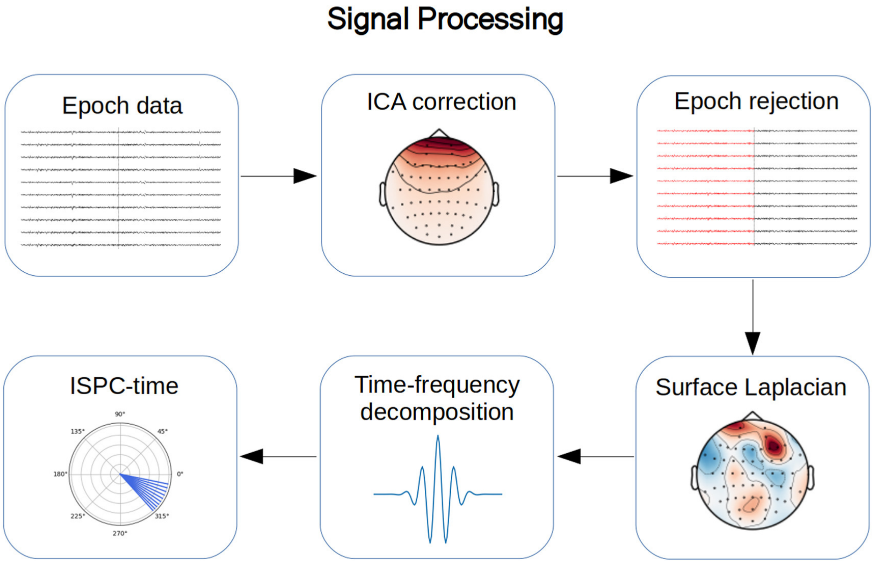


Figure 3.1 Signal processing diagram.

The *inter-site phase clustering* (ISPC) over time was computed for each epoch as an index of phase synchronization between signals. This index describes the consistency in phase difference between two signals over time and is defined as:

$$ISPC_f = |n^{-1} \sum_{t=1}^{n} \epsilon^{i(\phi_{it}-\phi_{jt})}| \tag{3.1}$$

where f is a given frequency, n is the number of time points and φ_{it} and φ_{jt} are the phases of two given signals at a given time point (Cohen, 2014). This was done for every frequency and every combination of two electrodes. Finally, ISPCs were averaged across frequencies. We excluded from subsequent analysis connections involving peripheral electrodes (Fp1, Fp2, FT9, FT10, TP9 and TP10) and connections where the two electrodes were less than 6 cm apart from each other, since these most likely reflect residual artifactual activity and volume conduction, respectively. This reduced the number of analyzed connections from 1830 to 1289.

Statistical analysis

In order to validate the time-weighted reported pleasantness measure, a generalized Bayesian multilevel linear model with this index as response variable, overall liking as explanatory variable and varying intercepts and slopes per subject was performed. A student-t likelihood function was assumed to explain the data in order to accommodate outliers (μ: identity; prior on σ: student-t, $\mu = 0$, $\sigma = 10$, $\nu = 3$; prior on ν: gamma, $\alpha = 2$, $\beta = 0.1$). Weakly informative priors were placed over the intercept and slope (normal, $\mu = 0$, $\sigma = 1$), as well as over the varying effects (gamma, $\alpha = 2$, $\beta = 2$). To test the group-level slope to be non-zero a 95% *highest density interval* (HDI) was used to check the inclusion of the null hypothesis (H_0: β_1=0) in the posterior assuming a *region of practical equivalence* (ROPE) of ±0.01 (Kruschke, 2015). The reported point estimate (β_1) corresponds to the mode of the posterior.

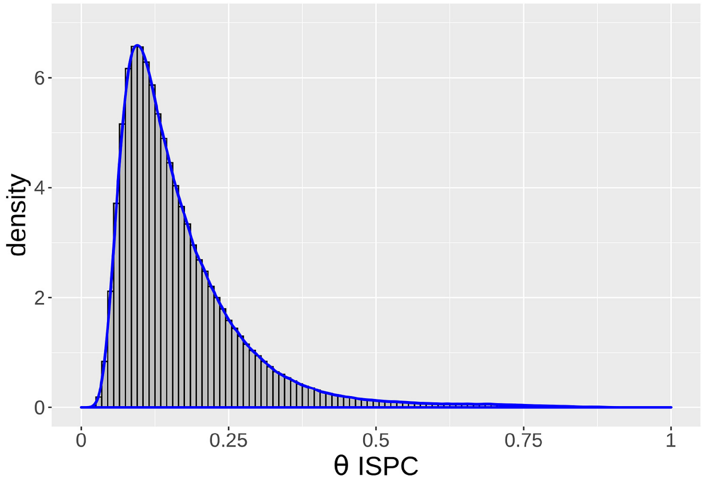


Figure 3.2 Distribution of ISPC values in theta pooled across subjects and connections. The histogram and its overlying line represent the values' densities.

In order to investigate the relationship between reported pleasantness and phase synchronization in theta, mass-univariate Bayesian multilevel beta regression models with ISPCs as response variables, (standardized) time-weighted reported pleasantness as explanatory variable and varying intercepts and slopes per subject were performed for every two-electrode combination. A beta likelihood function with the logit link function was assumed to explain the data (μ: logit(x); prior on φ: gamma, $\alpha = 0.01$, $\beta = 0.01$), since ISPC values are non-normally distributed in the unit interval (Figure 3.2). Weakly informative priors were placed over the overall intercepts and slopes (normal, $\mu = 0$, $\sigma = 1$), as well as over the varying effects (gamma, $\alpha = 2$, $\beta = 2$). Before the analysis was performed, bivariate outliers per connection and subject were identified and removed using bagplots (Rousseeuw et al., 1999). To test the group-level slopes to be non-zero a 95% HDI was used to check the inclusion of the null hypothesis (H_0: β_1=0) in the posteriors assuming a ROPE of ±0.01. Reported point estimates correspond to the mode of the posteriors.

Posterior distributions were approximated using 5 Markov chains of 1000 samples with no thinning, burning-in the first 200 samples. The No-U-turn sampler algorithm was used to draw samples. All chains were initialized at 0. All models converged as indicated by Gelman's split-R-hat equaling 1 (Gelman et al., 2013).

3.1.4 Results

Self-reported data

The distribution of the time-weighted reported pleasantness index per excerpt and subject is displayed in Figure 3.3. Figure 3.4 shows the relationship between time-weighted reported pleasantness and the overall liking Likert scale for every individual (thin blue lines) as well as at the group level (thick black line). Time-weighted reported pleasantness was highly predicted by the overall liking scale at the group level (β_1 = 0.52, 95% HDI = 0.49–0.55). Thus, this on-line continuous index is consistent with an overall recall measurement of evoked pleasantness.

EEG phase synchronization

Figure 3.5 shows the non-zero results of the phase-synchronization analysis in theta. Two non-zero right fronto-temporal connections showed an increase in synchronization with greater degrees of reported pleasantness at the group level (AF4-T8: β_1 = 0.04, 95% HDI = 0.02–0.06; F4-T8: β_1 = 0.04, 95% HDI = 0.02–0.06). Coefficients are expressed in log-odds.

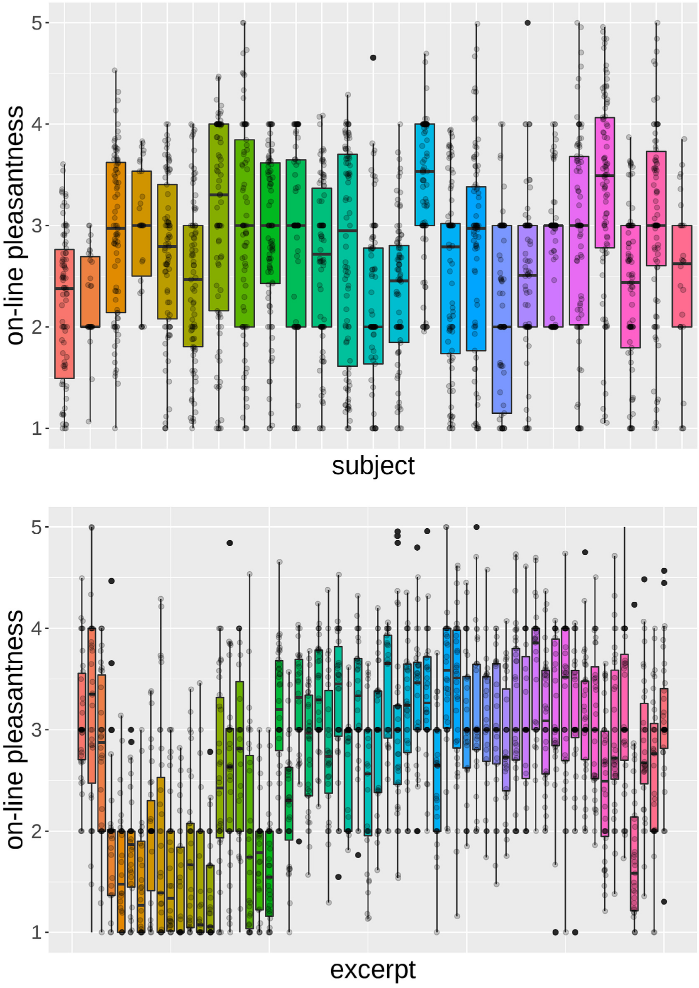


Figure 3.3 Distribution of time-weighted self-reported pleasantness per subject (top) and excerpt (bottom).

In order to compare these results with standard frequentist approaches, we represented the results of the mass-univariate regressions using different frequentist alpha levels (see Figure 3.6 in the appendix). As it can be seen, an uncorrected alpha level of 0.05 yields several connections, which are reduced if the alpha level is more restrictive. Only the rather arbitrary alpha level of 0.001 yields the same results as the proposed Bayesian approach. Importantly, none of the connections survived standard Family Wise or False Discovery Rate corrections, deemed too restrictive. Therefore, in contrast to the use of an arbitrary p-value or overly restrictive corrections to ameliorate the multiple testing problem, the proposed Bayesian approach yields non-inflated results with uncorrected inference standards.

3.1.5 Discussion

The goal of the present experiment was to study the oscillatory dynamics of the brain interactions underlying music-evoked pleasantness. To this purpose, we analyzed the relationship between phase synchronization of EEG signals in an oscillatory band of interest (theta) and reported pleasantness in a multilevel design where each participant listened to and rated several music stimuli.

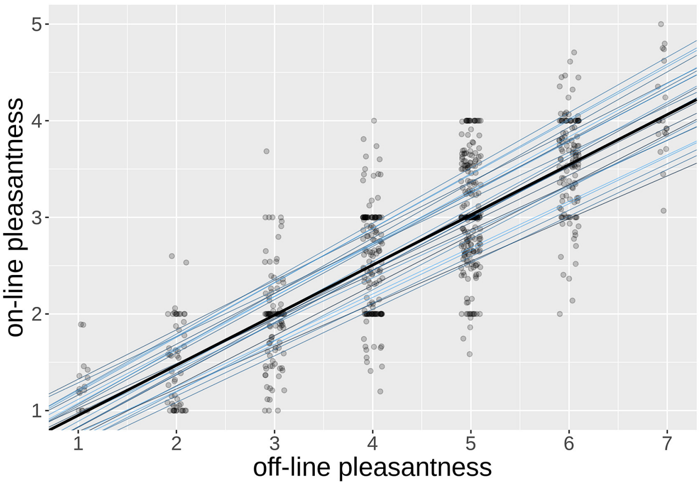


Figure 3.4 Time-weighted (on-line) self-reported pleasantness regressed on likert scale (off-line) self-reported pleasantness. Thin blue lines represent each participant's regression line. The thick black line represents the group-level regression line. Observations (jittered) are shown for illustration purposes.

We found increased synchronization between right temporal and right frontal nodes with higher degrees of reported pleasantness. These results are in agreement with previous findings showing the involvement of a cortical network associated with the process of giving value to music, which includes temporal and frontal areas (Salimpoor et al., 2013; Sachs et al., 2016; Martínez-Molina et al., 2019). In addition, frontal and parietal activations have been found in emotional control, both in reaction to music (Rogenmoser et al., 2016), and in general (Heller, 1993; Davidson, 2004). Interestingly, frontal and temporal areas have also been related to recognition processes during music listening, and to recognition of positively valenced music in particular (Altenmüller et al., 2014). Indeed, memory retrieval and working memory in musical contexts are tightly related to frontal function (Zatorre et al., 1994; Zatorre et al., 1996; Halpern and Zatorre, 1999; Zatorre and Halpern, 2005) and emotional processing (Eschrich et al., 2008). The results are also consistent with previous findings on the right hemispheric dominance in music processing (Zatorre and Gandour, 2008; Zatorre et al., 2002; Hyde et al., 2008; Özdemir et al., 2006; Martínez-Molina et al., 2016). Nevertheless, it is important to note that there is also evidence showing that inter-hemispheric interactions are necessary for normal music processing (Schuppert et al., 2000), as well as research showing no hemispheric specialization (e.g. Jäncke and Alahmadi, 2016).

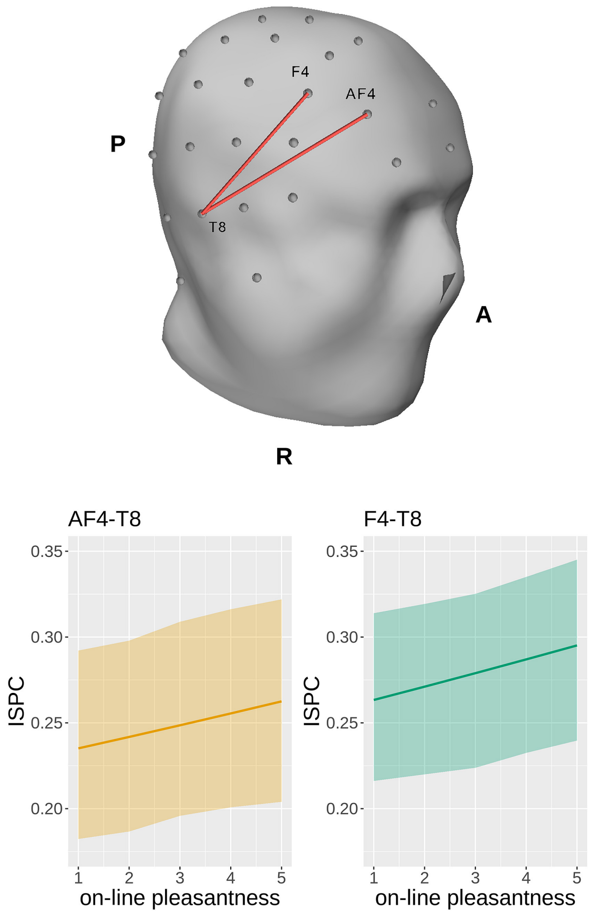


Figure 3.5 Non-zero connections in theta (top) and their corresponding prediction plots (bottom). Straight lines and their ribbons represent predictions of the response variables at each value of the explanatory variable following parameter estimates and their 95% HDIs, respectively. Predictions are made on the original scale of the variables.

In a different line of research, phase synchronization between temporal and frontal nodes has also been found in theta during auditory working memory tasks (Kaiser, 2015). Working memory, in turn, has been hypothesized to play an important role in music-evoked pleasantness, as it would allow the formation of musical patterns and multi-modal structures that go beyond single auditory events (Zatorre and Salimpoor, 2013). Low-frequency synchronization between temporal and frontal nodes has also been related to auditory and musical PE computation (Recasens et al., 2018; Omigie et al., 2019). Different accounts have proposed a key role of expectancies and PEs in the pleasurable experience of listening to music. For example, Salimpoor et al. (2015) proposed that the process of listening to music involves the generation of expectations. The resolution of such expectations would induce PEs which would be coded by dopaminergic neurons in a similar way as reward PEs. Regarding this latter interpretation, however, it must be noted that not all studies report activation in reward core areas, at least when studying the broader construct of evoked valence (e.g. Trost and Frühholz, 2015).

Although in this study we focused on theta, it must be noted that other frequency bands have been related to music listening elsewhere. For instance, the alpha band has been found to increase in power during music perception (Sammler et al., 2007;

Baumgartner et al., 2006). In addition, faster rhythms such as beta and gamma oscillations also exhibit an increase in power during music perception (Sammler et al., 2007; Martin et al., 2018). Future studies could be devoted to exploring these bands using appropriate settings (specially in the case of high-frequency analysis). On the other hand, frontal theta rhythms also appear to modulate evoked arousal, in addition to valence, suggesting a possible interaction between the two emotional dimensions (Sammler et al., 2007; Mikutta et al., 2012; Mikutta et al., 2014).

An important novelty of this study is the Bayesian multilevel models used to analyze the data. The application of this methodology had a double pursuit: first, the multilevel structure of the models allowed us to analyze the data taking into account both levels of inference (individual and group) simultaneously. This framework also allowed the adoption of appropriate assumptions about the distribution of the data (e.g. that ISPC values follow a beta distribution). Second, the use of this approach ameliorated the multiple testing problem by virtue of the statistical properties of Bayesian estimation.

Another methodological issue that we addressed is how music-evoked pleasantness was operationalized. In most previous related literature, music-evoked pleasantness was assumed to be related to the positive end of the valence dimension in a circumflex model of emotion (e.g., see Lin et al., 2010 or Rogenmoser et al., 2016). Whilst this holds true for most research in emotion, evoked pleasantness is sometimes found to be dissociated from valence in musical contexts (e.g. liking sad music, Sachs et al., 2015). This dissociation has often been attributed to the difference between perceived emotions (i.e. emotions identified by the listener) and evoked emotions (i.e. emotions evoked in the listener; Kawakami et al., 2014). According to this view, pleasant feelings to music belong to the realm of evoked emotions. This would justify paradigms using (evoked) valence to measure pleasantness. However, this dissociation can also be observed within evoked emotions themselves (e.g. liking music that makes one sad), which has motivated a different theoretical framework to resolve this confound. Schubert (2013) explains that in musical contexts evoked valence can be further broken down into two distinct dimensions, namely emotion valence (i.e. emotions felt by the listener) and affect valence (i.e. approach/avoidance toward these emotions).

From this standpoint, if the researcher seeks to study pleasant/unpleasant responses to music independently of the emotions evoked, music-evoked pleasantness should be operationalized as affect valence. Sammler et al. (2007) and Omigie et al. (2015) did so in using consonant and dissonant music as proxies for pleasant and unpleasant music. Nonetheless, because of the previously mentioned idiosyncrasies, individual differences may arise in such paradigms, where some people may like or dislike the music employed to a different extent, or even dislike/like music thought to be pleasant/unpleasant by the researcher. We argue that continuous self-reported pleasantness ratings, albeit subjective and less controlled, are better suited to capture these nuances regardless of emotion valence and music preferences. Although continuous ratings have been demonstrated to influence the extent to which neural signals respond to music and its associated states (Markovic et al., 2017), they seem well suited to study evoked emotions in musical contexts, where these most likely vary as music dynamics unfold (Arjmand et al., 2017).

The present study also presents a number of limitations. One of the most important is the low spatial resolution of EEG and its incapacity to capture subcortical signals. Nonetheless, it is clear from the literature that the striatal and limbic systems are pivotal in the process of giving value to music. The techniques here employed thus offer an incomplete picture of the brain mechanisms involved in such function. Subsequent studies must address this by combining different technical modalities, such as simultaneous EEG-fMRI recordings. This approach would benefit from both the good temporal resolution of EEG and the good spatial resolution of fMRI, providing a more complete picture of the processes studied. Furthermore, the fact that subjects evaluated the stimuli while listening to them might have imposed an active listening strategy, which could have influenced our results and interpretations (Jäncke et al., 2018). Yet another limitation is the fact that we studied the overall oscillatory dynamics of the music fragments, being these portions of their complete counterparts, rather than their specific time-courses over the whole pieces. The related acoustics and emotional features and how they unfold over longer periods of time can offer a rich and complementary view on the study of music-evoked pleasantness (e.g. Arjmand et al., 2017; Sturm et al., 2014; Sturm et al., 2015; Jäncke et al., 2015; Martin et al., 2018).

3.1.6 Conclusions

In summary, the pleasurable experience associated with listening to music is associated with interactions between right temporal and frontal areas with theta rhythms as means of communication. This functional and anatomical interplay adds up to existing literature showing the involvement of frontal and temporal areas and theta rhythms in the process of giving value to music and its related neuropsychological mechanisms. The latter must be furthered researched using more controlled paradigms and finer grained operationalizations, as well as multimodal neuroimaging techniques.

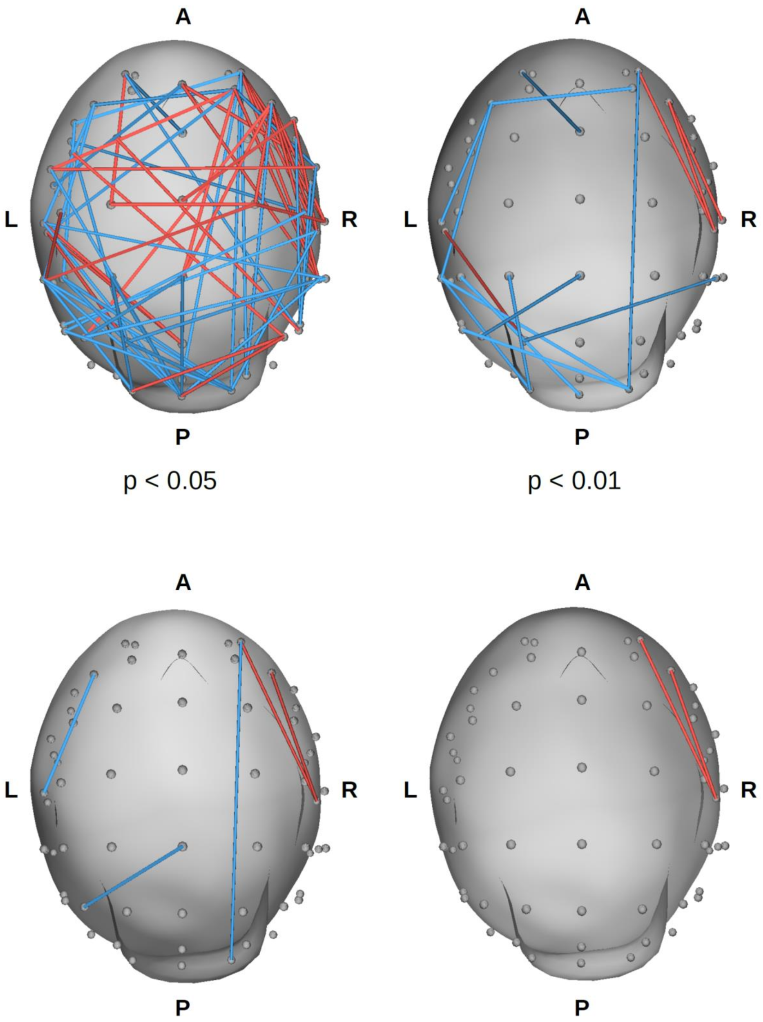
3.1.7 Appendix

Artist	Track
Anjulie	Boom
Atari Teenagers	New Blood
Atari Teenagers	Street Grime
Basshunter	All I ever wanted
Baz Corden	Hearts and Rainbows
Blinding	The Island
Buffalo	Dub trees
Caro Emerald	Just One Dance
Cashmere Cat	Mirror Maru
Combforce	Semantic Field
Conrad Schinitzer	Wurm
Daft Punk	The Game Has Changed
Dua Lipa	Blow Your Mind (Instrumental)
Errors	A Rumor in Africa
Finally Awake	Gone Away
Florence + The machine	Dog days are over (instrumental)
James Arthur	Coming Home for Summer
James Welsh	Nowt
JRY ft. Rooty	Pray
Kaskade ft. Martina of Dragonette	Fire your new shoes
Klingande	Jubel (original mix)
KSHRM	Kashmir (original mix)
Linkin Park	Heavy (instrumental)
Linkin Park	Battle Symphony (instrumental)
Marina and the Diamonds	Hollywood (instrumental)
Martin Solveig and GTA	Intoxicated (instrumental)
Martin Solveig ft. Sam White	+1
Maybeshewill	Opening
Metric	Combat Baby (instrumental)
Metric	Speed the collapse

Table 3.1 List of songs used in the experiment. Songs labeled as instrumental are instrumental versions of songs originally written with lyrics.

Artist	Track
Moguai ft. Cheat Codes	Hold On
Mumdance	Shook
Mumdance	Take time
Nine Inch Nails	8 ghosts I
Nine Inch Nails	14 ghosts II
Núria Graham	Unknown
Paloma Faith	Black and Blue
Paloma Faith	Only Love Can Hurt Like This (instrumental)
Passenger	Bullets
Quarta 330	Digital lotus flower
Richard Devine	Pallete
Richard Devine	Reneanalogueseq
Robin Bengtsson	Constellation Prize
Robin Dtjiernberg	Rain (Didrick remix)
Roco	Dealer
S-Type	Billboard (Lido Remix)
Scooter	Maria (I like it loud)
Scooter	My gabber
Sia	Alive (instrumental)
Special D	Alive (instrumental)
Special D	You
Stargate ft. Pink and Sia	Waterfall (instrumental)
Stephen Marley	Hey Baby (instrumental)
Subshock Evangelos	All Right
The Mad Trist	Pay the Piper
TNGHT	Goooo
Triana Park	Iron Blue
Ulver	Darling, didn’t we kill you?
Venetian Snares	Öngyilkos Vasárnap
ZAYN	Fool For You (instrumental)

Table 3.2 (continuation)



$p < 0.05$ $p < 0.01$

$p < 0.005$ $p < 0.001$

Figure 3.6 Significant connections in theta under the frequentist framework with different alpha levels. Red lines indicate positive relationships and blue lines negative relationships. No connection survived standard family-wise error or false discovery rate corrections.

Music-evoked pleasantness modulates theta synchronization within a fronto-temporal music-related network

3.2 Study 2

3.2.1 Abstract

Music processing and its associated hedonic value is characterized by a complex interplay of brain activations in relevant perceptual, cognitive and affective areas. Theta rhythms (4-8 Hz), on the other hand, have been recently proposed as a means of synchronization between this network's temporal and frontal nodes in the process of giving value to music. Nonetheless, this association has not been established empirically yet. In the present experiment, fMRI and EEG signals were recorded simultaneously while participants listened to a series of music excerpts and rated the degree of experienced pleasantness on a continuous basis. Subsequently, the fMRI networks associated with music-listening were extracted using *group independent component analysis* (gICA) and exerted to statistical analysis to study their relation with EEG theta synchronization and how evoked pleasantness might modulate this relationship. Music-related brain function as measured with fMRI was characterized by frontal and temporal co-activations. In addition, the relation between this fMRI network and fronto-temporal/parietal theta synchronization as measured with EEG was modulated by evoked pleasantness, showing an upward trend for music that was liked the most, and otherwise for music that was liked the least. These results show that theta fronto-temporal/parietal synchronization plays an important role in music-evoked pleasantness and the brain networks that support it.

3.2.2 Introduction

Music is arguably a very pleasurable stimulus for humans. However, it differs from primary reinforcers (which cover basic needs) or secondary reinforcers (which give access to the former) in so that it presents no evident adaptive advantages. For this reason, the mechanisms whereby pleasure emerges from music have motivated extensive research over decades. From a functional perspective, consistent results indicate that brain areas involved in working memory, auditory perception and reward processing are all entangled in the process of giving value to music. Auditory areas such as the STG and Heschl's gyrus; frontal areas such as the OFC and the IFG; as well as the ventral and dorsal striatum; are all involved in music-evoked pleasantness (Koelsch, 2014). Core areas in reward processing such as the NAcc in the ventral striatum have been reported to coactivate along auditory and frontal function areas during pleasant music listening (Blood and Zatorre, 2001). Furthermore, functional connectivity between auditory, frontal and reward processing structures is related to the associated value of music (Salimpoor et al., 2013), being the strength of white matter connectivity between these areas related to individual differences in music-reward sensitivity (Martínez-Molina et al., 2019). Moreover, magnetic stimulation/inhibition of fronto-striatal pathways during music listening modulates music-evoked pleasantness (Mas-Herrero et al., 2018), similar to the way dopaminergic agonism/antagonism leads to a respective increased/decreased music-related hedonic experience (Ferreri et al., 2019). Therefore, frontal and temporal cortices work together along the reward system during positive valuation of music.

Despite all this knowledge about the brain areas involved in music reward processing, it is unclear what are the neural dynamics involved in the coordination of the different nodes of such extensive network. It has been proposed that a suitable means of communication between brain areas is oscillatory synchronization. By oscillating in the same frequencies, different neural populations bind together and encode/decode representational information in order to accomplish a common task (Buzsáki and Draguhn, 2004). Interestingly, previous studies on music have consistently related frontal and fronto-temporal theta oscillations (4-8 Hz) to music-evoked pleasantness or related constructs. Frontal theta power has been observed to increase following consonant as opposed to dissonant music (Sammler et al., 2007; Omigie et al., 2015) and with positive valence in circumflex models of emotion (Lin et al., 2010; Mikutta et al., 2014; Rogenmoser et al., 2016). Moreoever, fronto-temporal theta phase synchronization has been associated with reported evoked pleasantness during music listening (Ara and Marco-Pallarés, 2020). On the other hand, both frontal theta power and fronto-temporal theta phase synchronization have also been related to pivotal processes for music perception and evaluation, such as auditory working memory and PE computation (Zatorre and Salimpoor, 2013; Kaiser, 2015; Recasens et al., 2018; Omigie et al., 2019). Therefore, theta oscillations could be responsible for the synchronization of the different brain regions identified to be involved in musical pleasure in the aforementioned neuroimaging literature.

However, whether the brain networks associated with music reward processing in the neuroimaging literature, on the one hand, and theta synchronization, on the other hand, are indeed intertwined has never been researched empirically. Indeed, the large-scale networks supporting this orchestration of cognitive and affective processes must work through slow rhythms, due to the physical constrains posed by far-off interactions (Buzsáki and Draguhn, 2004). One way to address this inquiry is to test whether the relationship between music-related functional connectivity as measured with fMRI and theta synchronization as measured with EEG is modulated by behavioral responses of pleasantness, combining the advantages of the two techniques. On the one hand, fMRI's excellent spatial resolution allows the identification of relevant areas and networks engaged during a task. On the other hand, EEG's fine temporal resolution allows the study of the associated neural oscillations.

Therefore, the goal of the present study was to establish whether there is a relationship between theta phase synchronization as measured with EEG and music-related brain function as measured with fMRI; and whether this relation is modulated by evoked pleasantness. To reach this goal, we used simultaneous fMRI-EEG recordings which combine fMRI's excellent spatial resolution with EEG's fine temporal resolution and capability of detecting oscillatory dynamics. We hypothesized that theta oscillatory synchronization as measured with EEG would be related to music-related brain networks as measured with fMRI, particularly when music evokes pleasant feelings in the listener.

3.2.3 Materials and Methods

Participants

Twenty right-handed individuals (M = 23.95 years old, SD = 4.13, 16 women) participated in the experiment. All participants were chosen to roughly have similar profiles of music reward and physical anhedonia as assessed with the BMRQ (Mas-Herrero et al., 2013; cut-off > 64) and the PAS (Chapman et al., 1976; males cut-off < 28, females cut-off < 20), respectively. None of the participant had received formal training in music for more than three years. All participants gave written informed consent and were paid 10€ per hour. Two participants were dropped from the study for different reasons: one participant recordings were severely artifacted and another participant decided to halt participation amidst the experiment. All procedures were approved by the local ethical committee.

Stimuli

Stimuli consisted in 12 fragments of 60s from well-known classical music pieces (see Table 3.3 of the appendix for the complete list of pieces employed). Six stimuli were selected to be very pleasant and other 6 to be moderately pleasant according to the norms collected by Martínez-Molina et al. (2016). The 60s fragments were chosen to be representative of the whole musical pieces (e.g. that they included more than one theme, that variations took place and/or that several instruments were present).

Experimental design

Before entering the scanner, participants were exposed to the 12 music excerpts in random order. Exposing participants to the music outside the scanner had the pursuit of making sure that all participants had listened to every music piece at least once.

In the scanner, participants were exposed again to the same music fragments in random order and were asked to rate the degree of evoked pleasantness on a continuous basis with as many responses as they wanted in an event-related design. Responses were given via two fMRI-compatible two-button controls, one held in each hand, with the following equivalences: left thumb: I don't like it; left index: I like it moderately; right index: I like it a lot; right thumb: I experience frissons. Response keys had to be held for as long as a rating applied for the individual. We introduced periods of rest in between excerpts. The event-related design was divided in two identical runs and went as follows: 15s of rest, 6 blocks of music (60s) followed by rest (30s), and a final block of 15s of rest. Figure 3.10 of the appendix shows the distribution of the average reported pleasantness (average of every response weighted by the time each response is held) per subject and excerpt. Figure 3.11 of the appendix shows the average time courses of the pleasantness ratings provided by all individuals for each excerpt with their associated dispersion.

fMRI data acquisition

Whole brain fMRI data were acquired using a 3T Trio scanner at the Mind, Brain and Behavior Research Centre in Granada (Spain). Functional images were obtained with a T2-weighted echo planar imaging sequence, with a *repetition time* (TR) of 2000 ms (two runs of 285 scans) and 35 descendent slices with a thickness of 3'5 mm^3 (echo time = 25 ms; flip angle = 80°; voxel size = 3'5 mm^3; matrix size = 68 x 68). In order to reduce susceptibility artifacts in the OFC and the anterior parts of the ventral striatum, slices were oriented with an angle of 30^o with the plane intersecting the anterior and the posterior commissures (Weiskopf et al., 2006). High resolution T1-weighted anatomical images were acquired after the functional task (192 slices; image matrix = 256 x 256; voxel size = 1 mm^3; TR = 2500 ms; echo time = 3.69 ms, flip angle = 7°). Inside the head coil, participants' heads were padded to restrict excessive motion.

EEG data acquisition

EEG was recorded from the scalp (0.01 Hz high-pass filter with a notch filter at 50 Hz; 1000 Hz sampling rate) using an fMRI compatible BrainAmp amplifier with fMRI-compatible electrodes mounted on an Easycap (Brain Products©), at 31 standard positions (Fp1/2, Fz, F7/8, F3/4, FC5/6, FC1/2, Cz, T7/8, C3/4, TP9/10, CP1/6, CP1/2, Pz, P7/8, P3/4, POz, Oz, O1/2). FCz served as the on-line reference and AFz served as ground. Electrode impedances were kept below 20 kΩ during the whole session. ECG was also recorded with an electrode placed as far down as possible on the back of the subjects along the paravertebral line. This electrode is necessary to clean out the cardioballistic artifact present in the EEG from simultaneous fMRI-EEG recordings. fMRI's TRs were registered in the EEG data with a specific trigger for subsequent data alignment.

fMRI signal processing

Pre-processing of whole brain images was carried out using the SPM12 Matlab toolbox (https://www.fil.ion.ucl.ac.uk/spm/software/spm12/). Functional runs were first slice timing-corrected (descending order, sinc interpolation, reference slice = 17) and realigned, and a mean image was created. The T1 image was co-registered to this mean image and segmented into gray matter by means of unified segmentation. Next, data were normalized via 4th degree B-spline interpolation. Finally, functional volumes were smoothed with an 8-mm 'full-width-at-half-maximum' kernel.

To study the brain networks involved in music processing, spatial gICa was carried out on the complete data set using the GIFT Matlab toolbox (https://trendscenter.org/software/gift/). Data were entered per subject and session accordingly. Before applying the algorithm, the number of independent components (ICs) was estimated to be 37 using the GIFT dedicated tool (the median across subjects was used as criterion). The regular stability analysis and the Infomax algorithm were chosen to fit the ICA. Prior to model fitting, processing steps included removing the image mean per time point; applying a mask to each subject/session to filter out voxels smaller than the average of the whole session in the first functional image; and employing a standard *principal components analysis* with a two-step reduction approach where dimensionality is first reduced at the subject level to then do so at the group level (number of principal components were set to 1.5 times the number of ICs at step 1: 37x1.5 = 56; and to the number of ICs at step 2: 37). The algorithm was fitted with the following parameter values: block = 129, stop = 1^{-6}, weight = 0, lrate = 0.005, maxsteps = 512, anneal

= 0.9, annealdeg = 60, momentum = 0; and with sphering and bias applied. Finally, the gICA back-reconstruction procedure was applied to project individual time courses and spatial maps, which were then converted to Z-scores.

EEG signal processing

Electrodes TP9 and TP10 were dropped because they mainly contained heartbeat signals. Electrode FC6 was also dropped because of poor data acquisition across sessions. The gradient artifact induced by fMRI fields was removed from all signals using Brainvision Analyzer©'s Template Drift Compensation algorithm (continuous artifact, average baseline correction, offset from TR marker = 0ms, templates per head position = 3). After the artifact was removed, signals were downsampled to 200 Hz, low-pass filtered at 35 Hz (FIR filter) and stop-band filtered at 17.5 Hz (bandwidth = 0.5 Hz). EEG was further high-pass filtered at 1 Hz, and ECG was high-pass filtered between 0.001 Hz and 1 Hz depending on the subject to optimally detect heartbeat in the next processing step (IIR filter, order = 8). Next, the cardioballistic artifact induced by the effect of the MRI fields on heartbeat signals captured by EEG was removed from all EEG signals using Brainvision Analyzer's dedicated algorithm (pulse properties: pulse length (ms) = 750±250; template search: time range (s) = 0-25, coherence = 0.6, amplitude range = 0.2-1.2; correction details: whole data used to compute time delay, pulses per average = 21). Before correction was applied, visual supervision was performed on the heartbeat template, and rectified if needed. Data were then epoched from –2s to 4s with respect to TR markers. Therefore, each epoch was 6s long, containing the TR corresponding to the fMRI volume of interest, plus the previous and next TRs to avoid edge artifacts in subsequent processing steps. Finally, ICA was used to remove residual artifactual activity and other artifacts such as blinks and muscular noise (epochs visually identified as too noisy were not considered for model fitting). After ICA correction, epochs visually identified as still noisy were marked as bad and electrode FC6 was interpolated.

In order to compute phase synchronization between signals the surface Laplacian transform was applied in order to reduce volume conduction and make the data reference-free (Perrin et al., 1989). Time-frequency decomposition was computed on each electrode and epoch using 5-cycle complex Morlet wavelets in the frequency band of interest (theta: 4–8 Hz). Phase values for each electrode and frequency were obtained from this decomposition over the time corresponding to each fMRI volume (i.e. excluding the first and last 2s of each epoch). To study synchronization between EEG signals the ISPC over time was computed for each one of these segments (Cohen, 2014). ISPCs were computed for every combination of two signals and every frequency, excluding Fp1/2 signals (likely reflecting residual blink and saccade activity) FC5/6 signals (likely unreliable due to FC6's interpolation, see above) and neighboring connections (i.e., less than 6 cms apart, likely reflecting residual volume conductivity). Finally, ISPCs were averaged across frequencies. The result was a time course of phase synchronization between EEG signals of the same length as fMRI measurements (i.e. 570 time points) for each considered electrode pair (25 × 24 – neighboring connections = 251 connections).

Model pre-processing

In order to time-match the self-reported ratings with the BOLD signals, self-reported pleasantness ratings were convolved with the canonical HRF after orthogonalizing responses per subject (demeaned and scaled to SD = 1) and coding passages with no music and/or no responses with zeros (Figure 3.7A). Observations from both sessions were concatenated.

The group independent components (gICs) time courses were band-pass filtered between 0.01 and 0.1 Hz (zero-phase-lag butterworth filter, order = 10) and pre-whitened according to the covariance structure of an autoregressive process of order 1 (AR(1)) to remove autocorrelation of the residuals, per subject (Figure 3.7B). Observations from both sessions were concatenated.

Phase synchronization time courses were also processed per subject. First, observations corresponding to segments marked as bad were linearly interpolated. Next, time courses were band-pass filtered between 0.01 and 0.1 Hz (zero-phase-lag butterworth filter, order = 10) and pre-whitened according to the covariance structure of an AR(1). These series were then convolved with the HRF. Finally, and since filtering centers signals at zero, the means of the unprocessed time courses were added to return them to their original center (Figure 3.7C). Observations from both sessions were concatenated.

The moderation effect of reported pleasantness on the relation between brain function and theta phase synchronization was operationalized as a statistical interaction between reported pleasantness and brain activity. It has been stressed that interactions between psychological variables and BOLD activity happen at the neural level, faster than hemodynamic responses (Gitelman et al., 2003). Accordingly, the interaction term was computed as the product between the un-convolved pleasantness series (Figure 1.3.7D top) and the deconvolved gICs series (Figure 3.7D middle). The latter was achieved by convolving the series with a deconvolution kernel. This was computed as the dot product between the gICs series and the inverse of the circulant matrix of the HRF function. This is:

$$D = xC' \tag{3.2}$$

where *D* is a deconvolved gIC series, *x* is a gIC series and *C'* is the inverse of the circulant matrix *C*, which is defined as:

$$C = \begin{bmatrix} c_0 & c_n - 1 & \dots & c_2 & c_1 \\ c_1 & c_0 & c_n - 1 & & c_2 \\ \vdots & c_1 & c_0 & \ddots & \vdots \\ c_n - 2 & & \ddots & \ddots & c_n - 1 \\ c_n - 1 & c_n - 2 & \dots & c_1 & c_0 \end{bmatrix} \tag{3.3}$$

where c is the HRF (right-padded with zeros to match the gICs series length) and *n* is the vector index. The interactions between the deconvolved gICs series and the un-convolved pleasantness series were again convolved with the HRF for subsequent analyses (Figure 3.7D bottom).

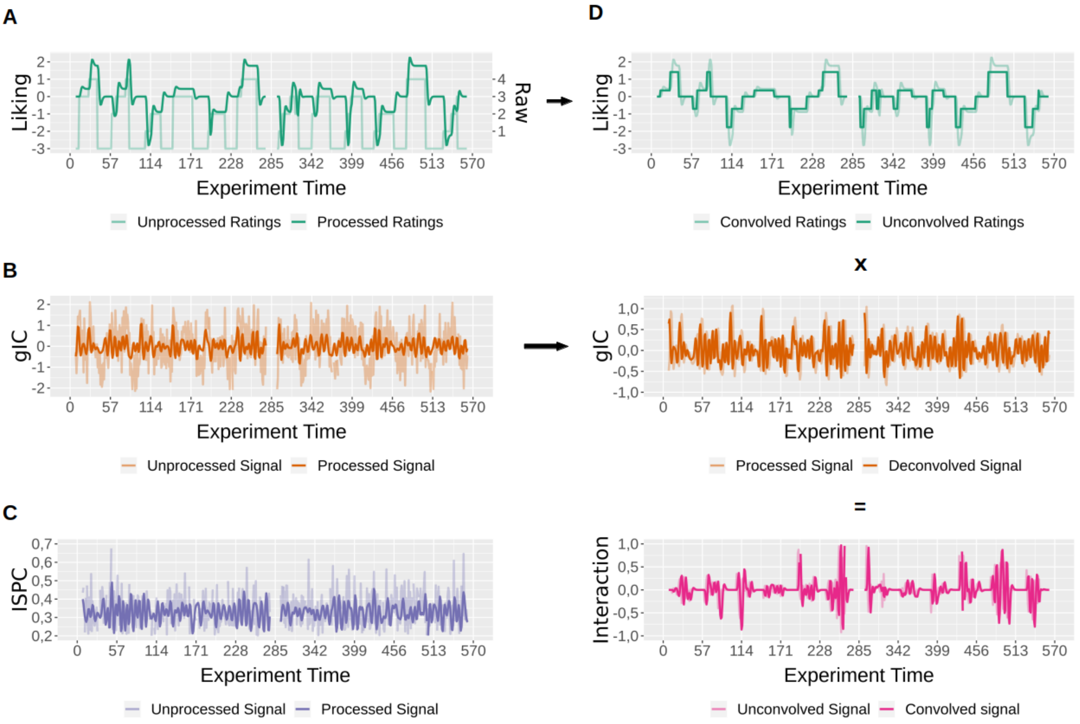


Figure 3.7 Example model pre-processing for one gIC and one participant. **A)** Pleasantness ratings before processing (shaded, right y-scale) and after being convolved (highlighted, left y-scale). **B)** Music-related gIC (fMRI) before processing (shaded) and after being filtered and pre-whitened (highlighted). **C)** Theta ISPC-time series (EEG) before processing (shaded) and after being interpolated, filtered, pre-whitened, convolved and back-mean-centered (highlighted). **D)** The moderation effect was operationalized as the convolved interaction between the unconvolved pleasantness series and the deconvolved, processed music-related gIC (highlighted elements). Observations corresponding to the first 7 and last 8 volumes of each session are not displayed.

After all processing was applied, observations corresponding to the first 7 and last 8 volumes of each session per subject were dropped. These observations corresponded to extra resting time at the beginning and end of each session and could contain edge artifacts.

Statistical Analysis

fMRI feature selection

In order to keep subsequent analyses grounded on music-related brain function, mass-univariate Bayesian multilevel robust regression models were carried out with the processed gICs series as response variables; the convolved experimental design as explanatory variable (music vs. rest); and varying intercepts and slopes per subject. A student-t likelihood function was assumed to explain the data in order to accommodate potential outliers (μ = identity; prior on σ: student-t: $\mu = 0$, $\sigma = 10$, $\nu = 3$; prior on ν: gamma: $\alpha = 2$, $\beta = 0.1$). Weakly informative priors were placed over the overall intercepts and slopes (normal, $\mu = 0$, $\sigma = 1$), as well as over the varying effects (gamma, $\alpha = 2$, $\beta = 2$). To test the group-level effects to be non-zero a 95% HDI was used to check the inclusion of the null hypothesis (H_0: $\beta_1 = 0$) in the posteriors assuming a ROPE of ± 0.1. Reported point estimates correspond to the mode of the posteriors.

Joint fMRI-EEG analysis

In order to investigate the relation between music-related brain function and theta phase synchronization, as well as the moderation effect of music-evoked pleasantness, mass-univariate Bayesian multilevel beta regression models were carried out with the processed phase-synchronization series as response variables; the processed music-related gIC series, pleasantness series and interaction term as explanatory variables; and varying intercepts and slopes per subject. A beta likelihood function with the logit link function was assumed to explain the data since ISPC-time values are non-normally distributed in the unit interval (μ: logit(x); prior on φ: gamma, $\alpha = 0.01$, $\beta = 0.01$). Weakly informative priors were placed over the overall intercepts and slopes (normal, $\mu = 0$, $\sigma = 1$), as well as over the varying effects (gamma, $\alpha = 2$, $\beta = 2$). To test the group-level moderation effects to be non-zero a 95% HDI was used to check the inclusion of the null hypotheses (H_0: $\beta_1, \beta_2, \beta_3 = 0$) in the posteriors assuming a ROPE of ± 0.01. Reported point estimates correspond to the mode of the posteriors.

In addition, we set out to repeat the analysis of any potential non-zero effects in theta in three other frequency bands (alpha: 9-12 Hz, beta: 13-25 Hz and gamma: 26-40 Hz) in order to test the specificity of effects in this frequency band, following the same processing pipelines (see EEG signal processing and model pre-processing sections).

Bayesian inference specification

The choice of Bayesian inference and the generalized linear model to estimate the parameters of interest obeyed the pursuit of ameliorating the multiple testing problem posed by mass-univariate analyses without incurring in neither arbitrary or overly restrictive post-hoc corrections usually associated with frequentist statistics, as well as assuming appropriate distributions for the dependent variables. These goals are achieved by virtue of Bayesian inference's statistical properties (see Ara and Marco-Pallarés, 2020 for a similar case). Given that this procedure is conservative, nonetheless, we repeated the joint fMRI-EEG analysis under the frequentist framework using different alpha levels in order to compare potential results to those of more liberal procedures.

Posterior distributions were approximated using 6 Markov chains of 2000 samples with no thinning, burning-in the first 1000 samples. The No-U-turn sampler algorithm was used to draw samples. All chains were initialized at 0. All models converged as indicated by Gelman's split-R-hat equaling 1 (Gelman et al., 2013).

3.2.4 Results

fMRI feature selection

In order to identify music-related brain function in the form of networks, we performed gICA on the fMRI signals and predicted the extracted components from the experimental design (music vs. rest). Only one gIC was predicted by the experimental design (gIC: β_1 = 0.15, 95% HDI = 0.14-0.16) and was considered as music-related brain activity. Figure 3.8A shows the cortical activations map of this music-related gIC, thresholded above a z-score of +1 and a cluster size of 50 voxels. Music-related co-activations included both STG, portions of both *rostral motor cortices* (RMCs), portions of the right IFG, as well as portions of the left cerebellum and the vermis (not shown). Figure 3.8B shows the average time course of the music-related gIC (across subjects) along the (convolved) experimental design. To check specific coordinates please visit this study's dedicated NeuroVault profile through the following link: https://neurovault.org/collections/HXMGAUPT/.

Joint fMRI-EEG analysis

In order to test whether music-related brain function is associated with theta synchronization and whether this relation is moderated by musical liking, we computed phase synchronization between EEG signals and predicted it from activity in a music-related brain network, reported pleasantness and the interaction between the two.

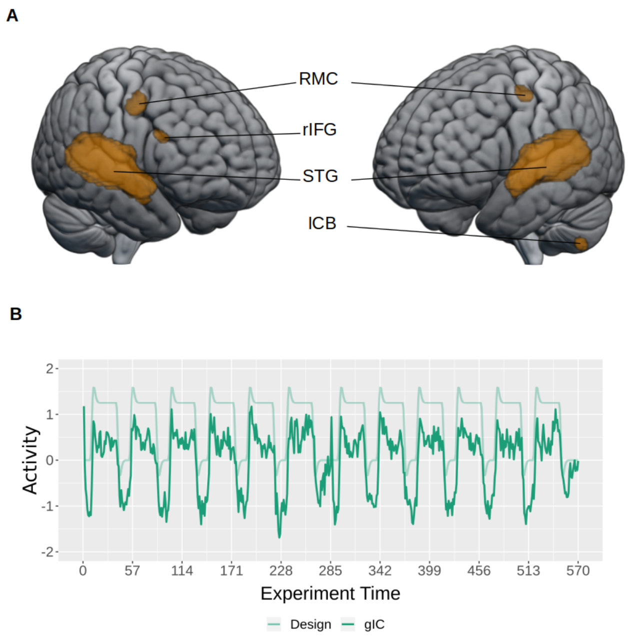


Figure 3.8 **A)** Music-related gIC spatial activations (STG: superior temporal gyri; RMC: rostral motor cortex; rIFG: right inferior frontal gyrus; ICB: left cerebellum). **B)** Average time course (across subjects) of the (unprocessed) music-related gIC along the (unconvolved) experimental design.

Main effects in the liberal frequentist analysis suggested fronto-parietal and fronto-occipital theta connectivity to decrease in synchronization with greater music-related brain function (see Figure 3.12 in the appendix for a comparison using different alpha levels). In the more conservative Bayesian analysis, only one of the fronto-occipital connections showed a non-zero decrease in theta synchronization with greater music-related brain function (Figure 3.9; FC1-O2: β_1 = -0.03, 95% HDI = -0.05-[-0.01]). No main effects of pleasantness were found to be non-zero in the Bayesian analysis.

In addition, interaction effects in the liberal frequentist analysis suggested fronto-temporal, fronto-parietal and fronto-occipital theta connections to be more associated with music-related brain function as reported pleasantness increased. In the more conservative Bayesian analysis, two fronto-temporal/parietal connections showed a non-zero interaction between music-related function and reported pleasantness, consisting in an increase in theta synchronization with greater music-related brain function when music was reported to be liked the most, as compared to when music was reported to be liked the least (Figure 3.9; F4-T8: $\beta_3 = 0.04$, 95% HDI = 0.01-0.08; FC1-CP6: $\beta_3 = 0.05$, 95% HDI = 0.01-0.08). Coefficients are expressed in log-odds.

None of the effects found in the Bayesian analyses were replicated in alpha, beta or gamma, indicating specificity of these effects in the theta oscillatory band.

3.2.5 Discussion

The goal of the present experiment was to study the link between theta phase synchronization and music-related brain function, as well as how this relation might be related to evoked pleasantness. We did so by employing fMRI-EEG simultaneous recordings in an experimental design where a cohort of participants listened to a series of musical fragments while reporting the degree of experienced pleasure, with rest periods between excerpts.

By studying fMRI gICs we found that music-related brain function (as opposed to rest in silence) mainly consisted in temporal (STG) and frontal (RMC and the IFG) co-activations, replicating previous findings (Zatorre et al., 1994). Most importantly, in our Bayesian analyses results we found that fronto-temporal/parietal phase synchronization in the theta band increased with greater music-related brain function when music was liked the most and decreased otherwise. In other words, when music was experienced to be most pleasant the right temporal and frontal nodes of a music-processing network synchronized more efficiently through theta rhythms. In turn, music that was liked the least was characterized by these nodes being less synchronized in this frequency band. This suggests that while fronto-temporal connectivity was consistently present during music listening, it was theta rhythmicity within this network what was modulated by evoked pleasantness. Interestingly, the location of both the EEG connectivity and the music-related gIC activations support the idea that theta oscillations are involved in the functional connectivity between the right temporal lobe and the frontal nodes of this network (e.g. RMC and IFG).

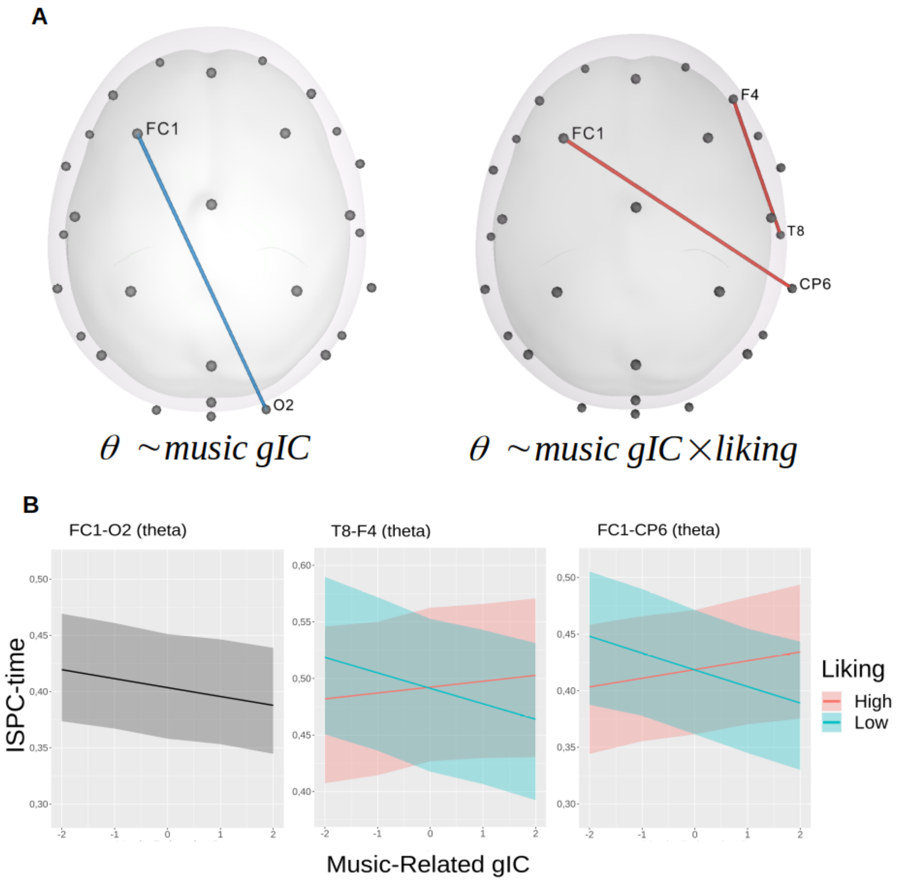


Figure 3.9 **A)** Non-zero main effects of music-related brain function (left) and interaction effects between music-related brain function and reported pleasantness (right) on theta phase synchronization. **B)** Corresponding prediction plots. Straight lines and their ribbons represent group-level predictions of ISPC-time across music-related gIC activity fixed at two representative values for high and low reported pleasantness (mean sample liking ± its associated standard deviation), following parameter estimates and their 95% HDIs.

Indeed, it has already been established that frontal and temporal brain function underlies music perception (Zatorre et al., 1994) and its associated hedonic value (Blood and Zatorre, 2001). Moreover, several electrophysiological studies have revealed that frontal and fronto-temporal theta rhythms are related to music-evoked pleasantness (Ara and Marco-Pallarés, 2020) or similar constructs such as consonance or evoked valence (Sammler et al., 2007; Omigie et al., 2015; Lin et al., 2010; Mikutta et al., 2014; Rogenmoser et al., 2016). In the present study we provide evidence that these two phenomena are indeed intertwined.

Our results also indicate a relative right-hemispheric dominance of this interaction effect. Particularly, the medial frontal activations of our gIC of interest displayed a right-hemispheric dominance, and we only found changes in theta phase synchronization between connections involving right temporal signals during pleasant music listening. This goes in line with previous research showing a right hemisphere dominance in music processing (Zatorre et al., 2002; Özdemir et al., 2006; Hyde et al., 2008; Zatorre and Gandour, 2008; Martínez-Molina et al., 2016). Nevertheless, there is also evidence that inter-hemispheric interactions are necessary for normal music processing (Schuppert et al., 2000). In our results, in fact, temporal and motor activations were found bilaterally, showing no hemispheric specialization whatsoever, and one EEG connection involved a left frontal node during pleasant music listening. This suggests a relative specialization of the right hemisphere in the processing of music, but not total specificity.

Right fronto-temporal loops have been hypothesized to support the necessary predictive processes to encode, maintain and decode musical representations within auditory working memory (Zatorre and Salimpoor, 2013). Indeed, functional connectivity between temporal, frontal and reward processing areas increases during pleasant music listening (Salimpoor et al., 2013). Interestingly, frontal theta activity and fronto-temporal theta synchronization have also been related to working memory and predictive coding in the auditory domain (Kaiser, 2015; Recasens et al., 2018; Omigie et al., 2019) The PEs generated in this process have been hypothesized to trigger the reward signals associated with music-evoked pleasantness (Salimpoor et al., 2015). Particularly, salient musical PEs, as opposed to excessive or insufficient PEs, would comprise an intermediate state between predictability and surprise responsible of pleasant responses (Hansen et al., 2017).

The relationship between theta rhythms and music-related brain function in this study (as well as others) is consistent with theories stating that slow rhythms are an optimal mechanism for large-scale connectivity between brain areas (Buzsáki and Draguhn, 2004). Given that we demonstrated liking effects on fronto-temporal synchronization to be intertwined with fronto-temporal brain function and theta oscillations, a tentative interpretation of our results is that theta oscillatory synchronization is the neural mechanisms underlying the computation of the PEs mediating musical enjoyment.

We also found parietal signals to synchronize with frontal signals in our moderation results. Anatomically, the fronto-temporal loops underlying auditory working memory and expectancy operate over two functional streams: a ventral pathway representing the “what” and a dorsal pathway the “when” of auditory events (Zatorre and Salimpoor, 2013). The former connects the STG with the IFG along the temporal lobe, while the latter connects the STG with the mPFC via the parietal lobe (Rauschecker and Scott, 2009), supporting the potential synchronization between dorso-frontal and parietal EEG nodes, in contrast to more medial fronto-temporal connectivity.

Finally, in studying how music-related brain function directly related to theta rhythms, we found that fronto-parietal and fronto-occipital synchronization decreased with activity in the music network, being significant only one fronto-occipital connection in the more conservative Bayesian approach. It is difficult to determine the nature of this negative relationship in the extent of this study. One possibility is that frontal, parietal and occipital sites are less synchronized by theta rhythms when the brain engages in the processing of music because of the disengagement of other networks that operate in this frequency band.

The present study presents several novelties in the neuroscientific study of music-evoked pleasantness. By acquiring fMRI-EEG co-registered data we could study contingent brain and EEG signals in the same experimental session. This acquisition modality, in combination with gICA and multilevel modeling, allowed us to infer multimodal processes common to a group of participants, while fully capturing phenomena taking place within individuals (i.e. how brain function and EEG signals respond to different degrees of evoked pleasantness). Furthermore, by adopting a generalized linear modeling framework, appropriate assumption about the distribution of the data could be made (i.e. that ISPC-time values follow a beta distribution). Finally, the choice of Bayesian inference to estimate the parameters of interest ameliorated the multiple testing problem posed by mass-univariate analysis by virtue of its statistical properties (Ara and Marco-Pallarés, 2020).

There are also limitations to our study. While our experimental design and signal processing methods allowed us to study how EEG signals and cortical activity relate to self-reported pleasantness ratings during music listening, it could not directly capture the more nuanced mechanics hypothesized to underlie music-evoked pleasantness such as predictive coding and PE computation, neither it captured reward signals in the striatum associated with peaks of pleasurable activity. Paradigms where induced pleasantness is experimentally controlled and predictive processes are operationalized are needed along co-registered data to test the extent of these claims. Non-invasive brain stimulation/inhibition paradigms can also offer an interesting window to test the results here presented in a more experimentally controlled manner. Another limitation of this study is the fact that subjects evaluated the stimuli while listening to them, which might have imposed an active listening strategy. This might have influenced our results and interpretations (Jäncke et al., 2018). In this same line, continuous ratings have been demonstrated to influence the extent to which neural signals respond to music and its associated states (Markovic et al., 2017). However, we argue that when no control can be exerted over pleasantness or its associated psychological mechanisms, continuous ratings over time seem well suited to study music-evoked emotions, where these most likely vary as music dynamics unfold (Arjmand et al., 2017).

3.2.6 Conclusions

In summary, in this study we show that fronto-temporal theta phase synchronization as measured with EEG is associated with music-related brain function as measured with fMRI, with more synchronization following greater brain activity when music is reported to be most pleasant. These results provide empirical evidence that two phenomena associated with music-evoked pleasantness in the literature are indeed intertwined, namely fronto-temporal theta oscillations and fronto-temporal brain networks. Further research must be conducted to unveil the concrete neuropsychological mechanisms underlying these brain and physiological interactions during pleasant music listening.

3.2.7 Appendix

Title	Composer
Symphony No.9, Op.125, Mov.2	Beethoven
Mazurka in A minor, Op.17, No.4	Chopin
New World Symphony No.9, Mov.4	Dvorak
Firebird Suite, Finale	Stravinsky
Dance Of The Sugar Plum Fairy	Tchaikovsky
The four seasons ”Spring” Mov.1	Vivaldi
The four seasons ”Winter” Mov.1	Vivaldi
Symphony No.4 in B Flat major, Op.60, Mov.2	Beethoven
Symphony No.38 in C major Mov.3	Haydn
Für Elise	Beethoven
Violin Sonata in A Major Mov. 1	Fauré
The Planets - Venus, The Bringer of Peace	Holst

Table 3.3 List of musical pieces used in the experiment.

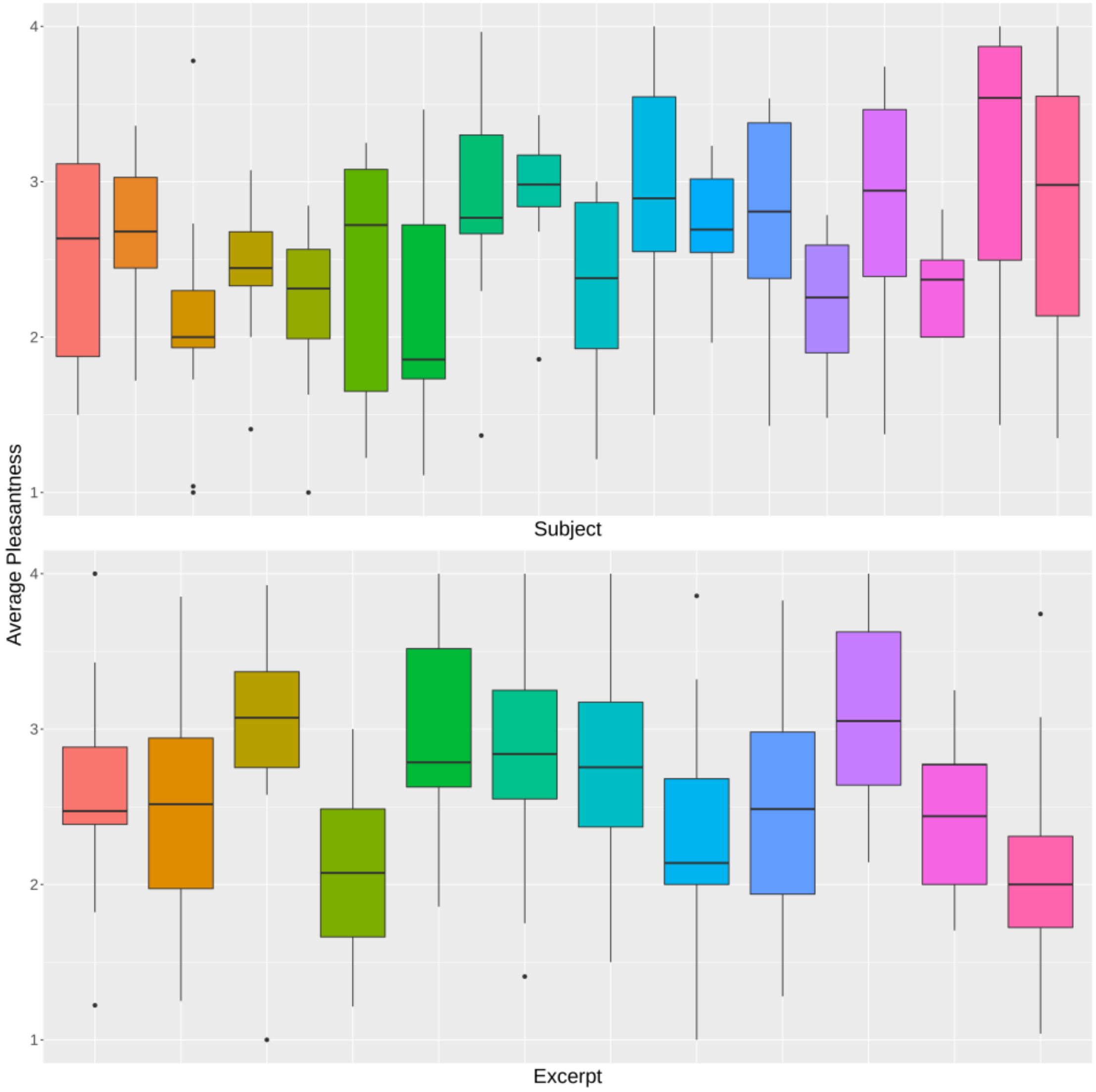


Figure 3.10 Distribution of time-weighted average reported pleasantness per subject (top) and excerpt (bottom).

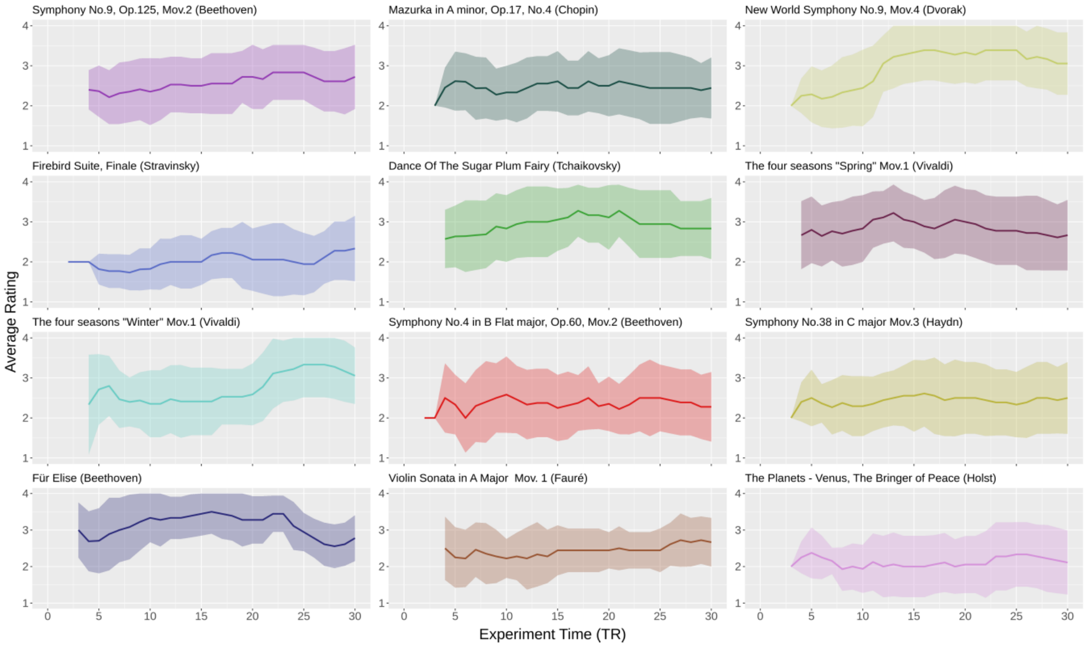


Figure 3.11 Average pleasantness time courses given for each excerpt. Straight lines represent the mean rating across participants at each time point (in TRs) and the ribbons around them represent these expectations ± their associated standard deviations).

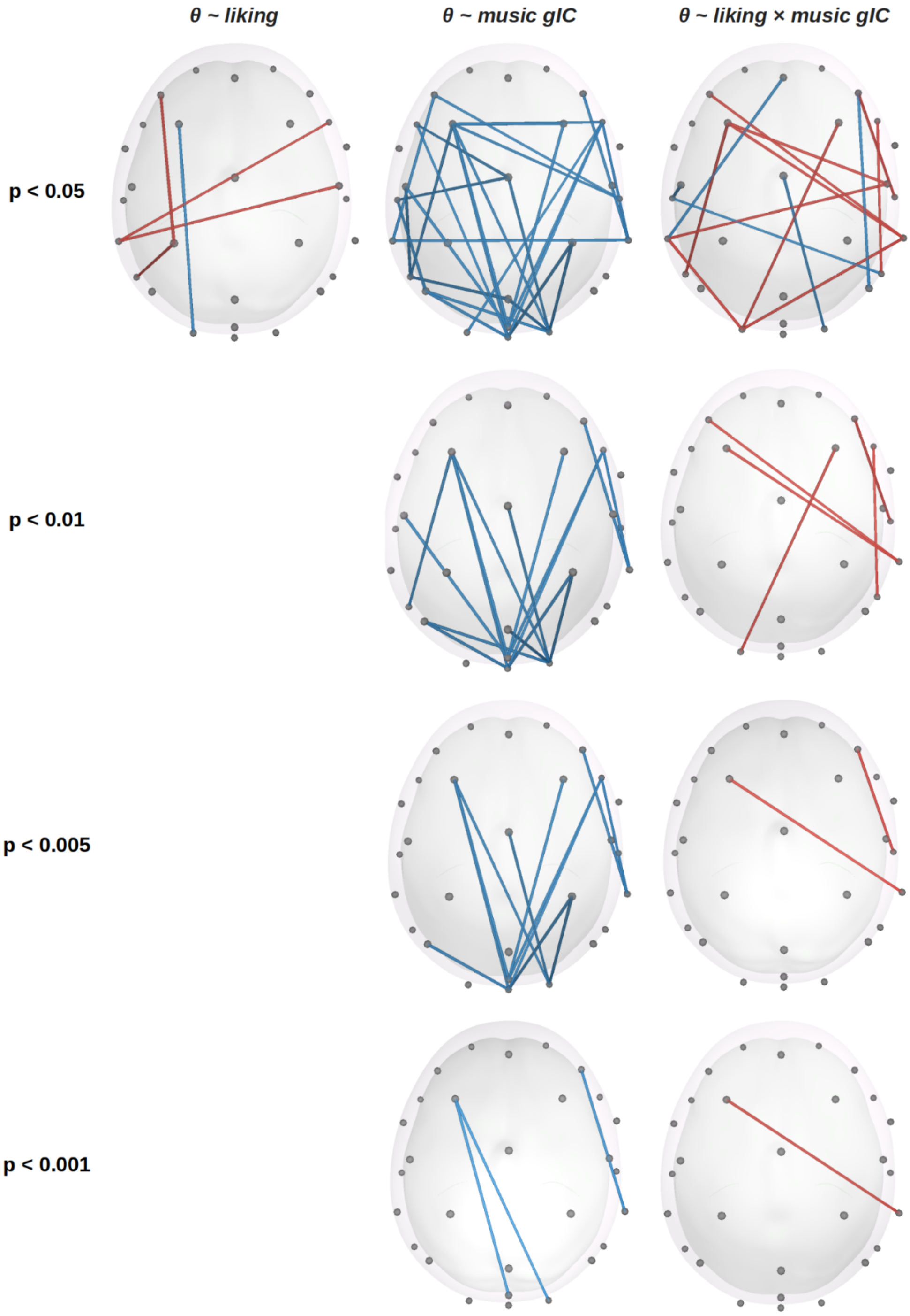


Figure 3.12 Significant connections in theta under the frequentist framework with different alpha levels for **A)** main effects of liking, **B)** main effects of music-related brain function and **C)** the interaction term. Red lines indicate positive relationships and blue lines negative relationships. No connection survived standard p-value corrections.

Different Theta Oscillatory Networks Underlie Pleasantness Evoked by Familiar and Unfamiliar Music

3.3 Study 3

3.3.1 Abstract

Music-evoked pleasantness has been extensively reported to be modulated by familiarity. Nevertheless, while the brain oscillatory dynamics underlying the process of giving value to music are beginning to be understood, little is known about how familiarity might modulate the oscillations associated with music-evoked pleasantness. The goal of the present experiment was to study the influence of familiarity in the relation between theta phase synchronization and music-evoked pleasantness. EEG was recorded from 22 healthy participants while they were listening to both familiar and unfamiliar music and rating the experienced degree of evoked pleasantness. By exploring interactions, we found that right fronto-temporal theta synchronization was positively associated with music-evoked pleasantness when listening to unfamiliar music. On the contrary, inter-hemispheric temporo-parietal theta synchronization was positively associated with music-evoked pleasantness when listening to familiar music. These results shed some light on the possible oscillatory mechanisms underlying fronto-temporal and temporo-parietal connectivity and its relationship with music-evoked pleasantness and familiarity.

3.3.2 Introduction

Music is undoubtedly a powerful source of pleasure for most human beings, despite its abstract nature. While multiple factors may contribute to music's hedonic impact, its relation to familiarity has drawn the attention of researchers across disciplines. Evidence suggests a trend in liking familiar music more than unfamiliar one (Chmiel and Schubert, 2017), indicating that familiarity is an important modulator of music evoked pleasantness. This has been traditionally observed in behavioral experiments describing a “mere exposure” effect on musical appreciation, consisting in an increased liking response for music that had been previously heard due to implicit psychological mechanisms (Peretz et al., 1998). This effect has been classically attributed to a reduction in perceived complexity. In other words, with repeated exposure, the listener implicitly learns the attributes and contingencies of the stimuli and therefore perceives them as less complex and more likeable (Berlyne, 1971). Indeed, influential theories propose that when individuals listen to music, they make predictions about how it is going to unfold based on both schematic expectations (implicit knowledge about the encultured rules of music) and veridical expectations (factual knowledge about concrete pieces of music) (Tillmann et al., 2014). When these predictions are compared to the actual incoming information, reward signals are believed to be triggered as a function of the certainty of the predictions and the surprisal of the outcomes (Salimpoor et al., 2015). In the case of music-evoked pleasantness as a function of factual familiarity, the most pleasurable musical events would be characterized by a compromise between predictability and surprise (Hansen et al., 2017). As individuals are exposed to music, predictions are updated, and so is their associated hedonic value. Familiarity effects on music evoked pleasantness could thus be explained by an increase in predictive precision as veridical expectations come into play, at least while there is still room for surprise.

Consistent with this theoretical account, neuroscientific research has associated the pleasurable experience of listening to music with predictive coding in the auditory domain via fronto-temporal loops (Salimpoor et al., 2015), as well as with the brain reward system via dopaminergic activation of the striatum (Salimpoor et al., 2011). The different nodes comprising this network carry out relevant functions for music perception to take place. On the one hand, the temporal lobe is crucial in the processing of auditory inputs (Koelsch, 2014). On the other hand, the PFC is a pivotal area for emotional control (Rogenmoser et al., 2016), the processing of time information (Abrams et al., 2011) and working memory (Zatorre et al., 1994) in the musical domain. Functional streams assembling these two structures have been hypothesized to underlie auditory working memory, which in turn enables the predictive dynamics ultimately necessary for music to become rewarding (Zatorre and Salimpoor, 2013). Indeed, temporal areas such as the STG and Heschl's gyrus along prefrontal areas such as the vmPFC, OFC and the IFG all have been related to pleasant music listening (Blood and Zatorre, 2001, Brown et al., 2004, Menon and Levitin, 2005, Koelsch et al., 2006). Moreover, both structural and functional connectivity between temporal and frontal nodes and the striatum have been found to be modulated by music-evoked pleasantness and individual differences in music-reward sensitivity (Salimpoor et al., 2013, Sachs et al., 2016, Martínez-Molina et al., 2016).

The oscillatory dynamics of the brain interactions underlying music-evoked pleasantness have also been studied. Most notoriously, both frontal theta power and fronto-temporal theta synchronization have been related to music-evoked pleasantness and related constructs (Rogenmoser et al., 2016, Sammler et al., 2007, Lin et al., 2010, Mikutta et al., 2014, Omigie et al., 2015, Ara and Marco-Pallarés, 2020). Interestingly, frontal and fronto-temporal theta rhythms have also been related to working memory and expectancy in the auditory and musical domains (Kaiser, 2015, Recasens et al., 2018), suggesting further evidence in favor of the predictive coding hypothesis of music-evoked pleasantness.

Despite this corpus of evidence, the neural underpinnings underlying liking for (factually) familiar music have not been extensively investigated. Among the few, an fMRI study by Green et al. (Green et al., 2012) linked listening to previously exposed music during a liking task to an increase of activity in the dlPFC cortex and the IPC. The authors interpreted this functional interplay as underlying unintentional memory retrieval of familiar content into working memory upon re-exposure. Regarding music-related familiarity, Jagiello et al. (2019) also found greater late amplitudes over frontal and parietal sites to be related to familiar music listening in an ERP study, phenomena related to recognition processes elsewhere (Yonelinas, 2002). Moreover, in a metanalysis by Freitas et al. (2018), listening to familiar music was found to be associated with activity in the *left superior frontal gyrus*, the *ventral lateral nucleus of the left thalamus* and the *left medial frontal gyrus*; while listening to unfamiliar music was associated to activity in the left insula, right *cingulate cortex* and right *middle frontal gyrus*. Interestingly, there is a great amount of overlap between the engaged areas found in these studies and the areas consistently found to be related to music-evoked pleasantness in other lines of research, particularly over frontal cortices. This would support the idea that familiarity and evoked pleasantness are indeed interlaced during music listening. Nonetheless, some degree of spatial differentiation is also observed, suggesting that other brain mechanisms may come into play when listening to and liking familiar music.

While the literature commented above identifies the spatial and temporal signatures of the studied phenomenon, these fMRI and ERP studies do not tackle the neural mechanisms that might explain how the different brain areas underlying liking for familiar music bind together. In these regards, neural oscillations have been hypothesized to be the means of communication between the different nodes of a brain network underlying cognition, with slow rhythms particularly well suited to synchronize distant brain areas (Buzsáki and Draguhn, 2004). To date, however, the connectivity dynamics between the brain nodes associated with liking for familiar music have not been addressed, neither their oscillatory signature.

In the present experiment we studied theta cortical rhythms associated with music-evoked pleasantness as modulated by familiarity. In order to reach a good compromise between ecologic validity and experimental control, we induced familiarity in an exposure session using (likely) unknown music stimuli that otherwise were naturalistic and conforming to the participants' preferences. Motivated by a connectivity approach and based on the results of previous studies (Ara and Marco-Pallarés, 2020, Green et al., 2012, Jagiello et al., 2019) and physiological plausibility (Buzsáki and Draguhn, 2004), we focused our analysis on theta synchronization between frontal, temporal and parietal signals. We hypothesized that the association between fronto-temporal theta synchronization and music-evoked pleasantness would be modulated by familiarity. In addition, we expected other connectivity patterns to show up as a result of taking familiarity into account.

3.3.3 Materials and methods

Participants

Twenty-two right-handed individuals (M = 21.86 years old, SD = 2.36, 17 women) participated in the experiment. All participants were chosen to roughly have similar music preferences toward indie, pop, electronic and folk music genres as assessed with the STOMP-R (cut-off ≥ 4; Rentfrow and Gosling, 2003) as well as similar profiles of music reward and physical anhedonia as assessed with the BRMQ (cut-off > 64; Mas-Herrero et al., 2013) and the PAS (males cut-off < 28, females cut-off < 20; Chapman et al., 1976), respectively. None of the participant had received formal training in music for more than three years. All participants gave written informed consent and were paid 10€ per hour. All procedures were approved by the Bioethical Comission of the University of Barcelona and all experimental procedures were carried out according to the relevant guidelines and regulations.

Stimuli

The musical stimuli used in this study were the same as in study 1 (see 3.1). Sixty musical fragments formed a pool of stimuli from which the experimental excerpts were taken. The stimuli consisted in fragments of 45s from commercially available songs of several music genres including indie, pop, electronic, folk and experimental music. These stimuli were selected to be likely unfamiliar and to elicit variable degrees of pleasantness based on the results of a pilot study with a separate sample of individuals. The 45s fragments were chosen to be representative of the whole musical pieces (e.g. that they included more than one theme, that variations took place and/or that several instruments were present).

Experimental procedure

The experimental design is depicted as a diagram in Figure 3.13. The experiment was divided in two sessions with a 24h inter-session lapse: an exposure session and an experimental session. In the exposure session, participants were exposed to 30 music excerpts randomly drawn from the pool of stimuli. After each excerpt had finished participants responded to a 7-point Likert familiarity scale, where 1 meant “I have never heard this song before”, 2 meant “it sounds familiar but I cannot recognize it”, 3 meant “I have listened to this song once”, 4 meant “I have listened to this song a few times”, 5 meant “I have listened to this son numerous times”, 6 meant “I have listened to this song a lot” and 7 meant “I know this song to perfection”. In the experimental session participants listened to the same materials plus a set of 30 novel excerpts, in random order, and were asked to rate the degree of evoked pleasantness on a continuous basis while listening to each excerpt with as many responses as they wanted. Responses were given via the numeric keys of a computer keyboard with the following equivalences: 1: “I don’t like it”; 2: “I like it a little”; 3: “I like it moderately”; 4: “I like it a lot”; and 5: “I experience frissons”. Response keys had to be held for as long as a particular rating applied for the individual. Participants had to look to a fixation cross while listening to the excerpts. If no response was given after half the stimulus was presented, that trial was halted and automatically rejected from all conditions for that subject. After each excerpt had finished participants responded to the same Likert familiarity scale.

Self-reported data

In order to have a metric index of online evoked pleasantness for each trial in the experimental session we computed the average of every response given for each excerpt weighted by the amount of time each response was held. For the statistical analysis of the EEG data, these data were dichotomized per subject by the means of a median split in order to ease model-fit and interpretation (excerpts rated below the median were coded as “least liked”, while excerpts rated equally or above the median were coded as “most liked”). The familiarity Likert scale was used to reject trials identified by the individuals to be familiar the first time they were presented (rejection cut-off > 2) from all conditions.

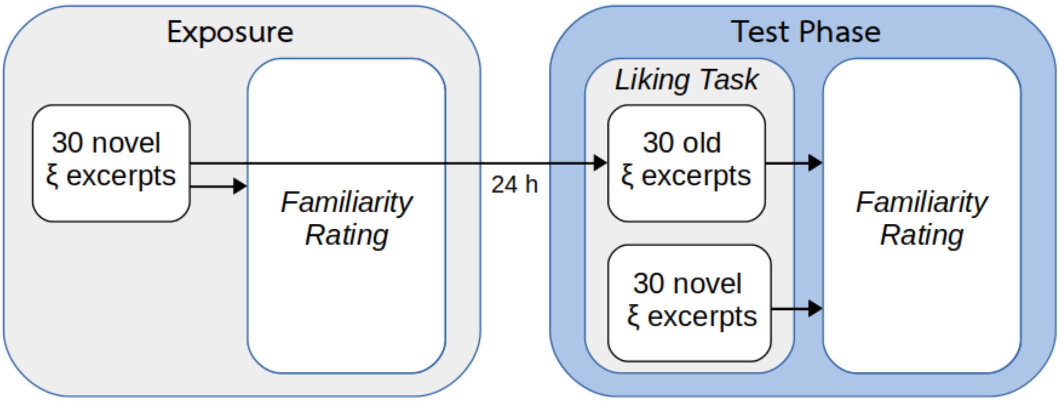


Figure 3.13 Experimental design diagram. During exposure, participants listened to 30 music stimuli randomly taken from a pool of 60 stimuli and rated their familiarity with the materials after each excerpt had been presented. Twenty-four hours later, participants listened to the same stimuli plus another 30 novel ones while continuously reporting the degree of pleasantness evoked. After each excerpt had been presented, participants rated their familiarity with the materials.

EEG data acquisition

EEG was recorded from the scalp during the second session (0.01 Hz high-pass filter with a notch filter at 50 Hz; 250 Hz sampling rate) using a BrainAmp amplifier with tin electrodes mounted on an Easycap (Brain Products©), at 61 standard positions (Fp1/2, AF3/4, Fz, F7/8, F5/6 F3/4, F1/2, FCz, FT9/10, FT7/8, FC5/6, FC3/4, FC1/2, Cz, T7/8, C5/C6, C3/4, C1/2, CPz, TP9/10, TP7/8, CP5/6, CP3/4, CP1/2, Pz, P7/8, P5/6, P3/4, P2/1, POz, PO7/8, PO3/4, Oz, O1/2) and left and right mastoids. An electrode placed at the lateral outer canthus of the right eye served as an on-line reference and an electrode at the infraorbital ridge of the right eye was used to monitor vertical eye movements. Electrode impedances were kept below 10 kΩ during the whole session.

EEG signal processing

The same signal processing procedures used in study 1 were applied to this study's EEG data. EEG was re-referenced off-line to the linked mastoids and band-pass filtered from 0.1 to 45 Hz. Epochs consisted in the whole time-window of each listening and were baseline-corrected using the average of the whole fragment. Artifacts in these epochs were identified and corrected using ICA. Epochs with absolute mean amplitude higher than 100 μV after ICA correction were rejected. One subject was excluded from the analysis because of poor physiological data quality. The surface Laplacian transform was applied to these data in order to reduce volume conduction and make the data reference-free (Perrin et al., 1989). To avoid effects of surprise at the beginning and end of the song, the first and last 2s were removed from the epochs for subsequent analysis. Time-frequency decomposition was computed on each epoch using 5-cycle complex Morlet wavelets in the frequency band of interest (theta: 4–8 Hz). Phase values for each electrode and frequency were obtained over time from this decomposition.

Then, ISPC-time was computed for each epoch as an index of phase synchronization between signals .This was done for every frequency in the band of interest and all electrode pairs involving frontal, temporal and parietal signals (AF3/4, Fz, F7/8, F5/6 F3/4, F1/2, FCz, FT7/8, FC5/6, FC3/4, FC1/2, Cz, T7/8, TP7/8, CP5/6, CP3/4, CP1/2, Pz, P7/8, P5/6, P3/4, P2/1, POz, PO7/8, PO3/4). Finally, ISPCs were averaged across frequencies. We excluded from subsequent analysis connections involving peripheral electrodes (Fp1/2, FT9/10, TP9/10) and connections where the two electrodes were less than 6 cm apart from each other, since these most likely reflect residual artifactual activity and volume conduction, respectively.

3.3.4 Statistical Analysis

Self-reported data

In order to investigate whether participants found target music presented in the experimental session (old music) more familiar than in the exposure session and as compared to novel music in the experimental session a Bayesian multilevel ordinal regression model was carried out with reported familiarity as response variable, condition as explanatory variable and varying intercepts and slopes per subject. A cumulative likelihood function with the probit link function was assumed to explain the data in order to treat the Likert scale as ordinal (μ = probit(x), σ = 1). Weakly informative priors were placed over the latent variable’s thresholds and slopes (normal: $\mu = 0$, $\sigma = 1$), as well as over the varying effects (gamma: $\alpha = 2$, $\beta = 2$). The reference explanatory condition was target music in the experimental session (old music). Therefore, the difference between target music in the experimental session and in the exposure session was quantified by coefficient β_1. The difference between old music and novel music in the experimental session was quantified by coefficient β_2. The difference between novel music in the experimental session and target music in the exposure session was quantified by the difference between slopes (β_2 - β_1). To test the group-level differences to be non-zero a 95% HDI was used to check the inclusion of the null hypotheses (H_0: β_1, β_2, β_2-β_1 = 0) in the posteriors assuming a ROPE of ±0.01. The reported point estimates correspond to the mode of the posteriors.

In order to investigate the difference between conditions of the experimental session (new vs. old) in reported pleasantness, a generalized Bayesian multilevel linear model was carried out with reported pleasantness as response variable, condition as explanatory variable and varying intercepts and slopes per subject. A student-t likelihood function was assumed to explain the data in order to accommodate outliers (μ = identity; prior on σ: student-t: $\mu = 0$, $\sigma = 10$, $\nu = 3$; prior on ν: gamma: $\alpha = 2$, $\beta = 0.1$). Weakly informative priors were placed over the intercept and slope (normal: $\mu = 0$, $\sigma = 1$), as well as over the varying effects (gamma: $\alpha = 2$, $\beta = 2$). To test the group-level slope to be non-zero a 95% HDI was used to check the inclusion of the null hypothesis (H_0: $\beta_1 = 0$) in the posterior assuming a ROPE of ±0.01. The reported point estimate corresponds to the mode of the posterior and quantifies the difference between conditions with new music as the reference explanatory condition.

EEG phase synchronization

In order to investigate the effects of music-evoked pleasantness on theta synchronization as moderated by familiarity in the experimental session, mass-univariate Bayesian multilevel beta regression models were carried out with ISPCs as response variables, dichotomous liking, familiarity condition and their interaction as explanatory variables and varying intercepts and slopes per subject. A beta likelihood function with the logit link function was assumed to explain the data since ISPC-time values are non-normally distributed in the unit interval (μ = logit(x); prior on φ: gamma: $\alpha = 0.01, \beta = 0.01$). Weakly informative priors were placed over the overall intercepts and slopes (normal: $\mu = 0$, $\sigma = 1$), as well as over the varying effects (gamma: $\alpha = 2$, $\beta = 2$). The moderation effects of familiarity on the relationship between liking and ISPCs were quantified by coefficients β_3. To test the group-level moderation effects to be non-zero a 95% HDI was used to check the inclusion of the null hypotheses (H_0: $\beta_3 = 0$) in the posteriors assuming a ROPE of ±0.01. When a non-zero interaction was found, post-hoc posterior inspection was carried out according to the model in order to explore non-zero differences between least liked and most liked reports in each familiarity condition (H_0: PH = 0; $PH_{new\_most-new\_least} = \beta_1$, $PH_{old\_most-old\_least} = \beta_1 + \beta_3$) with a 95% HDI assuming a ROPE of ±0.01. Only connections exhibiting non-zero results in these post-hoc explorations are considered. Reported point estimates correspond to the mode of the posteriors.

Bayesian inference specification

We used Bayesian inference in order to ameliorate the multiple testing problem posed by mass-univariate analyses without having to employ arbitrary thresholds nor the overly restrictive post-hoc corrections usually associated with frequentist statistics. This is achieved by virtue of Bayesian inference's statistical properties (see Ara and Marco-Pallarés, 2020 for a similar case). In addition, the generalized linear model allowed us to make appropriate assumptions about the dependent variables' distributions.

Posterior distributions were approximated using 5 Markov chains of 2000 samples with no thinning, burning-in the first 1000 samples. The No-U-turn sampler algorithm was used to draw samples. All chains were initialized at 0. All models converged as indicated by Gelman's split-R-hat equaling 1 (Gelman et al., 2013).

3.3.5 Results

Self-reported data

Figure 3.14 shows the familiarity ratings for the excerpts listened the first day (exposure), their repetition the second day (old music) and the new songs listened the second day (new music). As can be seen, ratings for the exposure and new music were mainly 1 ("I had never heard this song before") or 2 ("it sounds familiar but I cannot recognize it"), while for the old music the most selected rating was 3 ("I have listened to this song once"). This was further corroborated by the statistical analysis showing that familiarity ratings were higher for target music in the experimental session than in the exposure session (β_1 = -2.34, 95% HDI = -2.67 - [-2.02]) and as compared to novel music's in the experimental session (β_2 = -2.14, 95% HDI = -2.46 - [-1.79]) Coefficients are expressed in standard deviation units. These results demonstrate that participants correctly recognized those songs presented the day before.

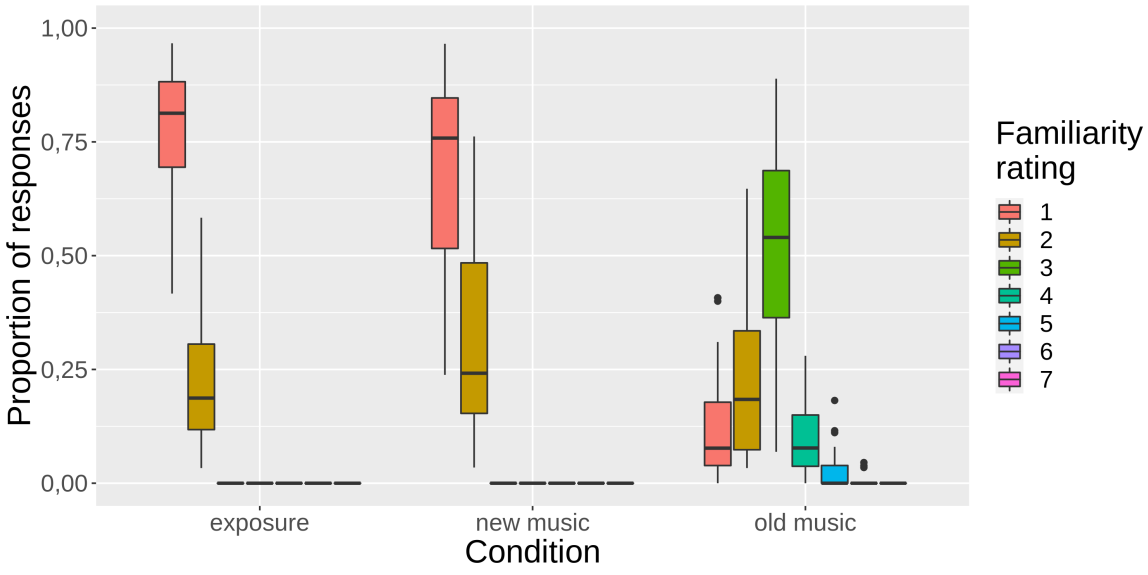


Figure 3.14 Distribution of average proportion of responses given for each familiarity rating across subjects in each familiarity condition (1: "I had never heard this song before"; 2: "it sounds familiar but I cannot recognize it"; 3: "I have listened to this song once"; 4: "I have listened to this song a few times"; 5: "I have listened to this son numerous times", 6: "I have listened to this song a lot" and 7: "I know this song to perfection"). Music recognized as familiar in the exposure session and in the new music condition of the experimental session are excluded from all conditions (rejection cutoff > 2).

In addition, time-weighted reported pleasantness was higher for old songs than for new songs in the experimental session (β_1 = 0.12, 95% HDI = 0.01 - 0.24). Figure 3.15 shows that the liking rates for all the participants were higher for the excerpts that were previously listened to than for the new ones. The distribution of time-weighted reported pleasantness per excerpt and subject is displayed in Figure 3.17 of the appendix.

EEG phase synchronization

Two right fronto-temporal connections exhibited a non-zero increase with reported pleasantness in the new condition only (AF4-FT8: β_3 = -0.08, 95% HDI = -0.13 - [-0.02], $PH_{new\_most-new\_least}$ = 0.05, 95% HDI = 0.02 - 0.09; AF4-T8: β_3 = -0.08, 95% HDI = -0.13 - [-0.02], $PH_{new\_most-new\_least}$ = 0.06, 95% HDI = 0.01 - 0.10). In addition, two right-temporal to left-parietal connections exhibited a non-zero increase with reported pleasantness in the old condition only (T8-CP5: β_3 = 0.14, 95% HDI = 0.06 - 0.22, $PH_{old\_most-old\_least}$ = 0.08, 95% HDI = 0.01 - 0.14; CP5-TP8: β_3 = 0.16, 95% HDI = 0.07 - 0.24, $PH_{old\_most-old\_least}$ = 0.10, 95% HDI = 0.03 - 0.16). Coefficients are expressed in log-odds. Results are displayed in Figure 3.17. In order to compare these results with standard frequentist approaches using different alpha levels please see Figure 3.18 in the appendix.

3.3.6 Discussion

The goal of the present experiment was to study effects of familiarity and music-evoked pleasantness on phase synchronization between frontal, temporal and parietal signals in the theta oscillatory band. We exposed a cohort of participants to a set of musical fragments and measured their EEG signals and evoked reported pleasantness 24h later in a second listening session, along a set of novel musical fragments.

Familiarity ratings for target stimuli were significantly greater in the experimental session than in the exposure session and as compared to novel stimuli in the experimental session, indicating that familiarity was indeed induced. Consistent with previous liter-

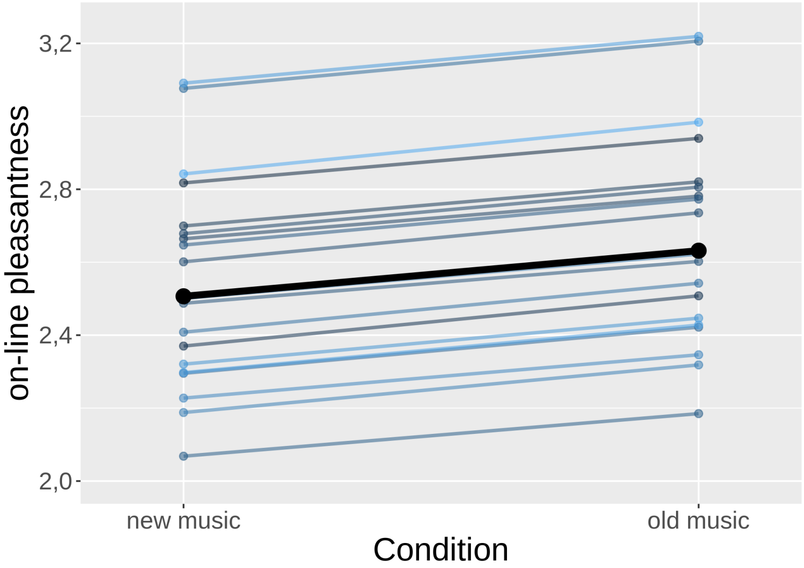
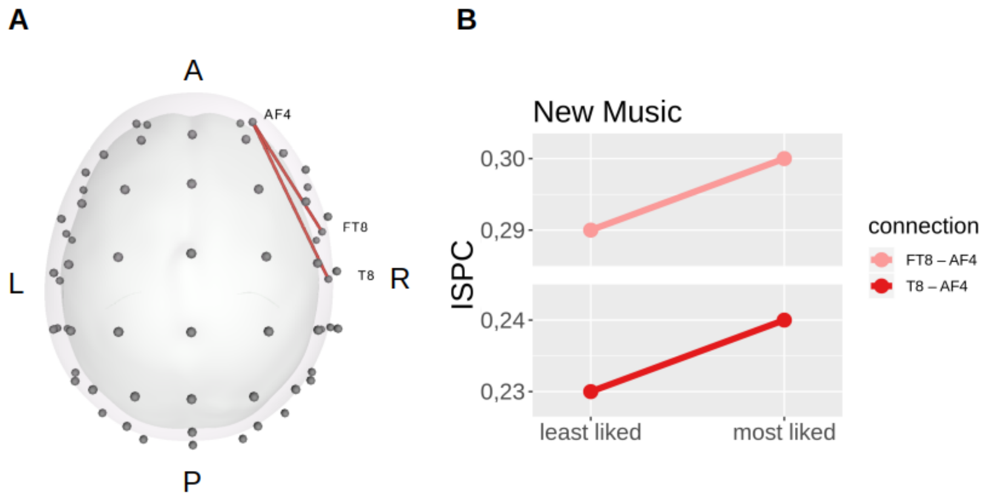


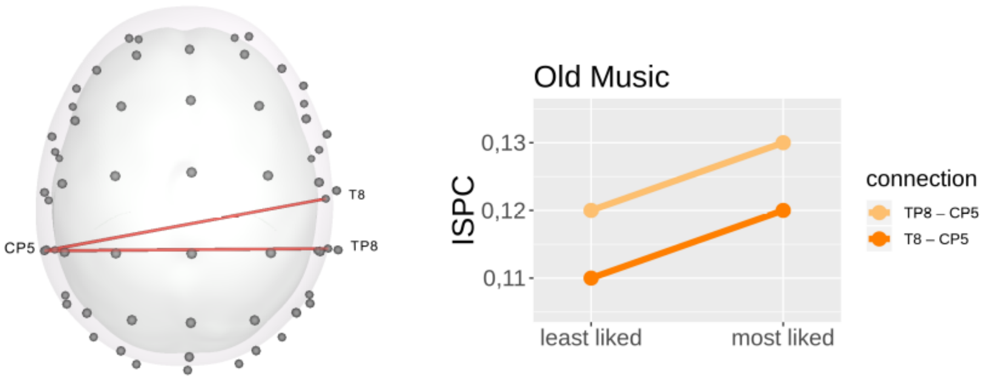
Figure 3.15 Time-weighted self-reported pleasantness in the two familiarity conditions of the experimental session (new vs old). Thin blue lines represent each participant's increase. The thick black line represents the group-level increase. Dots represent parameter estimates.

ature, liking for old songs was significantly greater than for new songs, revealing that one repetition and 24h of consolidation was enough to induce the mere exposure effect of exposure on liking. Seminal studies had already demonstrated that this effect is observed with as few as one repetition, even when explicit recognition fails (Peretz et al., 1998, Johnson et al., 1985). In the context of the current study, we consider the presence of the mere exposure effect relevant, since it demonstrates that familiarity was not only induced, but also interlaced with self-reported pleasantness, thus making subsequent analysis of EEG data pertinent.

In the EEG synchronization analysis, we observed an increase in right fronto-temporal theta synchronization with greater reported pleasantness for unfamiliar musical fragments. Conversely, liking for familiar music revealed greater theta synchronization between right temporal and left parietal signals. These results suggest that different theta connectivity patterns are involved in the process of giving value to music depending on whether the stimuli are familiar or unfamiliar to the listener.



most liked > least liked
(new music)



most liked > least liked
(old music)

Figure 3.16 Non-zero results **A)** with their corresponding prediction plots **B)** in the theta connections of interest. Straight lines represent predictions of the response variables in each liking × familiarity condition of interest following parameter estimates. Predictions are made on the original scale of the dependent variable.

Right fronto-temporal cortices have been found to co-activate during pleasant music listening and to be related to reward-processing areas during peak pleasurable events (Blood and Zatorre, 2001, Salimpoor et al., 2013). Furthermore, frontal and parietal areas have been related to emotional control in reaction to music (Rogenmoser et al., 2016). Fronto-temporal loops also underlie working memory and PE processing in the auditory and musical domains (Kaiser, 2015, Recasens et al., 2018), functions hypothesized to be involved in music-evoked pleasantness by enabling the temporal representations and predictive dynamics necessary for music perception and its subsequent affective evaluation (Salimpoor et al., 2015).

In addition, theta oscillations have been revealed to play a role in music-evoked pleasantness. Frontal theta power has been associated with music-evoked pleasantness and related constructs such as evoked positive valence and musical consonance (Rogenmoser et al., 2016, Sammler et al., 2007, Lin et al., 2010, Mikutta et al., 2014, Omigie et al., 2015). Importantly, right fronto-temporal theta synchronization in similar areas to the ones found in Ara and Marco-Pallarés (2020) was observed to increase with reported pleasantness when listening to novel music. These consistent results suggest that music-evoked pleasantness critically depends on right fronto-temporal connectivity when the musical stimuli are unknown, possibly due to the processing of schematic expectations while music is unfolding within auditory working memory.

On the other hand, frontal and parietal cortices have been reported to correlate with music-induced familiarity. This functional complex has been interpreted to underlie memory retrieval of known musical materials (Green et al., 2012). Likewise, EEG activity over right frontal and left parietal regions has been related to familiar music listening (Jagiello et al., 2019) and left temporo-parietal theta activity is thought to be involved in recognition memory (Jacobs et al., 2006). We found theta synchronization between right temporal and left parietal signals to increase with liking for familiar music. This association suggests that music-evoked pleasantness relies more strongly on the neuropsychological mechanisms emerging from these connections when the musical stimuli are known, possibly recognition processing in the form of veridical expectations in the auditory domain.

It is difficult to determine from these results whether both connectivity profiles are completely dissociated in different familiarity conditions, or whether they work in communion but assuming different roles in each context. A tentative interpretation is that both fronto-temporal and temporo-parietal theta connections are engaged during music listening, but positive valuation of the stimuli relies on fronto-temporal connectivity when music is novel and shifts its focus over temporo-parietal connectivity as music becomes familiar. Positive value would thus be assigned to efficient online predictive processing in the former case (schematic expectancy) and to efficient recognition in the latter (veridical expectancy). This latter case would be associated with a greater likelihood of reporting the most evoked pleasantness, considering our behavioral results and previous evidence (Chmiel and Schubert, 2017). It must be noted, however, that a variety of evidence exists showing how liking for music correlates with fronto-temporal activations using potentially familiar stimuli (e.g. Blood and Zatorre, 2001; or Martínez-Molina et al., 2016). Therefore, while we show a predominance of these connections during positive valuation of unfamiliar music, we cannot completely rule out its involvement in the valuation of familiar music.

It is also interesting to note that our results add up to several studies pointing out certain right hemispheric dominance in music processing (e.g. Zatorre and Gandour, 2008, Zatorre et al., 2002, Hyde et al., 2008, Özdemir et al., 2006, Martínez-Molina et al., 2016 or Ara and Marco-Pallarés, 2020), since all our results involve right temporal nodes, and frontal nodes are also right-lateralized. This right-hemispheric dominance could be attributed to the specialization of right temporal and frontal areas in pitch perception and auditory working memory, as well as in the detection of pattern violations (Zatorre and Salimpoor, 2013). However, evidence showing no hemispheric specialization also exists (e.g. Jäncke and Alahmadi, 2016), as well as research noting that inter-hemispheric interactions are needed for normal music listening (Schubert and Pearce, 2016). Therefore, the involvement of the left temporal lobe cannot be completely ruled out in music-related cognition. Instead, we interpret our results as showing a relative right hemisphere dominance, rather than an absolute specialization.

The present study is not absent of limitations. While the use of EEG provided us with a good temporal resolution to study oscillatory dynamics, it lacks the appropriate spatial resolution to make more precise anatomical inferences, neither it captures the subcortical signals associated with the process of giving value to music. Multimodal experiments are necessary to replicate and link the results here present with reward signals in the striatum during peak pleasurable events, as well as to precise the cortical localization of the EEG signals. Other limitations include the fact that subjects evaluated the musical stimuli while listening to them, which might have imposed an active listening strategy (Jäncke et al., 2015), and analyzing the data relative to the whole music fragments rather than studying the particular EEG, behavioral and acoustic time-courses, which may offer a complementary view on how temporal dynamics of interest unfold (e.g. see Arjmand et al., 2017, Sturm et al., 2014, Sturm et al., 2015, Jäncke et al., 2018, Martin et al., 2018). Finally, we only counted on one repetition and 24h of consolidation to induce familiarity. While this resulted to be enough to observe the mere exposure effect and differences in the EEG data, more repetitions and tests would be necessary to see the extent to which these effects are stable or change over time.

3.3.7 Conclusions

Considering our results, the relation between music-evoked pleasantness and temporal theta synchronization is moderated by familiarity, with fronto-temporal connectivity underlying liking for novel music and temporo-parietal connectivity underlying liking for familiar music, the latter being associated with greater liking responses. These distinct mechanisms could be reflecting how positive valuation of musical stimuli shifts its focus from schematic expectations to veridical expectations as music becomes familiar. This claim must be furthered researched with the appropriate paradigms and methodology.

3.3.8 Appendix

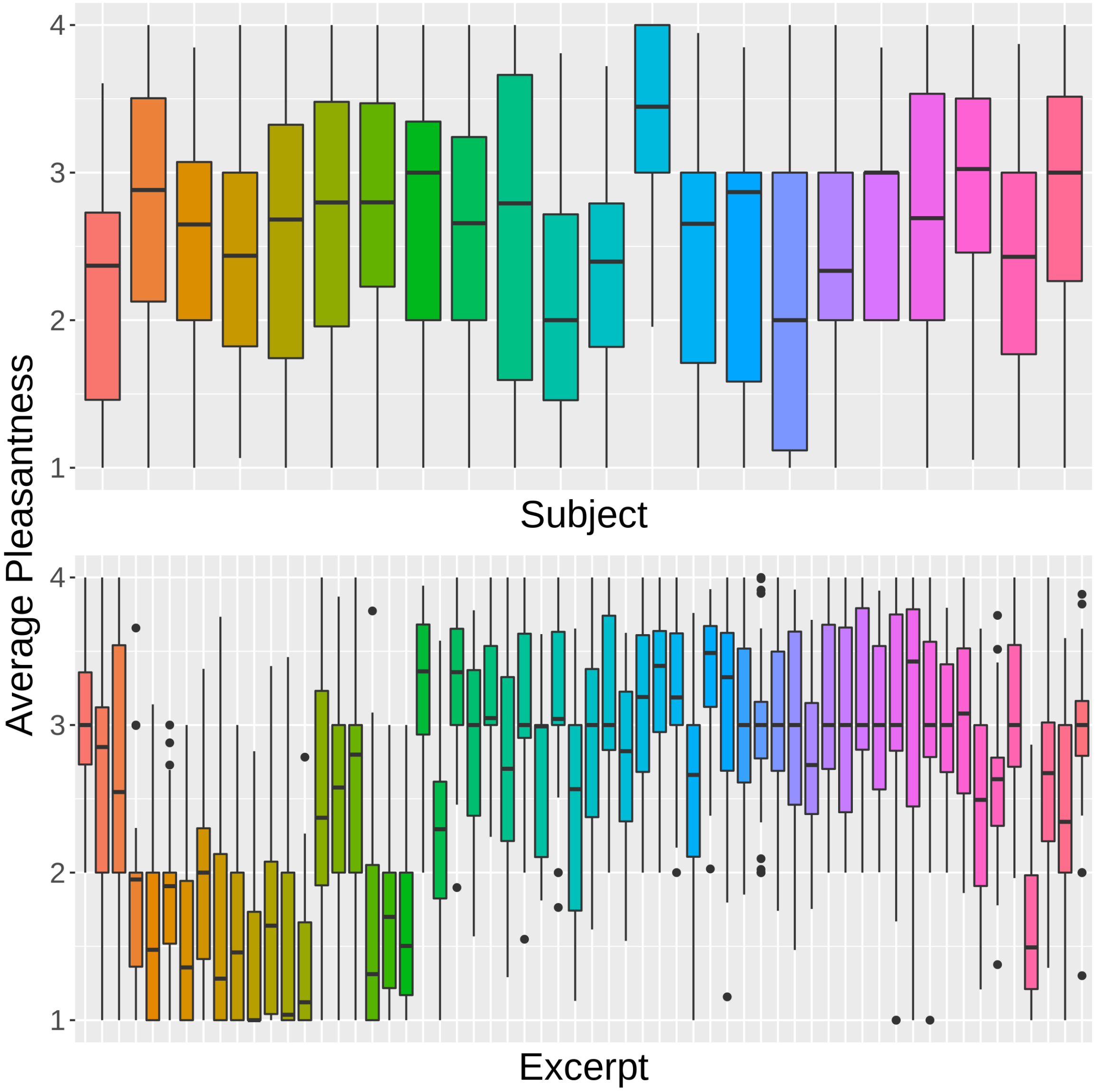


Figure 3.17 Distribution of time-weighted self-reported pleasantness per subject (top) and excerpt (bottom).

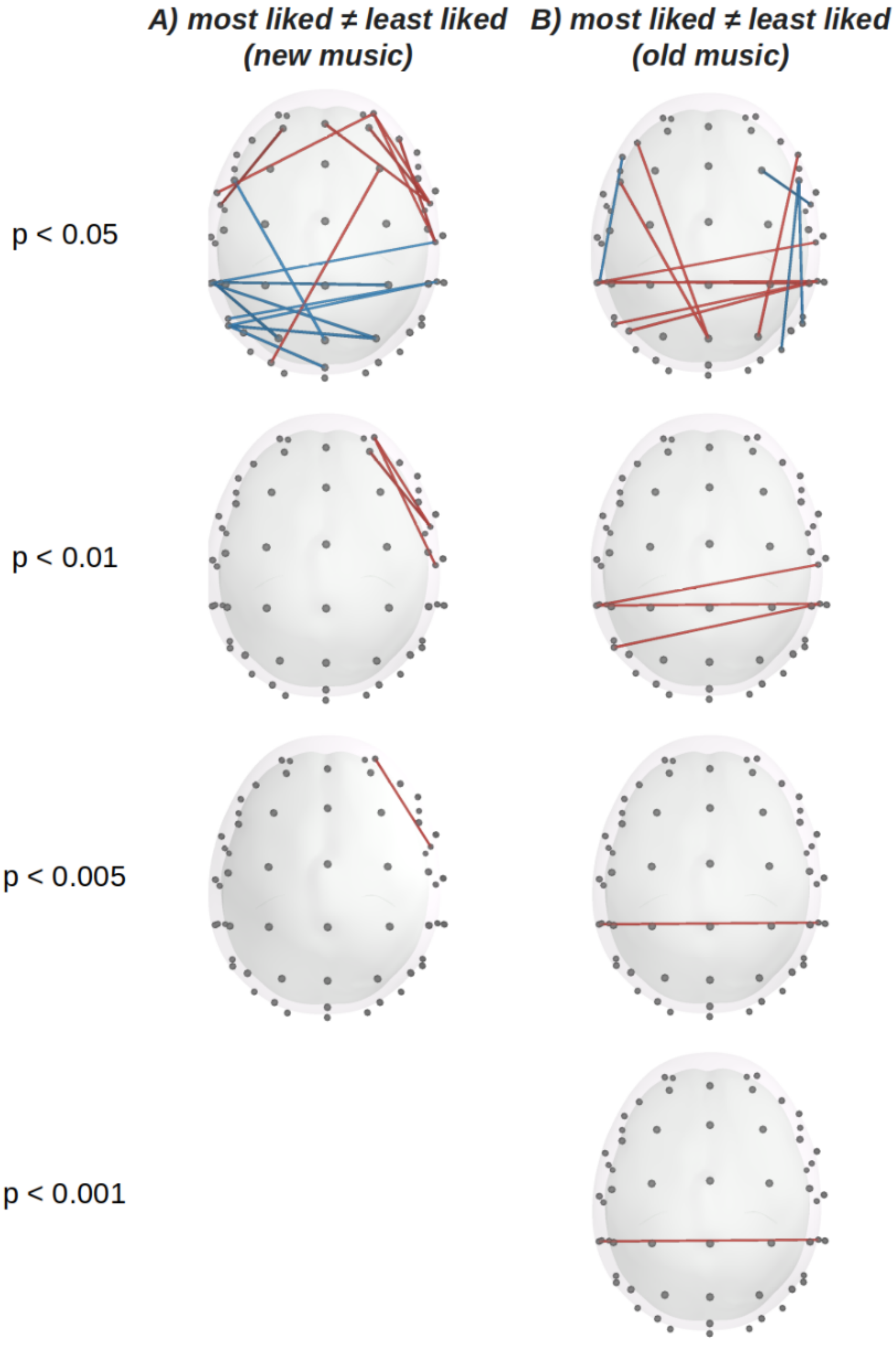


Figure 3.18 Significant connections in theta under the frequentist framework with different alpha levels for **A)** effects of liking for novel music and **B)** effects liking for familiar music. Red lines indicate positive relationships and blue lines negative relationships. No connection survived standard p-value corrections.

4. Discussion

In the three studies presented in this thesis we empirically addressed a number of research inquiries regarding music-evoked pleasantness and its associated brain rhythms. Particularly, these consisted in identifying what brain nodes theta rhythms synchronize during pleasant music listening and their associated anatomic activations, as well as the modulatory effect of familiarity on these connectivity topologies. In order to test the extent of our hypotheses, neuroimaging and physiological techniques were used along behavioral paradigms.

In the following sections the results of these three studies will be discussed in an integrative fashion. It will be evaluated to which extent the research inquiries have been answered as well as how they relate to each other. Furthermore, the theoretical contributions of this thesis to the state of the art of the neuroscience of music reward will be drawn. Likewise, the methodological aspects present in this thesis will be commented, paying attention to both advantages and caveats. Finally, future directions in the topic given the results and discussion will be proposed.

4.1 Research inquiries and experimental results

Motivated by previous literature in the topic of music-evoked pleasantness and its neural substrates, three research inquiries were set out in this thesis. The first one consisted in *identifying what functional nodes theta rhythms synchronize during pleasant music listening*, following studies that had identified theta power to correlate with music-evoked pleasantness and related constructs. In the first study we tried to answer this question by exposing a cohort of participants to several music stimuli while they reported the degree of evoked pleasantness in real time in an EEG design. After determining the overall theta phase synchronization between all considered electrodes and the overall liking response for every excerpt across subjects we examined how and where these two phenomena were associated. We found that the more music was liked, the more synchronized right fronto-temporal nodes were by theta oscillations.

Previous literature had already revealed that right fronto-temporal connectivity is not only relevant in music perception (Zatorre et al., 1994) but also play an active part in music-reward processing (Blood and Zatorre, 2001). This importance resides in that these loops allow the processing of patterns that go beyond simple auditory percepts in a working memory system (Zatorre and Salimpoor, 2013). Ultimately, reward signals responding to musical stimuli have been related to the predictive and monitoring dynamics generated within this system (Salimpoor et al., 2015), processes that operate through theta rhythms in these connections (Kaiser, 2015; Recasens et al., 2018; Omigie et al., 2019). In study 1 we provide evidence that right fronto-temporal theta connectivity is actively involved in the process of assigning value to music, adding up to previous literature pointing out at frontal theta rhythms as a correlate of music-evoked pleasantness (Sammler et al., 2007; Omigie et al., 2015; Lin et al., 2010; Mikutta et al., 2014; Rogenmoser et al., 2016).

The second inquiry consisted in *understanding the neural networks underlying theta synchronization during pleasant music listening*. While in the first study we identified fronto-temporal theta synchronization to be related to musical liking, converging with previous evidence identifying fronto-temporal networks to be actively involved in music perception and reward (Blood and Zatorre, 2001), the link between these fMRI and EEG findings had not been empirically tested. In the second study we investigated the relationship between activity in music-related fMRI networks and EEG theta synchronization. In order to do so we exposed a cohort of participants to a series of musical excerpts alternated with periods of rest while they rated the degree of evoked pleasantness in a simultaneous fMRI-EEG design. We then investigated how theta synchronization was associated with music-related fMRI activations and how musical liking moderated this relationship.

Firstly, we identified an fMRI network that was consistently engaged during music listening that included both STG and RMCs as well as a portion of the right IFG, consistent with previous neuroimaging literature (Zatorre et al., 1994). Most importantly, fronto-temporal/parietal theta synchronization within this music-related network was modulated by evoked pleasantness, with more synchronization being related to music processing the more music was liked. Coherently with our hypotheses, study 2 shows that while fronto-temporal networks are always engaged during music listening, it is theta rhythms within these loops that are related to affective reactions to music. On the other hand, right-hemispheric specialization in this study was not clear, with left nodes also being involved in our findings.

Finally, our third inquiry consisted in *studying how familiarity modulates theta synchronization during pleasant music listening*. Familiarity has been one of the phenomena observed to be most influential on music-evoked pleasantness (Chmiel and Schubert, 2017) and neuroimaging studies had revealed that listening to (factually) familiar music engages a slightly different network than otherwise (Green et al., 2012). In the third study we explored whether the theta brain connectivity found during pleasant music listening was different depending on whether music was novel or familiar. In order to do so, we familiarized a cohort of participants with some musical stimuli and registered their EEG and liking responses to these excerpts 24 hours later along a new set of musical stimuli. We then studied what nodes theta rhythms synchronized as a function of evoked pleasantness during novel ad familiar music listening, respectively.

Firstly, we confirmed that participants were familiarized with the excerpts presented during exposure. In addition, we replicated previous findings indicating that familiar music is overall preferred over novel music (Johnson et al., 1985; Peretz et al., 1998). Most importantly, by looking at interactions between familiarity and liking we revealed that the right fronto-temporal theta topology found in studies 1 and 2 appeared to be related to liking for novel music, while liking for familiar music was related to temporo-parietal theta synchronization instead. These results are consistent with literature showing that parietal cortices are involved in familiar music listening (Green et al., 2012). Therefore, in study 3 we provided evidence that temporal nodes are engaged in different theta connectivity topologies depending on familiarity during pleasant music listening, with frontal nodes involved in liking for novel music and parietal nodes involved in liking for familiar music.

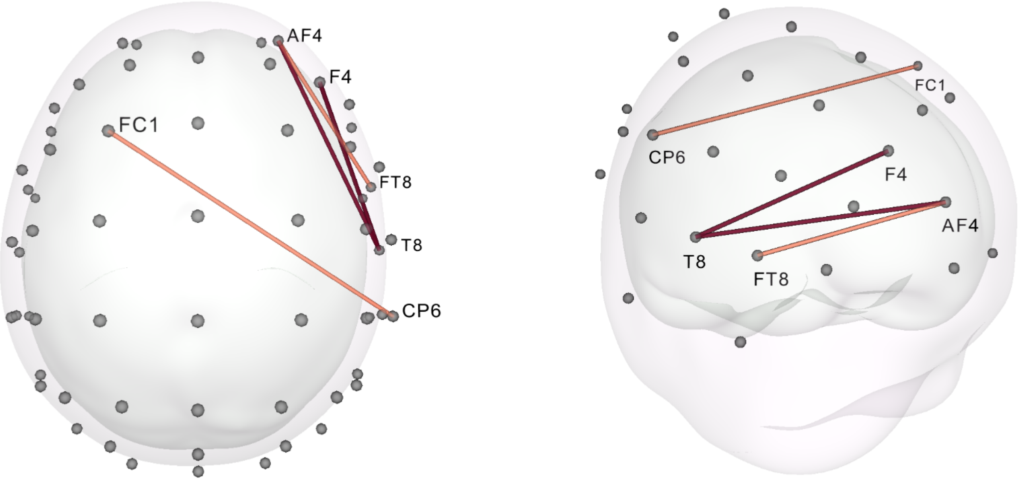


Figure 4.1 Fronto-temporal theta synchronization found across all three studies. (left: dorsal view. right: right lateral view). Right fronto-temporal connections increased in theta synchronization with greater music-evoked pleasantness in studies 1 and in study 3 for the case of novel music. Likewise, right fronto-temporal theta synchronization engaged to a greater extent within a music-related brain network the more musical liking took place in study 2, in addition to a cross-hemispheric fronto-parietal connection. Color intensity represents overlapping connections across the studies.

Altogether, the empirical results of this thesis show that theta rhythms are relevant for synchronizing key brain nodes during pleasant music listening. Particularly, fronto-temporal theta connectivity was consistently found to be associated with music-evoked pleasantness across all three studies (Figure 4.1). Nonetheless, the third study revealed that this topology is more associated with liking for novel music than with familiar music. Familiarity was not controlled in the first and second studies, and while in the first study melodies were overall likely unfamiliar, this was not the case in the second study, where some melodies were classical anthems. Therefore, while in study 3 we provide evidence of fronto-temporal theta connectivity being more strongly involved in liking for novel music, we cannot completely rule out their involvement in overall musical liking, given the results of studies 1 and 2 -a topic to which we shall return later.

Another consistency across all three studies is that we found a relative right-hemispheric dominance of the brain nodes associated with musical liking. This specialization was unequivocal for frontal and temporal nodes synchronized by theta rhythms in study 1 and in the case of liking for novel music in study 3. In addition, in study 2 this specialization was observed for temporal and parietal nodes that were theta-synchronized with frontal nodes as a function of music-related brain function and liking, as well as in music-related IFG activations. Finally, in study 3 only right temporal nodes were theta-synchronized with parietal nodes in relation to liking for familiar music. Importantly, these results are not only consistent across all studies comprising this thesis, but they are also consistent with a growing corpus of literature showing that the processing of music in the brain is right-lateralized to some extent (Zatorre et al., 2002; Özdemir et al., 2006; Hyde et al., 2008; Zatorre and Gandour, 2008; Martínez-Molina et al., 2016).

4.2 Theoretical implications

4.2.1 The role of theta oscillatory activity in music reward

Throughout this thesis it has been conveyed the relevance of theta rhythms in the coupling of brain areas involved in the process of assigning value to music. The results of studies 1, 2 and 3 add up to existing literature showing that theta oscillations increase as a function of music-evoked pleasantness or related constructs (Sammler et al., 2007; Omigie et al., 2015; Lin et al., 2010; Mikutta et al., 2014; Rogenmoser et al., 2016), especially over frontal areas. The EEG and fMRI sites we identified to be synchronized by theta rhythms as a function of music-evoked pleasantness had also been pinpointed in other lines of research to be actively involved in the processing of music perception (Zatorre et al., 1994), music reward (Blood and Zatorre, 2001) and music recognition

(Green et al., 2012). In addition, fronto-temporal synchronization in the theta band had been related to working memory and predictive dynamics in the auditory domain (Kaiser, 2015; Recasens et al., 2018; Albouy et al., 2017; Omigie et al., 2019), processes hypothesized to be intimately intertwined with music hedonic's impact (Zatorre and Salimpoor, 2013; Salimpoor et al., 2015).

We adopted a connectivity approach to analyze the brain data in all three studies. We particularly focused on oscillatory phase synchronization as a candidate physiological mechanism that integrates the areas involved in music-evoked pleasantness. In order to do so, we analyzed long segments of EEG data and studied them along the overall associated liking response. In addition to this, we acquired fMRI data in study 2 along EEG's to identify the anatomic networks associated with music listening and their relationship with liking and the EEG data. This connectivity approach had the advantage of capturing how different brain areas work together in relation to a cognitive phenomenon of interest, rather than simply identifying the brain nodes involved. However, given the correlational nature of the designs presented in this thesis, we cannot infer empirically what precise cognitive operations underlie the observed relationship between theta synchronization and music-evoked pleasantness. Nonetheless, previous findings as well as theories on the topic offer a window for interpretation. Firstly, the fronto-temporal connections characteristic of all three studies are consistent with findings showing temporal areas and frontal areas to engage during music listening (Zatorre et al., 1994). While the temporal lobe is crucial in the processing of auditory percepts, it is through interactions with the frontal lobe that auditory streams are represented. These fronto-temporal loops are the basis of auditory working memory and are responsible for processing auditory patterns that go beyond single auditory events, such is the case of music (Barton and Brewer, 2019).

These fronto-temporal loops take place via two different, though converging streams: the ventral pathway, which connects belt and parabelt areas of the temporal lobe with the inferior frontal cortex along the temporal lobe; and the dorsal stream, which does so through the parietal lobe and dorsally along the frontal lobe. These two loops have been hypothesized to encode information about the "what" and "when" of auditory events, respectively. These streams are bidirectional, this is, frontal areas also project back to the temporal seeds. This allows the system to not only enable bottom-up perception and working memory, but also to generate top-down predictions (Zatorre and Salimpoor, 2013). Likewise, bottom-up projections are not only responsible for transmitting sensory information up to planning systems, but also for monitoring and encoding how close incoming information is to the aforementioned top-down predictions (Schönwiesner et al., 2007).

These working memory and expectancy processes have been hypothesized to enable the ulterior reward processing of musical stimuli, through decoding of certainty and surprise interactions (Salimpoor et al., 2015). This information would be ultimately encoded by the brain reward system to motivate learning (Gold, Mas-Herrero, et al., 2019). A recent metaanalysis by Mas-Herrero, Maini, et al. (2021) shows that indeed these frontal and temporal areas work along the brain reward system during pleasant music listening, similarly to other types of rewards such as food. The fact that the reward system is both responsive to music and to other rewards but through different neural pathways supports the idea that the reward system is a common hub accessed via different routes depending on the nature of the input (Marco-Pallarés and Mas-Herrero, 2015). The utility of this input can thus vary from ensuring intake of nutrients (i.e. food) or keeping the auditory system engaged and flexible to better understand our environment (i.e. music). Our results overlap to a great extent with these results displaying specific frontal and temporal activations during music reward processing, pinpointing a physiological mechanism through which communication between these cortical areas might take place. Moreover, and coinciding with the idea that music reward is intertwined with auditory expectancy and working memory, it has been observed that fronto-temporal connectivity underlying auditory working memory and expectancy takes place through rhythmic synchronization in theta (Kaiser, 2015; Recasens et al., 2018; Omigie et al., 2019). In our studies, we found that theta synchronization of these areas was also related to music-evoked pleasantness as reported by participants. Thus, given previous findings and theories, a tentative interpretation of our findings is that this relationship is explained by those predictive processes directly related to music reward processing that take place within fronto-temporal loops.

In the present thesis we focused on theta rhythms (4-8 Hz) to study synchronization because they had already been observed to increase in power as a function of musical liking and related constructs in previous studies over frontal areas (Sammler et al., 2007; Omigie et al., 2015; Lin et al., 2010; Mikutta et al., 2014; Rogenmoser et al., 2016). Given the distance between the different nodes involved in these topologies, slow rhythms pose the most likely synchronization and information transfer mechanism. Following the interpretation of Buzsáki and Draguhn (2004), slow rhythms are better suited to transmit information between distal areas, since the physical constrain posed by cycling over long connections makes it unlikely for fast rhythms to synchronize efficiently. We wanted to test to which extent these oscillations could be synchronizing relevant areas for music processing and reward. Indeed, theta rhythms were observed to synchronize far-off relevant brain nodes in all three conducted studies, partially validating our physiological assumptions. In addition to auditory working memory and expectancy, theta rhythms have been identified as a key physiological mechanism in hippocampal working memory (Tesche and Karhu, 2000) and in cognitive control over frontal areas, a cognitive process associated with PE computation (Cavanagh and Frank, 2014). Therefore, it seems that this oscillatory band is particularly well suited to foster contextual information. It must be noted that in our studies we analyzed brain activity over long segments of music listening, rather than event-related activity. Thus, a complementary interpretation of our results is that we captured a more sustained process integrating contextual information, with more successful integration of music being associated with more chances of evoking pleasure. Indeed, theta rhythms have been proposed to maintain information in working memory while integrating it with new inputs, especially in the temporal lobe and the hippocampus (Tesche and Karhu, 2000).

The nodes we identified in our studies are part of a wider network that includes reward related areas such as the NAcc (Blood and Zatorre, 2001; Brown et al., 2004; Menon and Levitin, 2005; Koelsch et al., 2006; Salimpoor et al., 2013; Salimpoor et al., 2011; Martínez-Molina et al., 2016; Martínez-Molina et al., 2019). Thus, our results along this literature shows that these cortical networks take on affective significance beyond music comprehension. Given the techniques and designs used in this thesis we did not capture how these cortical networks synchronize with the brain reward system. Whether the frontal areas that serve as integrative hubs to pass on musical information synchronize with the reward system via theta rhythms is yet to be determined. Evidence from human intracranial recordings point to alpha oscillations as a candidate physiological mechanism supporting reward processing (Lega et al., 2011), but further research is needed to determine the precise rhythms operating in reward-related areas in response to musical stimuli. Another commonly area reported in the literature on music-evoked pleasantness and that we did not observe in our neuroimaging data is the vmPFC (Mas-Herrero, Maini, et al., 2021). This area has been hypothesized to be an integrative hub where different sensory inputs are processed similarly so that their hedonic impact can be evaluated on a common scale by the brain reward system (Kringelbach and Radcliffe, 2005). In fact, the fronto-temporal slow synchronization underlying PE computation observed in Recasens et al. (2018) operated over the vmPFC, supporting the idea that expectancy dynamics are evaluated for likability. In our neuroimaging data, however, neither this area nor the NAcc were observed, probably because these were extracted as a function of music perception alone, regardless of hedonic impact. A complete model of the neural oscillations synchronizing all the areas involved must also include both subcortical and cortical regions of the reward system, with slow rhythms in the theta-alpha range as candidate dynamics for coupling the different paths of the network.

4.2.2 Oscillatory networks of familiar and novel music

In addition to the correlational methodology of studies 1 and 2, in study 3 we familiarized participants with some stimuli in an experiment designed to compare liking between novel and familiar music. In this experiment, participants were exposed to a set of novel stimuli and tested 24 hours later for the likeability of the same stimuli along a set of novel ones. This design allowed us to observe effects of familiarity on liking with only one repetition, replicating previous findings (Peretz et al., 1998), as well as to tease apart two different connectivity topologies underlying musical liking depending on the familiarity treatment. To our knowledge, this poses the first attempt in the literature to study how different brain areas synchronize during pleasant music listening in response to familiar and unfamiliar excerpts, adding up to an otherwise classic line of research studying how musical liking an familiarity are intertwined (Chmiel and Schubert, 2017).

Particularly, we found right fronto-temporal theta synchronization to increase as a function of liking only when participants listened to novel music. This was virtually the same topology found in study 1, where we used likely unfamiliar music. In turn, increased temporo-parietal synchronization was observed when participants reported to like familiar music. Parietal activations have been observed in the literature in response to familiar music (Green et al., 2012, Jagiello et al., 2019), and left temporo-parietal theta rhythms have been attributed to recognition memory elsewhere (Jacobs et al., 2006). Indeed, the parietal cortex has been identified to be crucial for the recognition of familiar materials across a different number of modalities (Green et al., 2012). Nonetheless, we also found fronto-temporal theta synchronization within music-related brain function to be modulated by liking using well known classical music in study 2. Therefore, we cannot attribute the processes underlying musical liking to opposing networks depending on whether the stimuli are familiar for the listener, despite the results of study 3.

Instead, we propose that these two different networks underlie the processing of different, though not exclusive, expectancy sources. Fronto-temporal loops would underlie the processing of schematic expectations (i.e. abstract, statistical rules), while temporo-parietal would underlie the processing of veridical expectations (i.e. recognition of familiar materials). According to this model, in studies 1 and 2 we observed liking as a function of schematic expectations supported by fronto-temporal connectivity, even when some degree of familiarity with the stimuli could be expected. In study 3, however, participants were exposed to the familiar stimuli 24 hours before test in a similar experimental setting. It is possible that under these circumstances veridical expectations took over when listening to recognized stimuli, while schematic expectations only took place with novel music. Thus, it is expected that in more ecologic contexts the two networks coexist, and even interact, to different extents. In fact, the parietal lobe acts as a mediator in the dorsal stream between the temporal lobe and the frontal lobe (Rauschecker and Scott, 2009). This stream has been hypothesized to process the “when” information of auditory stimuli. While timing information is important in schematic expectations as well, it could be possible that veridical information enhances this source of predictions through the parietal lobe as it interacts with the areas along this stream to convey when familiar musical events will take place.

An important aspect to note throughout this thesis is that we used naturalistic stimuli, taking a more ecologically valid approach. Along self-reported data, this allowed us to study affect valence responses in an ecological fashion without assuming a priori the likability of the stimuli, as had been done in other studies (Sammler et al., 2007; Omigie et al., 2015). In addition, this was particularly relevant in study 3 where we familiarized participants with some stimuli to investigate how liking and familiarity are intertwined. While controlled stimuli are well suited to study brain responses to concrete musical events, we argue that naturalistic stimuli are more adequate when studying sustained brain responses to familiar music. This ensures that every attribute characteristic of music is present in the materials, facilitating the familiarization process.

Finally, and on a different note, it is important to stress that music is not the only “abstract reinforcer” that has been studied in the literature. Other modalities of art have also drawn the attention of researchers in the cognitive and brain sciences. Interestingly, while common mechanisms could be expected to underlie liking for different types of aesthetic stimuli (e.g. music and pictorial art), other seem to be domain-specific (Tiihonen et al., 2017). For instance, while the relationship between complexity and evoked pleasantness may follow similar patterns in both the auditory and visual domains, complexity might mean very different things in each case. While in music this might be more related to the observer’s learning history, in pictorial art it could be more related to how physically rich the stimulus is. Furthermore, other psychological processes can take place to different extents depending on the art form. For example, pictorial art might be more prone to convey a concept subject to aesthetic evaluation, whereas the acoustic aspects of music could make it more prone to conditioning. Likewise, while different stimuli can engage the brain reward system in similar ways, the access routes must be naturally different, given the different sensory systems (Marco-Pallarés and Mas-Herrero, 2015). These different routes and the different cognitive operations that they support likely operate over different oscillatory dynamics in order to transfer the information efficiently. For example, in this thesis theta rhythms were identified as a means of communication between relevant areas associated with musical liking, while other lines of research have identified beta rhythms over occipital areas to be related to positive evaluation of pictorial stimuli after aesthetic judgment (Cela-Conde et al., 2013).

4.3 Statistical framework

An important novelty in this thesis was the statistical analytic framework employed. In all three studies we chose to analyze our data with multilevel modeling under the generalized linear model framework and using Bayesian inference. Analyzing the data in a multilevel fashion allowed us to retain every observation from each subject while performing inferences at the group level. Other procedures to make inferences at the group level about phenomena happening within individuals work on summary statistics or two-level procedures. While these procedures are convenient in many situations, they carry the disadvantage of not explaining variance at the individual level, thus resulting in loss of statistical power and parameter specificity (Baayen et al., 2008).

Multilevel modeling, on the other hand, is inherently parametric. This means that assumptions about the distribution of the explained data must be made. And while data is usually normally distributed in most cognitive neuroscience applications, this is not always the case. For instance, the phase synchronization metric that we used in all three studies (ISPC) is expressed as a rate in the unit interval, and visual inspection revealed that this index is not normally distributed. For this reason we adopted the generalized linear model to analyze all data in our studies. This type of models link predictors to the explained data assuming appropriate distributions (Stroup, 2012). Thus, by adopting this framework we could faithfully approximate phenomena of interest, for example assuming that ISPC values are Beta-distributed or that Likert scales are ordinal and not continuous.

Last but not least, all our statistical models were estimated using Bayesian inference, in contrast to the classic frequentist framework usually used in cognitive neuroscience. This proved to be a good conservative procedure for null-hypothesis testing that did not need arbitrary thresholding or overly restrictive corrections to keep potential false alarms from dominating results in our mass-univariate analyses. Because of the statistical properties of Bayes rule, specifying informative priors around the null hypothesis resulted in shrinkage of the likelihood toward it, making it more difficult for weak results to turn non-zero even when using standard, uncorrected criteria (Han and Park, 2018). Moreover, looking at the likelihood of parameter estimates given the data instead of computing multiple test statistics with the same degrees of freedom also made the multiple testing problem conceptually less problematic (Kruschke, 2015).

4.4 Limitations

The present thesis is not absent of limitations. Most of them have already been discussed in each study's discussion as well as in this section. However, there are a number of limitations common to all studies comprising this thesis that are worth mentioning. Firstly, all of our experiments studied music-evoked pleasantness in a correlational manner. While this was useful insofar it allowed us to successfully study sustained brain responses during pleasant music listening, this approach is not appropriate to tackle the more concrete cognitive operations underlying pleasant reactions to music, such as the certainty associated with the anticipation of musical events or the surprise generated when musical events take place. More controlled paradigms are needed to track finer-grained neural responses to pleasurable musical events. On the other hand, in study 3 we used an experimental manipulation to induce familiarity with some of the musical materials. This allowed us to successfully induce familiarity to study its relation with music-evoked pleasantness and theta synchronization of different brain areas. However, from this design it was not possible to assess the effects of long-term familiarization with music on liking response and these connectivity topologies. Designs manipulating the number of repetitions and/or the interval between sessions would be needed to do so.

Another important limitation is the type of connectivity measures used in this thesis. We set out to use a connectivity approach to analyze our brain data and its relation with musical affective phenomena, for which we used different measures. However, these synchronization and network measures are all informative of functional connectivity. This was valuable insofar it allowed us to easily elucidate connectivity patterns in an exploratory fashion in the spatial domain. However, given the statistical formulation of these indexes, we did not tackle the physical streams that could support the studied brain interactions, nor the causality that the different nodes exert on each other. Other type of measures are needed along the appropriate designs to take a closer look at the temporal dynamics of the brain oscillatory synchronization underlying musical liking, such as effective connectivity indexes.

Finally, although our choice of analytic framework posed a number of advantages, some modeling aspects still need to be refined. Particularly, we used a mass-univariate approach for our brain data instead of fully modeling commonalities across effects. This latter approach would make it possible to protect results against false alarms without having to specify multiple informative priors over multiple null hypotheses, which can be considered arbitrary, since common hierarchical distribution could be constructed empirically. However, this type of models are computationally challenging, specially when the response variable is not normally distributed and the number of brain sites is numerous. Future advances in computer software and hardware will make it possible to implement this type of models more efficiently in the future.

4.5 Future Directions

The findings and discussions presented throughout this thesis open up a number of questions to be addressed in future research endeavors. First of all, it must be researched whether the expectancy dynamics generated within auditory working memory are indeed at the basis of the theta-synchronized fronto-temporal and temporo-parietal connections associated with music-evoked pleasantness in our studies, as convergence with other lines of research suggests (Recasens et al., 2018). Whether brain activity in frontal, temporal and reward areas is related to musical liking through predictive certainty, PE or an interaction between the two has been researched in fMRI studies with promising results (Gold, Pearce, et al., 2019; Cheung et al., 2019; Shany et al., 2019). However, to date no study has tested empirically to which extent the oscillatory correlates of affect valence underlie the associated expectancy dynamics computed in cortical loops and ultimately encoded by the brain reward system. In these regards, some experimental and computational approaches are promising to study predictive coding and schematic knowledge acquisition in musical contexts along brain oscillatory data. For instance, it remains unclear whether changes in theta synchronization between relevant areas during pleasant music listening reflect PE computation. Since its inception, the Information Dynamics of Music model (IDyOM; Pearce, 2018) has proved to be useful in simulating the otherwise unobserved predictive dynamics behind music perception and reward (Gold, Pearce, et al., 2019; Gold, Mas-Herrero, et al., 2019). Using this model important hypotheses have already been proven true, such as that musical PEs are generated in temporal cortices via theta rhythms (Omigie et al., 2019) and that these predictive dynamics, when salient, are ultimately encoded by the NAcc, correlating with liking response (Shany et al., 2019). It would be interesting to test whether musical expectancy quantified by this model would be useful in explaining the theta connectivity found to be associated with musical liking in this thesis.

Another interesting question is how the schematic and veridical expectations hypothesized to be at the basis of music reward processing are acquired. In order to study this learning process a promising approach is the design of experimental paradigms using artificial grammars and learning protocols. Studies using artificial grammars have revealed that humans are capable or generalizing a musical artificial grammar after a short period of exposure (e.g. 30 minutes), as well as recognizing and developing preference for artificial familiar melodies (Loui et al., 2010; Loui, 2012). Future studies employing artificial grammars with more and longer sessions of training could elucidate whether generalization effects on liking can also take place with enough exposure, providing evidence for the assumption that musical liking is indeed learned. Together with the proper neuroimaging techniques these designs could reveal what changes in brain function accompany changes in learning and liking response.

Other brain networks and dynamics beyond the scope of this thesis also deserve further exploration. One unknown is how the oscillatory dynamics studied in this thesis relate to the mesolimbic reward system. Despite being such an important part of the music reward literature, we did not observe the subcortical activity usually associated with musical liking (e.g. in the NAcc). This was due to the limitations of our analytic methods to capture subcortical areas, particularly due to our focus on cortical synchronization. Future studies must be conducted with different designs that allow to study how hedonic signals in the subcortical brain reward system are associated with the cortical oscillatory dynamics identified in this thesis. In these regards, one interesting method is brain stimulation, where activity in different brain areas can be disrupted or boosted along their associated neural paths during performance of a task. As an example, Mas-Herrero et al. (2018) successfully modulated the liking response of participants during music listening using transcranial magnetic stimulation (TMS) over the left dlPFC, which in turn directly modulated fronto-striatal function. In a subsequent neuroimaging study, the same authors proved that this stimulation indeed modulated activity in the NAcc and its connectivity with temporal and frontal areas (Mas-Herrero, Dagher, Farrés-Franch, et al., 2021). Thus, similar procedures can be used in the future to test whether these findings are replicated in the oscillatory domain.

On a different note, in the introduction it was conveyed that in addition to auditory expectancy, another candidate cognitive mechanism that could contribute to music-related affect valence is evaluative conditioning. This is described as a mechanisms through which musical stimuli can be associated with other external or internal events, such as memories, emotions or other stimuli evoking pleasure (Juslin, 2013). It was thus proposed that music-reward processing could also emerge from these associations. However, this idea has not been explored in the literature nor in this thesis. In order to test the extent to which these high order associations can engage the brain reward system experiments inducing the generation of pleasant elements associated with music must be conducted. It will also be interesting to see the brain spatial distribution and oscillatory dynamics of these associative-driven liking responses.

5. Conclusions

The aim of this thesis was to better understand the oscillatory dynamics associated with music-evoked pleasantness. In order to do so, we set out three experiments to elucidate what brain nodes are synchronized by theta rhythms during pleasant music listening, which relation these rhythms have with the music processing network, and the modulation effect of familiarity on these connections. In all our experiments participants listened to naturalistic music stimuli while rating the degree of evoked pleasantness in real time, which allowed us to study sustained oscillatory dynamics and their relation to affect valence in response to music. In addition, in experiment 3 participants were familiarized with some of the materials 24h prior to the experimental session in order to further study whether different theta connectivity topologies underlie the processing of pleasant familiar and novel music, respectively.

Grounded on a connectivity approach we made some important discoveries. Firstly, we found that theta synchronization between right frontal and temporal areas increased with reported pleasantness in study 1. In addition, in study 2 we found that this fronto-temporal theta synchronization, was only associated with music-related fronto-temporal networks when music was reported to be liked. In this study music-related networks were extracted using blind source separation of fMRI signals, which were acquired simultaneously with the EEG data, and included both STG, both RMCs and portions of the right IFG. From these results we interpreted that theta rhythms are a key oscillatory mechanisms in the coupling of the brain areas involved in music listening, particularly relevant when music is pleasurable for the listener.

Altogether, these findings add up to a growing body of literature pointing out that frontal and temporal brain areas are actively involved in music-reward processing and that theta rhythms are key to this process. In addition, these findings also converge with other lines of research and theories. Particularly, theta synchronization between frontal and temporal areas has been found to be at the basis of expectancy dynamics and working memory in the auditory system. This does not only converge with our findings in the spatial and frequency domains, but also with theories stating that music-evoked pleasantness is precisely enabled by the expectancy dynamics taking place within auditory working memory, processes supported by these fronto-temporal loops. Future studies must be devoted to test whether these information processing accounts are indeed at the basis of the results found in this thesis.

Finally, in study 3 we found that these fronto-temporal theta connections were more related to pleasantness evoked by novel music than pleasantness evoked by familiar music, which was instead related to temporo-parietal theta synchronization. These results are consistent with previous research showing that parietal brain function is associated with familiar music listening along other music-related areas. We propose that while fronto-temporal loops might be more related to the processing of schematic expectations, temporo-parietal loops might be the source of veridical expectations during music listening. More efficient theta synchronization within these loops would be associated with increased liking response, congruent with literature on the effect of familiarity on music-evoked pleasantness. Future research will elucidate the extent of these hypotheses and how these two networks interact.

References

Abrams, D. A., Bhatara, A., Ryali, S., Balaban, E., Levitin, D. J., & Menon, V. (2011). Decoding temporal structure in music and speech relies on shared brain resources but elicits different fine-scale spatial patterns. *Cerebral Cortex*, *21*(7), 1507–1518.

Akam, T. E., & Kullmann, D. M. (2012). Efficient Communication through Coherence Requires Oscillations Structured to Minimize Interference between Signals. *PLoS Computational Biology*, *8*(11).

Albouy, P., Weiss, A., Baillet, S., & Zatorre, R. J. (2017). Selective Entrainment of Theta Oscillations in the Dorsal Stream Causally Enhances Auditory Working Memory Performance. *Neuron*, *94*(1), 193–206.e5.

Altenmüller, E., Siggel, S., Mohammadi, B., Samii, A., & Münte, T. F. (2014). Play it again, Sam: Brain correlates of emotional music recognition. *Frontiers in Psychology*, *5*(114), 1–8.

Ara, A., & Marco-Pallarés, J. (2020). Fronto-temporal theta phase-synchronization underlies music-evoked pleasantness. *NeuroImage*, *212*.

Arjmand, H. A., Hohagen, J., Paton, B., & Rickard, N. S. (2017). Emotional responses to music: Shifts in frontal brain asymmetry mark periods of musical change. *Frontiers in Psychology*, *8*(2044), 1–13.

Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language*, *59*(4), 390–412.

Bandettini, P. A. (2002). The spatial, temporal, and interpretive limits of functional MRI. *Neuropsychopharmacology: The fifth generation of progress*, *21*, 343–356.

Barascud, N., Pearce, M. T., Griffiths, T. D., Friston, K. J., & Chait, M. (2016). Brain responses in humans reveal ideal observer-like sensitivity to complex acoustic patterns. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(5), E616–E625.

Barton, B., & Brewer, A. A. (2019). Attention and Working Memory in Human Auditory Cortex. In S. Hatzopoulos, A. Ciorba, & P. H. Skarzynski (Eds.), *The human auditory system - basic features and updates on audiological diagnosis and therapy* (pp. 137–144). IntechOpen.

Bassett, D. S., & Sporns, O. (2017). Network neuroscience. *Nature Neuroscience*, *20*(3), 353–364.

Bastos, A. M., & Schoffelen, J. M. (2016). A tutorial review of functional connectivity analysis methods and their interpretational pitfalls. *Frontiers in Systems Neuroscience*, *9*(175), 1–23.

Baumgartner, T., Esslen, M., & Jäncke, L. (2006). From emotion perception to emotion experience: Emotions evoked by pictures and classical music. *International Journal of Psychophysiology*, *60*(1), 34–43.

Berlyne, D. E. (1971). *Aesthetics and psychobiology.* Appleton-Century-Crofts.

Berridge, K. C., Robinson, T. E., & Aldridge, J. W. (2009). Dissecting components of reward: 'liking', 'wanting', and learning. *Current Opinion in Pharmacology*, *9*(1), 65–73.

Blood, A. J., & Zatorre, R. J. (2001). Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(20), 11818–11823.

Bolam, J. P., Brown, M. T., Moss, J., & Magill, P. J. (2009). Basal Ganglia: Internal Organization. *Encyclopedia of Neuroscience*, 97–104.

Brown, S., Martinez, M. J., Hodges, D. A., Fox, P. T., & Parsons, L. M. (2004). The song system of the human brain. *Cognitive Brain Research*, *20*(3), 363–375.

Bryk, A. S., & Raudenbush, S. W. (1988). Heterogeneity of Variance in Experimental Studies: A Challenge to Conventional Interpretations. *Psychological Bulletin*, *104*(3), 396–404.

Buzsáki, G., & Draguhn, A. (2004). Neuronal olscillations in cortical networks. *Science*, *304*(5679), 1926–1929.

Cavanagh, J. F., & Frank, M. J. (2014). Frontal theta as a mechanism for cognitive control. *Trends in Cognitive Sciences*, *18*(8), 414–421.

Cela-Conde, C. J., Garcfa-Prieto, J., Ramasco, J. J., Mirasso, C. R., Bajo, R., Munara, E., Flexasa, A., Del-Pozo, F., & Maestu, F. (2013). Dynamics of brain networks in the aesthetic appreciation. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(SUPPL2), 10454–10461.

Chabin, T., Gabriel, D., Chansophonkul, T., Michelant, L., Joucla, C., Haffen, E., Moulin, T., Comte, A., & Pazart, L. (2020). Cortical Patterns of Pleasurable Musical Chills Revealed by High-Density EEG. *Frontiers in Neuroscience*, *565815*(November), 1–11.

Chapman, L. J., Chapman, J. P., & Raulin, M. L. (1976). Scales for physical and social anhedonia. *Journal of Abnormal Psychology*, *85*(4), 374–382.

Cheung, V. K., Harrison, P. M., Meyer, L., Pearce, M. T., Haynes, J. D., & Koelsch, S. (2019). Uncertainty and Surprise Jointly Predict Musical Pleasure and Amygdala, Hippocampus, and Auditory Cortex Activity. *Current Biology*, *29*(23), 4084–4092.e4.

Chmiel, A., & Schubert, E. (2017). Back to the inverted-U for music preference: A review of the literature. *Psychology of Music*, *45*(6), 886–909.

Ciaramelli, E., Grady, C. L., & Moscovitch, M. (2008). Top-down and bottom-up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia*, *46*(7), 1828–1851.

Cohen, M. X. (2014). *Analyzing neural time series data*. The MIT Press.

Craig, A. D. (2005). Forebrain emotional asymmetry: A neuroanatomical basis? *Trends in Cognitive Sciences*, *9*(12), 566–571.

Critchley, H. D., Mathias, C. J., & Dolan, R. J. (2001). Neural activity in the human brain relating to uncertainty and arousal during anticipation. *Neuron*, *29*(2), 537–545.

Davidson, R. J. (1995). Cerebral asymmetry, emotion, and affective style. In R. J. Davidson & K. Hugdahl (Eds.), *Brain asymmetry* (pp. 361–387). The MIT Press.

Davidson, R. J. (2004). What does the prefrontal cortex ”do” in affect: Perspectives on frontal EEG asymmetry research. *Biological Psychology*, *67*(1-2), 219–234.

Eschrich, S., Münte, T. F., & Altenmüller, E. O. (2008). Unforgettable film music: The role of emotion in episodic long-term memory for music. *BMC Neuroscience*, *9*, 1–7.

Ferreri, L., Mas-Herrero, E., Zatorre, R. J., Ripollés, P., Gomez-Andres, A., Alicart, H., Olivé, G., Marco-Pallarés, J., Antonijoan, R. M., Valle, M., Riba, J., & Rodriguez-Fornells, A. (2019). Dopamine modulates the reward experiences elicited by music. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(9), 3793–3798.

Flores-Gutiérrez, E. O., Díaz, J. L., Barrios, F. A., Guevara, M. Á., del Río-Portilla, Y., Corsi-Cabrera, M., & del Flores-Gutiérrez, E. O. (2009). Differential alpha coherence hemispheric patterns in men and women during pleasant and unpleasant musical emotions. *International Journal of Psychophysiology*, *71*(1), 43–49.

Flores-Gutiérrez, E. O., Díaz, J. L., Barrios, F. A., Favila-Humara, R., Guevara, M. Á., del Río-Portilla, Y., & Corsi-Cabrera, M. (2007). Metabolic and electric brain patterns during pleasant and unpleasant emotions induced by music masterpieces. *International Journal of Psychophysiology*, *65*(1), 69–84.

Freitas, C., Manzato, E., Burini, A., Taylor, M. J., Lerch, J. P., & Anagnostou, E. (2018). Neural correlates of familiarity in music listening: A systematic review and a neuroimaging meta-analysis. *Frontiers in Neuroscience*, *12*(686), 1–14.

Fries, P. (2005). A mechanism for cognitive dynamics: Neuronal communication through neuronal coherence. *Trends in Cognitive Sciences*, *9*(10), 474–480.

Friston, K. J., Buechel, C., G. R., F., Morris, J., Rolls, E., & Dolan, R. J. (1997). Psychophysiological and Modulatory Interactions in Neuroimaging. *Neuroimage*, *6*, , 218–229.

Friston, K. J. (1994). Functional and effective connectivity in neuroimaging: A synthesis. *Human Brain Mapping*, *2*(1-2), 56–78.

Garrido, S., & Schubert, E. (2015). Moody melodies: Do they cheer us up? A study of the effect of sad music on mood. *Psychology of Music*, *43*(2), 244–261.

Gelman, A., Carlin, J., Stern, H., & Rubin, D. (2013). *Bayesian Data Analysis* (3rd). Chapman; Hall/CRC.

Gitelman, D. R., Penny, W. D., Ashburner, J., & Friston, K. J. (2003). Modeling regional and psychophysiologic interactions in fMRI: The importance of hemodynamic deconvolution. *NeuroImage*, *19*(1), 200–207.

Gold, B. P., Frank, M. J., Bogert, B., & Brattico, E. (2013). Pleasurable music affects reinforcement learning according to the listener. *Frontiers in Psychology*, *4*(541), 1–19.

Gold, B. P., Mas-Herrero, E., Zeighami, Y., Benovoy, M., Dagher, A., & Zatorre, R. J. (2019). Musical reward prediction errors engage the nucleus accumbens and motivate learning. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(8), 3310–3315.

Gold, B. P., Pearce, M. T., Mas-Herrero, E., Dagher, A., & Zatorre, R. J. (2019). Predictability and uncertainty in the pleasure of music: A reward for learning? *Journal of Neuroscience*, *39*(47), 9397–9409.

Green, A. C., Bærentsen, K. B., Stodkilde-Jorgensen, H., Roepstorff, A., & Vuust, P. (2012). Listen, learn, like! Dorsolateral prefrontal cortex involved in the mere exposure effect in music. *Neurology Research International*, *2012*(846270).

Haber., S. N. (2011). Neuroanatomy of Reward: A View from the Ventral Striatum. In J. A. Gottfried (Ed.), *Neurobiology of sensation and reward* (pp. 255–282). CRC Press/Taylor Francis.

Hallam, S., Cross, I., & Thaut, M. (2014). Oxford University Press.

Halpern, A. R., & Zatorre, R. J. (1999). When that tune runs through your head: A PET investigation of auditory imagery for familiar melodies. *Cerebral Cortex*, *9*(7), 697–704.

Han, H., & Park, J. (2018). Using SPM 12's second-level bayesian inference procedure for fMRI analysis: Practical guidelines for end users. *Frontiers in Neuroinformatics*, *12*(1), 1–17.

Hansen, N. C., Dietz, M. J., & Vuust, P. (2017). Commentary: Predictions and the brain: How musical sounds become rewarding. *Frontiers in Human Neuroscience*, *11*(168), 10–12.

Heller, W. (1993). Neuropsychological mechanisms of individual differences in emotion, personality, and arousal. *Neuropsychology*, *7*(4), 476–489.

Honey, C. J., Kötter, R., Breakspear, M., & Sporns, O. (2007). Network structure of cerebral cortex shapes functional connectivity on multiple time scales. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(24), 10240–10245.

Hyde, K. L., Peretz, I., & Zatorre, R. J. (2008). Evidence for the role of the right auditory cortex in fine pitch resolution. *Neuropsychologia*, *46*(2), 632–639.

Jacobs, J., Hwang, G., Curran, T., & Kahana, M. J. (2006). EEG oscillations and recognition memory: Theta correlates of memory retrieval and decision making. *NeuroImage*, *32*(2), 978–987.

Jagiello, R., Pomper, U., Yoneya, M., Zhao, S., & Chait, M. (2019). Rapid Brain Responses to Familiar vs. Unfamiliar Music – an EEG and Pupillometry study. *Scientific Reports*, *9*(1), 1–13.

Jäncke, L., & Alahmadi, N. (2016). Detection of independent functional networks during music listening using electroencephalogram and sLORETA-ICA. *NeuroReport*, *27*(6), 455–461.

Jäncke, L., Kühnis, J., Rogenmoser, L., & Elmer, S. (2015). Time course of EEG oscillations during repeated listening of a well-known aria. *Frontiers in Human Neuroscience*, *9*(401), 1–18.

Jäncke, L., Leipold, S., & Burkhard, A. (2018). The neural underpinnings of music listening under different attention conditions. *NeuroReport*, *29*(7), 594–604.

Jarbo, K., & Verstynen, T. D. (2015). Converging structural and functional connectivity of orbitofrontal, dorsolateral prefrontal, and posterior parietal cortex in the human striatum. *Journal of Neuroscience*, *35*(9), 3865–3878.

Johnson, J. K., Kim, J. K., & Risse, G. (1985). Do alcoholic Korsakoff's syndrome patients acquire affective reactions? *Journal of experimental psychology. Learning, memory and cognition*, *1*(11), 22–36.

Juslin, P. N. (2013). From everyday emotions to aesthetic emotions: Towards a unified theory of musical emotions. *Physics of Life Reviews*, *10*(3), 235–266.

Juslin, P. N., & Sloboda, J. A. (2001). Psychological perspectives on music and emotion. In P. N. Juslin & J. A. Sloboda (Eds.), *Music and emotion. theory and research* (pp. 71–103). Oxford University Press.

Juslin, P. N., & Västfjäll, D. (2008). Emotional responses to music: The need to consider underlying mechanisms. *Behavioral and Brain Sciences*, *31*(5), 559–621.

Kaiser, J. (2015). Dynamics of auditory working memory. *Frontiers in Psychology*, *6*(613), 1–6.

Kawakami, A., Furukawa, K., & Okanoya, K. (2014). Music evokes vicarious emotions in listeners. *Frontiers in Psychology*, *5*(431), 1–7.

Koelsch, S. (2013). *Brain and music*. Wiley Blackwell.

Koelsch, S. (2014). Brain correlates of music-evoked emotions. *Nature Reviews Neuroscience*, *15*(3), 170–180.

Koelsch, S., Fritz, T., Cramon, D. Y. V., Müller, K., & Friederici, A. D. (2006). Investigating emotion with music: An fMRI study. *Human Brain Mapping*, *27*(3), 239–250.

Koelsch, S., Rohrmeier, M., Torrecuso, R., & Jentschke, S. (2013). Processing of hierarchical syntactic structure in music. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(38), 15443–15448.

Koelsch, S., Vuust, P., & Friston, K. (2019). Predictive Processes and the Peculiar Case of Music. *Trends in Cognitive Sciences*, *23*(1), 63–77.

Kringelbach, M. L., & Radcliffe, J. (2005). The human orbitofrontal cortex: Linking reward to hedonic experience. *Neuroscience*, *6*(September), 691–702.

Kruschke, J. (2015). *Doing Bayesian Data Analysis: A Tutorial with R, JAGS and Stan* (2nd). Elsevier Academic Press.

Kunst-Wilson, W. R., & Zajonc, R. B. (1980). Affective discrimination of stimuli that cannot be recognized. *Science*, *207*(4430), 557–558.

Lega, B. C., Kahana, M. J., Jaggi, J., Baltuch, G. H., & Zaghloul, K. (2011). Neuronal and oscillatory activity during reward processing in the human ventral striatum. *NeuroReport*, *22*(16), 795–800.

Lin, Y. P., Duann, J. R., Chen, J. H., & Jung, T. P. (2010). Electroencephalographic dynamics of musical emotion perception revealed by independent spectral components. *NeuroReport*, *21*(6), 410–415.

Loui, P. (2012). Learning and Liking of Melody and Harmony: Further Studies in Artificial Grammar Learning. *Topics in Cognitive Science*, *4*(4), 554–567.

Loui, P., Wessel, D. L., & Hudson Kam, C. L. (2010). Humans rapidly learn grammatical structure in a new musical scale. *Music Perception*, *27*(5), 377–388.

Madison, G., & Schiölde, G. (2017). Repeated listening increases the liking for music regardless of its complexity: Implications for the appreciation and aesthetics of music. *Frontiers in Neuroscience*, *11*(147), 1–13.

Marco-Pallarés, J., & Mas-Herrero, E. (2015). The Quartet does not play alone. Comment on ”The quartet theory of human emotions: An integrative and neurofunctional model” by S. Koelsch et al. *Physics of Life Reviews*, *13*, 71–72.

Marco-Pallarés, J., Münte, T. F., & Rodríguez-Fornells, A. (2015). The role of high-frequency oscillatory activity in reward processing and learning. *Neuroscience and Biobehavioral Reviews*, *49*, 1–7.

Markovic, A., Kühnis, J., & Jäncke, L. (2017). Task context influences brain activation during music listening. *Frontiers in Human Neuroscience*, *11*(342), 1–14.

Martin, S., Mikutta, C., Leonard, M. K., Hungate, D., Koelsch, S., Shamma, S., Chang, E. F., Millán, J. D. R., Knight, R. T., & Pasley, B. N. (2018). Neural encoding of auditory features during music perception and imagery. *Cerebral Cortex*, *28*(12), 4222–4233.

Martínez-Molina, N., Mas-Herrero, E., Rodríguez-Fornells, A., Zatorre, R. J., & Marco-Pallarés, J. (2016). Neural correlates of specific musical anhedonia. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(46), E7337–E7345.

Martínez-Molina, N., Mas-Herrero, E., Rodríguez-Fornells, A., Zatorre, R. J., & Marco-Pallarés, J. (2019). White matter microstructure reflects individual differences in music reward sensitivity. *Journal of Neuroscience*, *39*(25), 5018–5027.

Mas-Herrero, E., Dagher, A., Farrés-Franch, M., & Zatorre, R. J. (2021). Unraveling the temporal dynamics of reward signals in music-induced pleasure with TMS. *Journal of Neuroscience*, *JN-RM-0727*.

Mas-Herrero, E., Dagher, A., & Zatorre, R. J. (2018). Modulating musical reward sensitivity up and down with transcranial magnetic stimulation. *Nature Human Behaviour*, *2*(1), 27–32.

Mas-Herrero, E., Maini, L., Sescousse, G., & Zatorre, R. J. (2021). Common and distinct neural correlates of music and food-induced pleasure: A coordinate-based meta-analysis of neuroimaging studies. *Neuroscience and Biobehavioral Reviews*, *123*(November 2020), 61–71.

Mas-Herrero, E., Marco-Pallares, J., Lorenzo-Seva, U., Zatorre, R. J., & Rodriguez-Fornells, A. (2013). Individual differences in music reward experiences. *Music Perception*, *31*(2), 118–138.

Mas-Herrero, E., & Marco-Pallarés, J. (2014). Frontal Theta Oscillatory Activity Is a Common Mechanism for the Computation of Unexpected Outcomes and Learning Rate. *Journal of Cognitive Neuroscience*, *26*(3), 447–458.

Mas-Herrero, E., & Marco-Pallarés, J. (2016). Theta oscillations integrate functionally segregated sub-regions of the medial prefrontal cortex. *NeuroImage*, *143*, 166–174.

McDermott, J. H., Schultz, A. F., Undurraga, E. A., & Godoy, R. A. (2016). Indifference to dissonance in native Amazonians reveals cultural variation in music perception. *Nature*, *535*(7613), 547–550.

Mckeown, M. J., Makeig, S., Brown, G. G., Jung, T.-P., Kindermann, S. S., Bell, A. J., & Sejnowski, T. J. (1998). Analysis of fMRI data by blind separation into independent spatial components. *6*(3), 160–188.

Menon, V., & Levitin, D. J. (2005). The rewards of music listening: Response and physiological connectivity of the mesolimbic system. *NeuroImage*, *28*(1), 175–184.

Mikutta, C., Maissen, G., Altorfer, A., Strik, W., & Koenig, T. (2014). Professional musicians listen differently to music. *Neuroscience*, *268*, 102–111.

Mikutta, C., Altorfer, A., Strik, W., & Koenig, T. (2012). Emotions, arousal, and frontal alpha rhythm asymmetry during beethoven's 5th symphony. *Brain Topography*, *25*(4), 423–430.

Mišić, B., & Sporns, O. (2016). From regions to connections and networks: New bridges between brain and behavior. *Current Opinion in Neurobiology*, *40*, 1–7.

Murray, E. A. (2007). The amygdala, reward and emotion. *Trends in Cognitive Sciences*, *11*(11), 489–497.

Nemati, S., Akrami, H., Salehi, S., Esteky, H., & Moghimi, S. (2019). Lost in music: Neural signature of pleasure and its role in modulating attentional resources. *Brain Research*, *1711*, 7–15.

Omigie, D., Dellacherie, D., Hasboun, D., George, N., Clement, S., Baulac, M., Adam, C., & Samson, S. (2015). An intracranial EEG study of the neural dynamics of musical valence processing. *Cerebral Cortex*, *25*(11), 4038–4047.

Omigie, D., Pearce, M., Lehongre, K., Hasboun, D., Navarro, V., Adam, C., & Severine, S. (2019). Intracranial Recordings and Computational Modeling of Music Reveal the Time Course of Prediction Error Signaling in Frontal and Temporal Cortices. *Journal of Cognitive Neuroscience*, *31*(6), 855–873.

Özdemir, E., Norton, A., & Schlaug, G. (2006). Shared and distinct neural correlates of singing and speaking. *NeuroImage*, *33*(2), 628–635.

Park, H. J., & Friston, K. (2013). Structural and functional brain networks: From connections to cognition. *Science*, *342*(6158).

Pearce, M. T. (2018). Statistical learning and probabilistic prediction in music cognition: Mechanisms of stylistic enculturation. *Annals of the New York Academy of Sciences*, *1423*(1), 378–395.

Peretz, I., Gaudreau, D., & Bonnel, A. M. (1998). Exposure effects on music preference and recognition. *Memory and Cognition*, *26*(5), 884–902.

Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. (1989). Spherical splines for scalp potential and current density mapping. *Electroencephalography and Clinical Neurophysiology*, *72*(2), 184–187.

Posse, S., Ackley, E., Mutihac, R., Rick, J., Shane, M., Murray-Krezan, C., Zaitsev, M., & Speck, O. (2012). Enhancement of temporal resolution and BOLD sensitivity in real-time fMRI using multi-slab echo-volumar imaging. *NeuroImage*, *61*(1), 115–130.

Rauschecker, J. P., & Scott, S. K. (2009). Maps and streams in the auditory cortex: Nonhuman primates illuminate human speech processing. *Nature Neuroscience*, *12*(6), 718–724.

Recasens, M., Gross, J., & Uhlhaas, P. J. (2018). Low-Frequency Oscillatory Correlates of Auditory Predictive Processing in Cortical-Subcortical Networks: A MEG-Study. *Scientific Reports*, *8*(1), 1–12.

Rentfrow, P. J., & Gosling, S. D. (2003). The Do Re Mi's of Everyday Life: The Structure and Personality Correlates of Music Preferences. *Journal of Personality and Social Psychology*, *84*(6), 1236–1256.

Roeder, J. G. (2008). *The Physics and Psychophysics of Music* (4th ed.). Springer-Verlag.

Rogenmoser, L., Zollinger, N., Elmer, S., & Jäncke, L. (2016). Independent component processes underlying emotions during natural music listening. *Social Cognitive and Affective Neuroscience*, *11*(9), 1428–1439.

Rousseeuw, P. J., Ruts, I., & Tukey, J. W. (1999). The bagplot: A bivariate boxplot. *American Statistician*, *53*(4), 382–387.

Rubinov, M., & Sporns, O. (2010). Complex network measures of brain connectivity: Uses and interpretations. *NeuroImage*, *52*(3), 1059–1069.

Russell, J. (1980). A Circumplex Model of Affect. *Journal of Personality and Social Psychology*, *39*(6), 1161–1178.

Sachs, M. E., Damasio, A., & Habibi, A. (2015). The pleasures of sad music: A systematic review. *Frontiers in Human Neuroscience*, *9*(404), 1–12.

Sachs, M. E., Ellis, R. J., Schlaug, G., & Loui, P. (2016). Brain connectivity reflects human aesthetic responses to music. *Social Cognitive and Affective Neuroscience*, *11*(6), 884–891.

Salimpoor, V. N., Benovoy, M., Larcher, K., Dagher, A., & Zatorre, R. J. (2011). Anatomically distinct dopamine release during anticipation and experience of peak emotion to music. *Nature Neuroscience*, *14*(2), 257–264.

Salimpoor, V. N., Benovoy, M., Longo, G., Cooperstock, J. R., & Zatorre, R. J. (2009). The rewarding aspects of music listening are related to degree of emotional arousal. *PLoS ONE*, *4*(10).

Salimpoor, V. N., van den Bosch, I., Kovacevic, N., McIntosh, A. R., Dagher, A., & Zatorre, R. J. (2013). Interactions Between the Nucleus Accumbens and Auditory Cortices Predict Music Reward Value. *Science*, *340*(6129), 216–219.

Salimpoor, V. N., Zald, D. H., Zatorre, R. J., Dagher, A., & McIntosh, A. R. (2015). Predictions and the brain: How musical sounds become rewarding. *Trends in Cognitive Sciences*, *19*(2), 86–91.

Sammler, D., Grigutsch, M., Fritz, T., & Koelsch, S. (2007). Music and emotion: Electrophysiological correlates of the processing of pleasant and unpleasant music. *Psychophysiology*, *44*(2), 293–304.

Schönwiesner, M., Novitski, N., Pakarinen, S., Carlson, S., Tervaniemi, M., & Näätänen, R. (2007). Heschl's gyrus, posterior superior temporal gyrus, and mid-ventrolateral prefrontal cortex have different roles in the detection of acoustic changes. *Journal of Neurophysiology*, *97*(3), 2075–2082.

Schubert, E. (2013). Emotion felt by the listener and expressed by the music: Literature review and theoretical perspectives. *Frontiers in Psychology*, *4*(837), 1–18.

Schubert, E., & Pearce, M. (2016). A new look at musical expectancy: The veridical versus the general in the mental organization of music. *Lecture Notes in Computer Science (including subseries Lecture Notes in Artificial Intelligence and Lecture Notes in Bioinformatics)*, *9617*, 358–370.

Schultz, W. (2016). Dopamine reward prediction-error signalling: A two-component response. *Nature Reviews Neuroscience*, *17*(3), 183–195.

Schuppert, M., Münte, T. F., Wieringa, B. M., & Altenmüller, E. (2000). Receptive amusia: Evidence for cross-hemispheric neural networks underlying music processing strategies. *Brain*, *123*(3), 546–559.

Sescousse, G., Caldú, X., Segura, B., & Dreher, J. C. (2013). Processing of primary and secondary rewards: A quantitative meta-analysis and review of human functional neuroimaging studies. *Neuroscience and Biobehavioral Reviews*, *37*(4), 681–696.

Shany, O., Singer, N., Gold, B. P., Jacoby, N., Tarrasch, R., Hendler, T., & Granot, R. (2019). Surprise-related activation in the nucleus accumbens interacts with music-induced pleasantness. *Social Cognitive and Affective Neuroscience*, *14*(4), 459–470.

Singer, W. (1993). Synchronization of cortical activity and its putative role in information processing and learning. *Annual Review of Physiology*, *55*, 349–374.

Skov, M., & Nadal, M. (2020). There are no aesthetic emotions: Comment on Menninghaus et al. (2019). *Psychological review*, *127*(4), 640–649.

Sporns, O. (2007). Brain connectivity. *Scholarpedia*, *2*(10), 4695.

Stroup, W. W. (2012). *Generalized Linear Mixed Models. Modern Concepts, Methods and Applications*. CRC Press.

Sturm, I., Biankertz, B., Potes, C., Schaik, G., & Curio, G. (2014). ECoG high gamma activity reveals distinct cortical representations of lyrics passages, Harmonic and timbre-related changes in a rock song. *Frontiers in Human Neuroscience*, *8*(798), 1–14.

Sturm, I., Dähne, S., Blankertz, B., & Curio, G. (2015). Multi-variate EEG analysis as a novel tool to examine brain responses to naturalistic music stimuli. *PLoS ONE*, *10*(10), 1–30.

Sutterer, M. J., & Tranel, D. (2017). Neuropsychology and cognitive neuroscience in the fMRI era: A recapitulation of localizationist and connectionist views. *Neuropsychology*, *31*(8), 972–980.

Tesche, C. D., & Karhu, J. (2000). Theta oscillations index human hippocampal activation during a working memory task. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(2), 919–924.

Thanh Vu, A., Jamison, K., Glasser, M. F., Smith, S. M., Coalson, T., Moeller, S., Auerbach, E. J., Uğurbil, K., & Yacoub, E. (2017). Tradeoffs in pushing the spatial resolution of fMRI for the 7T Human Connectome Project. *NeuroImage*, *154*, 23–32.

Tiihonen, M., Brattico, E., Maksimainen, J., Wikgren, J., & Saarikallio, S. (2017). Constituents of music and visual-art related pleasure - A critical integrative literature review. *Frontiers in Psychology*, *8*(JUL), 1–12.

Tillmann, B., Poulin-Charronnat, B., & Bigand, E. (2014). The role of expectation in music: From the score to emotions and the brain. *Wiley Interdisciplinary Reviews: Cognitive Science*, *5*(1), 105–113.

Trost, W., Ethofer, T., Zentner, M., & Vuilleumier, P. (2012). Mapping aesthetic musical emotions in the brain. *Cerebral Cortex*, *22*(12), 2769–2783.

Trost, W., & Frühholz, S. (2015). The hippocampus is an integral part of the temporal limbic system during emotional processing. Comment on ”The quartet theory of human emotions: An integrative and neurofunctional model" by S. Koelsch et al. *Physics of Life Reviews*, *13*, 87–88.

Trost, W., Frühholz, S., Cochrane, T., Cojan, Y., & Vuilleumier, P. (2014). Temporal dynamics of musical emotions examined through intersubject synchrony of brain activity. *Social Cognitive and Affective Neuroscience*, *10*(12), 1705–1721.

van den Bosch, I., Salimpoor, V. N., & Zatorre, R. J. (2013). Familiarity mediates the relationship between emotional arousal and pleasure during music listening. *Frontiers in Human Neuroscience*, *7*(534), 1–10.

Vessel, E. A., Gabrielle Starr, G., & Rubin, N. (2012). The brain on art: Intense aesthetic experience activates the default mode network. *Frontiers in Human Neuroscience*, *6*(66), 1–17.

Vilberg, K. L., & Rugg, M. D. (2008). Memory retrieval and the parietal cortex: A review of evidence from a dual-process perspective. *Neuropsychologia*, *46*(7), 1787–1799.

Weiskopf, N., Hutton, C., Josephs, O., & Deichmann, R. (2006). Optimal EPI parameters for reduction of susceptibility-induced BOLD sensitivity losses: A whole-brain analysis at 3 T and 1.5 T. *NeuroImage*, *33*(2), 493–504.

Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, *46*(3), 441–517.

Zajonc, R. B. (2001). Mere exposure: A gateway to the subliminal. *Current Directions in Psychological Science*, *10*(6), 224–228.

Zajonc, R. B. (1968). Attitudinal Effects of Mere Exposure. *Journal of Personality and Social Psychology*, *9*(2, Pt.2), 1–27.

Zatorre, R. J., Belin, P., & Penhune, V. B. (2002). Structure and function of auditory cortex: Music and speech. *Trends in Cognitive Sciences*, *6*(1), 37–46.

Zatorre, R. J., Evans, A. C., & Meyer, E. (1994). Neural mechanisms underlying melodic perception and memory for pitch. *Journal of Neuroscience*, *14*(4), 1908–1919.

Zatorre, R. J., & Gandour, J. T. (2008). Neural specializations for speech and pitch: Moving beyond the dichotomies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1493), 1087–1104.

Zatorre, R. J., & Halpern, A. R. (2005). Mental concerts: Musical imagery and auditory cortex. *Neuron*, *47*(1), 9–12.

Zatorre, R. J., Halpern, A. R., Perry, D. W., Meyer, E., & Evans, A. C. (1996). Hearing in the mind's ear: A PET investigation of musical imagery and perception. *Journal of Cognitive Neuroscience*, *8*(1), 29–46.

Zatorre, R. J., & Salimpoor, V. N. (2013). From perception to pleasure: Music and its neural substrates. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(Suppl 2), 10430–10437.

Annex

Abbreviations List

Acronyms / Abbreviations

ACC	Anterior Cingulate Cortex
AR(1)	Autoregressive Process of Order 1
BMRQ	Barcelona Music Reward Questionnaire
BOLD	Blood Oxygenation Level Dependent
BRECVEMA	Brainstem reflexes, Rhythmic entrainment, Evaluative conditioning, Emotional contagion, Visual imagery, Episodic memory, Musical expectancy and Aesthetic judgment
dlPFC	Dorsolateral Prefrontal Cortex
EDA	Electrodermal Activity
EEG	Electroencephalography
ERF	Event-related Field
fMRI	functional Magnetic Resonance Imaging
gICA	group Independent Components Analysis
gIC	Group Independent Component
HDI	Highest Density Interval
HRF	Hemodynamic Response Function
ICA	Independent Components Analysis
IC	Independent Component
IPC	Inferior Parietal Cortex
ISPC	Inter-Site Phase Clustering

MEG	Magnetoencephalography
mPFC	Medial Prefrontal Cortex
NAcc	Nucleus Accumbens
OFC	Orbitofrontal Cortex
PAS	Physical Anhedonia Scale
PE	Prediction Error
PET	Positron Emision Tomography
PFC	Prefrontal Cortex
PPI	Psychophysiological Interactions
RMC	Rostral Motor Cortex
ROPE	Region of Practival Equivalence
SN/VTA	Substantia Nigra/Ventral Tagmental Area
STG	Superior Temporal Gyrus
STOMP-R	Short Test of Music Preferences Revised
suTG	Supratemporal Gyrus
TMS	Transcranial Magnetic Stimulation
TR	Repetition Time
vmPFC	Ventromedial Prefrontal Cortex

Figures Index

Tables Index