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Making sense of music: Insights from neurophysiology and connectivity analyses in naturalistic listening conditions

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ABSTRACT

According to the latest frameworks, auditory perception and memory involve the constant prediction of future sound events by the brain, based on the continuous extraction of feature regularities from the environment. The neural hierarchical mechanisms for predictive processes in perception and memory for sounds are typically studied in relation to simple acoustic features in isolated sounds or sound patterns inserted in highly certain contexts. Such studies have identified reliable prediction formation and error signals, e.g., the N100 or the mismatch negativity (MMN) evoked responses. In real life, though, individuals often face situations in which uncertainty prevails and where making sense of sounds becomes a hard challenge. In music, not only deviations from predictions are masterly set up by composers to induce emotions but sometimes the sheer uncertainty of sound scenes is exploited for aesthetic purposes, especially in compositional styles such as Western atonal classical music. In very recent magnetoencephalography (MEG) and electroencephalography (EEG) studies, experimental and technical advances in stimulation paradigms and analysis approaches have permitted the identification of prediction-error responses from highly uncertain, atonal contexts and the extraction of prediction-related responses from real, continuous music. Moreover, functional connectivity analyses revealed the emergence of cortico-hippocampal interactions during the formation of auditory memories for more predictable vs. less predictable patterns. These findings contribute to understanding the general brain mechanisms that enable us to predict even highly uncertain sound environments and to possibly make sense of and appreciate even atonal music.

1. Introduction

For us humans, one of the most common, universal activities dealing with sounds and a highly common source of pleasure in daily life consists in music listening. When, as scientists, we observe musical behaviour and its related affective connotations, though, what becomes immediately evident is their high variability among individuals and across cultures.

Sounds in music acquire sense, namely, show a sort of internal “formal perfection” – paraphrasing Cochrane (2011) – when their parts relate to each other in some kind of structured and organized way. This organization is dictated by each musical culture and by its historically established conventions (e.g., Western tonal music, pentatonic Arabic music and so on). Hence, sounds make sense in idiosyncratic ways across societies. They even acquire different meanings across individuals within the same musical culture or within the same individuals across time. Such semantic instability and uncertainty for music is what makes it more a form of art than a cognitive function. For instance, the same rough vocal timbre of a heavy rock singer might give chills of pleasure to one aficionado and be totally repulsive for a classical music lover. Or else, the same song can be meaningless for one person or be of utmost importance to another, representing strong desires and values of the inner self or transporting to the dearest memories of one’s own life.

The semantic variability and ambiguity of music across and within societies are the reasons why the scientific study of music perception and appreciation is challenging up to fall into a risk of reductionism when the musical experience gets identified with strictly perceptual or cognitive processes related to the brain processing of specific syntactic rules or their violations. Lately, to overcome the risk of reductionism and encompass the phenomenological richness of music, scholars have proposed a new research agenda, the neuroaesthetics of music, to investigate the neuroscientific foundations of music listening as an

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aesthetic experience, fractionating it into perceptual, cognitive, emotional and evaluative processes similarly to those occurring for other forms of arts (painting, literature, dance, and so on; Brattico, 2021; Hodges, 2016; Stark et al., 2018). Within this research agenda, several factors are considered to explain the individual variations in the musical experience. A very recent proposal by Thomson and colleagues (2023) identifies three main ways in which individuals engage with music and appreciate it: first, understanding and internalizing the musical structure; second, activating self-oriented responses to the music that reinforce the sense of self and impact on well-being (e.g., by activating autobiographical memories); third, identifying and engaging with the sources of music making, including the biomechanical way a piece is performed as well as its cultural, historical and even political context.

Neuroscientific research on music has much advanced, including within the neuroaesthetics agenda; however, the largest focus has been on the first source of music engagement and appreciation as identified by Thompson et al. (Thompson et al., 2023), namely understanding and internalising the musical structure, and more precisely, one specific type of musical structure, i.e., Western tonal music. The reason for such emphasis can be found in the Western geographical origin of the researchers and in the initial motivations for investigating Western classical musicians as a good cognitive and neuroscience model for, respectively, expertise and brain plasticity (for a brief history of the field, cf. Brattico, 2021). However, a musical meaning can emerge even in the presence of highly complex, indefinite sounds, and this meaning formation process might be affected by the constant process of learning by exposure to the environment. A small body of neuroimaging research has very recently focused on the contemporary style of atonal music, exploiting its richness and unpredictability to understand how the brain deals with the cognitive uncertainty of the auditory environment, in the theoretical framework of the predictive coding model (PCM) of music (Vuust et al., 2022).

2. Making sense of musical sounds by predicting them

Music typically consists of repeated acoustic features and patterns organized according to specific rules that vary by epoch, by composer or artist and even by composition or song. Composers and interpreters play with those features, patterns, and rules by allowing them to be fulfilled or betrayed. Hence, in music perception, musical rules allow listeners to form expectations, based on biologically acceptable acoustic features (e.g., within a physiologically acceptable range for loudness, roughness, or frequency) as well as on statistical learning of what is most or least common and accepted. Listeners, by being daily exposed to the music or their own culture learn the features and patterns rules specific of a musical style or piece. Schematic expectations exist for culture-specific conventions of harmony or rhythmic progressions (Hansen et al., 2017, ; Hansen and Pearce, 2014) whereas veridical expectations occur in the case of familiarity with a certain piece or genre of music (E. Brattico et al., 2013; Kliuchko et al., 2019; Vuust et al., 2012). Dynamic expectations rely on short-term memory and attention for the immediate musical past (Altenmüller, 2001; Reybrouck et al., 2021). The neuronal mechanisms and functional architectures underlying all these different kinds of expectations in music are shaped by the musical culture of a specific period and society as well as by the level of familiarity to that culture, which is dependent on the personal listening history, education and other person-related biological factors (Brattico, Bogert, et al., 2013; Reybrouck et al., 2021; (Vuust et al., 2022).

A single theoretical framework, i.e., the predictive coding model (PCM) of music (Koelsch et al., 2019; Tsogli et al., 2022) explains the formation of all kinds of expectations in the brain, how they impact on music perception and even how they might originate pleasurable emotions in listeners. The latter implications of PCM miss to cover the richness of the aesthetic experience of music as described by Thompson et al. (Thompson et al., 2023) or Brattico (Brattico, 2022) but it is considered a powerful framework for predicting several aspects of music perception, emotion, action, and learning, specifically dealing with positive (pleasurable) affect in Western tonal music, in its various manifestations, from classical to jazz and pop/rock style (Vuust et al., 2022).

According to PMC, when we listen to music, the brain works like a hierarchical Bayesian machine (Clark, 2013), since it deploys a predictive model based on prior listening experience of music to guide the perception of incoming sounds (posterior). Supporting evidence for PCM derives from neurophysiological studies using the mismatch negativity (MMN) a pre-attentive marker of prediction error (Garrido et al., 2008; Näätänen et al., 1978; Paavilainen, 2013). When the input (posterior) does not match the predictions (priors) such as when a tone is mistuned or arrives later than expected in an isochronous rhythm, a MMN error signal is generated in the neuronal assemblies located in the superior temporal gyrus extending to frontal and parietal regions, depending on the level of hierarchical predictions ((L. Bonetti et al., 2022), Carlomagno, et al., 2022; (Lumaca et al., 2019)). More specifically, when the infrequent sounds in the stimulation break expectations related to the acoustic features of the musical motifs sounding like performance mistakes by the artist, an MMN is originated mainly in the feedback loops of supratemporal neuronal assemblies whereas when the infrequent sounds are rather structural changes introducing unexpected musical keys or new rhythms then the bidirectional loops detecting the error and feeding back the prediction model locate higher in the cortical hierarchy, namely in cingulate, infero-frontal and insular regions (L. Bonetti et al., 2022).

In the laboratory, since the early 1980s the typical stimulation paradigm eliciting MMN responses in the brain is the oddball one, where repetitive sounds are replaced by one or more errors (also named deviants) violating the predictive sound stream with a low probability of occurrence. That stimulation arrangement made the experimental sessions rather long, repetitive, and distant from an ecological musical listening situation ((Tervaniemi, 2023)niemi, 2023). Later efforts were undertaken to evoke MMNs in a shorter time and with paradigms more music-sounding, such as the “multifeature” paradigm, and where the sounds are presented in a looped manner in randomly varying keys with several different deviants, each eliciting an MMN in just few minutes of recordings (Kliuchko et al., 2016; Vuust et al., 2012; Vuust et al., 2016). In all the stimulation paradigms the MMN is elicited when attention is diverted from the sounds toward another primary task, typically watching a silenced movie or performing a behavioural test (Näätänen et al., 2019). Such preattentive condition for MMN elicitation reflects the MMN function, namely detection of an infrequent change or error in the prediction and a fast, automatic updating of the predictive model (Koelsch et al., 2019). Very recent studies have further linked this prediction error signal to an automatic emotional reaction of the brain to aversive and unexpected features of the auditory scene (Ringer et al., 2023). In this sense, MMN could be an index of surprise and might be even related to a curiosity and exploratory instinct towards the environment.

The link between predictive processes in the brain and emotional responses to unexpected sudden changes in the environment has been hypothesized even in the aesthetic context, under the PCM framework. Some scholars have proposed that positive aesthetic responses to musical sounds might derive from the rewarding value of optimally dosed prediction violations and their related brain-bound predictive models. For example, tonality in Western music, i.e., the hierarchy of relations pointing towards a tonal centre in melody and harmony, constitute a strong predictive model for sound pitches, whereas metre, i.e., the experience of regularly recurring rhythmic patterns and accents (especially binary or ternary), which underwrites the way we move regularly to sometimes highly irregular musical rhythms, constitute a robust predictive model for the temporal occurrence of sounds in music (Vuust and Witek, 2014). According to PCM, aesthetic pleasure derives when the musical predictive models are neither precise nor too obscure, allowing the listener to reach the optimal dopaminergic activity when the model mismatches can be smoothly resolved by model updating and active sensorimotor regulation (Vuust et al., 2022). Such mismatch resolution is subjectively experienced as positive, not only in music but also in other forms of art, due to the evolutionarily positively valenced and arousing experience of resolving the uncertainties in the environment (van de Cruys & Wageman, 2011).

These predictive rewarding processes are enacted in the phenomenon of groove, which, according to the psychological literature, consists in the pleasurable urge to move to rhythmic music and depends on the level of complexity in specific musical features, particularly in the rhythm (Stupacher et al., 2022). The relationship between rhythmic complexity and groove is illustrated by an inverted U curve since the groove pleasurable hotspot lies in the medium level of complexity allowing precision in prediction and sensorimotor predictive inference (the drive to move) whereas too low complexity does not necessitate any sensorimotor involvement and too high rhythmic complexity leads to low precision and prediction failure (Matthews et al., 2023; Stupacher et al., 2022). This thrive towards optimal precision of predictions related to the multiple aspects of music, from rhythm to tonality features to the precise memorized models of each sound constituting our favourite song, is what might explain why we repeat musical listening experiences across our life (Gebauer et al., 2012).

The listening experience becomes highly interesting in the case of ambiguous musical stimuli, when the listener must choose between two models which is the one to adopt for enabling predictive processes. Hence, depending on their musical competence and listening biography, the listener makes an active decision to listen attentively to the same piece of music adopting a specific metric or tonal model. Think of polyrhythm in Subsaharian or Jazz music or polytonality in some modern pieces, e.g., by Alberto Ginastera or Bela Bartók or Arthur Honegger. In the context of PCM framework, music listening, and appreciation does not occur without referring to a model.

In this respect, a crucial concept in PCM is the notion that prediction errors are weighted by their expected precision or predictability, namely a neuromodulatory gain is applied depending on the strength and accuracy of the model based on prior experience, which might be more or less precise (Barron et al., 2020). When listening to less familiar music (whether consisting of melodies or rhythmic patterns), the listener's brain predicts the incoming sounds based on a weaker model than if the musical context would consist of highly familiar music, whose style-dependent features and conventions are very well known. In neurophysiological recordings, this model precision is indexed by the MMN magnitude to acoustic errors, which is reduced when those errors are inserted in unfamiliar as opposed to familiar contexts, as well as by the compromised behavioural performance in detecting the errors.

Supporting evidence for the role of model precision in PCM comes from magnetoencephalography (MEG) studies utilizing unfamiliar melodic sequences made of several pitches changing across multiple tonalities vs. melodies made of few repetitive pitches or rhythmic sequences with a variable metric vs. sequences with isochronous rhythms (Quiroga-Martinez, Hansen, et al., 2020; Quiroga-Martinez et al., 2021; Quiroga-Martinez et al., 2019; D.R. Quiroga-Martinez et al., 2020). MEG findings on MMN prediction errors support the role played by model precision with stronger MMN to errors within melodic or rhythmic contexts that closely conform to the conventions of Western tonal music and that are very repetitive as opposed to errors inserted in contexts musical sequences that are more varying in the pitch or metric content (D.R. Quiroga-Martinez et al., 2020; D.R. Quiroga-Martinez et al., 2020; Quiroga-Martinez et al., 2019). Remarkably, model precision acts as a neuromodulatory gain for MMN prediction error signals even for congenital amusia participants, suffering from an inborn music-specific deficit in pitch perception (Quiroga-Martinez, Tillmann, et al., 2020). Overall, these studies succeeded in proving that the more precise the model for musical predictions, based on culture-dependent statistical learning (such as in professional musicians vs laypersons), the larger the MMN at surprising notes (Vuust et al., 2022).

The majority of neurophysiology studies concerning PMC from the past decade have focused on Western tonal music and its predictive models of reference, namely tonality and metre. Western tonal music is well apt for PCM testing since it is characterized by tonal hierarchical organization, a high degree of consonance, and a tendency to provide the listener with a tonic as a reference point or a binary beat during the listening experience (Mencke et al., 2018). In real life, though, individuals often face situations in which uncertainty prevails and where making sense of sounds becomes a hard but necessary perceptual (and possibly even aesthetic) challenge. Echoing recent calls for action (Tervaniemi, 2023; Mencke et al., 2019, 2022; Brattico, 2019; Brattico and Alluri, 2021), brain research on PCM and, more broadly, on neuroaesthetics of music, should broaden its horizons to explore sound environments that are more unpredictable than the simplified and repetitive one-voice melodic or rhythmic patterns typically used, in favour of stimuli that rely even more than earlier on learning and uncertainty, towards increasing the ecological validity of our inferences.

3. The perceptual challenge of atonal music and the role of expertise

In music, the sheer uncertainty of sounds and acoustic features is exploited for aesthetic purposes and the continuous invention of novel compositional techniques and practices has ultimately led to the pluralism of music styles and idioms seen today (Taruskin, 2006). One common element of twentieth/twenty-first century Western art music is its aesthetic premise of creating and presenting something completely novel if not merely experimental (Hiekel and Utz, 2016; Nyman, 1999). Contemporary musical styles such atonal music are, indeed, less expected, with a highly uncertain auditory environment (Mencke et al., 2018, 2022, 2023). Consequently, a specific challenge of atonal music is that listeners must try to continuously generate new predictive models that can be composer-specific or, sometimes, even piece-specific. Listeners should not only try to refrain from applying available tonal models to the heard music, but they also should actively search for statistical regularities within each piece and to try to make sense of novel rules that may be related to musical properties other than pitch, such as timbre, dynamics, or even sound localisation in the space. Good examples of the use of sound localisation for aesthetic purposes are the pieces "La voce dell'Inferno" by S. Sciarrino or the "Dialogue de l'ombre double" for solo clarinet, tape, and live electronics by P. Boulez.

With the brain's prioritisation of auditory input containing cognitive reference points such as the tonic or the cadence in Western tonal music, due to its global diffusion, it is no wonder that contemporary atonal music is, in turn, widely recognized as a perceptual, cognitive and aesthetic challenge for both listeners and empirical researchers (Mencke et al., 2022). Nevertheless, atonal musical styles such as classical contemporary or experimental electronic music count a small but devoted niche of aficionados (Mencke et al., 2023). It has been recently proposed that listeners and musicians who prefer atonal music share personality traits that make them prone to internal states related to exploration (Mencke et al., 2019; 2022). The reward that derives from the process of continuously confronting with the uncertainty in the environment, which has been widely studied in relation with animals and their exploratory behaviour, might explain the motivational drive towards atonal music by its niche of aficionados, within the PCM account (Mencke et al., 2019). This mechanism might be combined with another one, proposed first by Menninghaus et al. (Menninghaus et al., 2017) and adapted to the atonal music case by Mencke et al. (2022), namely the increased tolerance for negative feelings originating from the dissonance and cognitive load typical of atonal music, being those feelings induced within an art context and for the purpose of intensifying the emotional engagement.

While little research has been conducted on the emotional responses to atonal music in relation to PCM, some cornerstones in the scarce neuroscientific investigations exist in relation to the neural correlates of predictive processes for atonal music. In magnetoencephalography (MEG) and electroencephalography (EEG) studies, we recently introduced stimulation paradigms and analysis approaches (exploiting knowledge from computational fields such as Music Information Retrieval (Lartillot et al., 2008) and information theory models of melodic expectancy, namely IDyOM ((Pearce and Wiggins, 2012)e & Wiggins, 2012) that allowed us to identify prediction-error- and memory-related responses in the brain even from AM contexts during a realistic music listening condition, towards understanding the neural mechanisms that possibly enable us to make sense of and appreciate even highly complex sounds.

First, we conducted an MEG study with 20 non-musically trained participants, focusing on how the high uncertainty of AM modulates predictive processes as indexed by the MMN and behavioural responses (Mencke et al., 2021). For this study, we implemented an atonal version of the "multifeature" paradigm (Vuust et al., 2011). Findings demonstrated that the magnetic MMN in response to pitch, intensity, timbre, and location errors was evoked in both tonal and atonal contexts, with no significant differences between conditions ((Mencke et al., 2021)e et al., 2021). In contrast, in a separate behavioural experiment, the 39 non-musicians were more accurate and had higher confidence in detecting pitch errors when inserted in the tonal than in the atonal "multifeature" stimulation context. This study, in terms of the consequences that the lack of a regular and hierarchically structured input has on neural and cognitive processing, suggests that the generation of predictive models is strongly impeded on the higher processing levels on which conscious behavioural discrimination relies. In contrast, the lower levels of processing within the auditory cortex that are indexed by the MMN did not seem to be affected by a lack of tonal hierarchies. Consequently, it was proposed that at least two distinctive types of expectations could be at work during music listening. A similar dual explanation of predictive processes has been posed by Tsogli et al. (Tsogli et al., 2019). They recorded with MEG the brain responses to experiment-made non-tonal sounds, namely tone triplets having an ending that could be predicted based on a custom-made (non-tonality related) statistical rule as well as according to their superficial acoustic features. When errors were introduced either in the statistical ending of the triplets or on their acoustic feature an MMN was elicited, showing interaction between sensory-based predictions and statistical predictions with a smaller MMN for statistical errors when they co-occurred with the acoustic errors. This evidence further demonstrates that several predictions operate in the brain during listening in bidirectional information loops operating in parallel in both bottom-up and top-down directions (Rauss and Pourtois, 2013), even in presence of non-tonal musical material.

4. The brain dynamics of predictive (and unpredictive) processes for atonal sounds

The above-mentioned findings seem to indicate that the encoding and prediction of structurally complex sounds is a perceptual and cognitive challenge that relies on neural mechanisms that have not yet been fully elucidated. Moreover, they point at the limit of preattentive predictive processes calling for investigations on conscious encoding and memory predictions of atonal sounds. For those processes, we likely depend on the temporal, dynamic organisation of stimulus features in the brain and on our individual memory functions ((Gabrieli, 1998)eli, 1998). For elucidating these dynamics, modern neurophysiological methods such as MEG combined with MRI offer unprecedented opportunities.

Recently, we adapted the old/new paradigm (Rugg and Curran, 2007) from (visual and verbal) memory research and applied it to MEG (combined with MRI for source reconstruction) (Bonetti, Brattico, et al., 2022) with the goal of understanding the temporal brain dynamics behind the conscious recognition of music, including AM. In our MEG/MRI study (Fernández-Rubio et al., 2022 ández-Rubio et al., 2022), after listening four times to a one-voice version of the prelude in C minor by J. S. Bach and it de-tonalised variation, 71 participants were asked to recognize whether 5-note melodic motifs were extracted from the prelude or from its atonal variation ('old') or were never heard before ('new') while their brain activity was recorded with MEG. Source reconstructions of the MEG envelope amplitude were performed in the 0.1–1 Hz and 2–8 Hz frequency bands. For both bands, distinct neural activations were obtained in association with recognizing the two types of musical stimuli. While the recognition of tonal sequences mainly recruited a widespread brain network involving cingulate gyrus and hippocampus in the right hemisphere (especially for the 0.1–1 Hz band), the recognition of atonal sequences was mainly associated with a sustained, slow activity in left-hemispheric auditory regions.

A first interpretation of the findings obtained by Fernández-Rubio et al. (2022) relies on acoustic processing rather than predictive processes and refers to relation between tonality and the harmonic series, a natural sequence of sound frequencies that are integer multiples of the fundamental frequency in a complex sound. Environmental sounds are typically nonharmonic, whereas both human voice and animal vocalisations contain harmonic structures, akin to the ones present in musical sounds (Di Stefano et al., 2022, ; Frühholz et al., 2016, ; Lewicki, 2002). The tonotopic organisation of the human auditory cortex is particularly sensitive to harmonic tones, suggesting that this region developed to process harmonics due to their relevance for social communication (Norman-Haignere et al., 2019). In this direction, it could be inferred that the distinct neural pathways obtained in relation to tonal vs. atonal music, such as found by Fernández-Rubio et al. (2022), might be related to sounds that are not coherent with the natural harmonic series and thus arguably more complex to process. On the other hand, harmonious sounds are also more common and hence, more familiar to listeners, being more widespread and hence priors for them do exist to guide our perception and memory. Hence, another interpretation relies on PCM, focusing on the memory-based predictive processes that are at play for tonal music: being atonal music more complex and harder to memorize, as evident from the behavioural findings with the same participants, the predictive processes necessary for recognising the learned motifs were confined to auditory areas for atonal music, and extended to higher-order areas for the tonal learned motifs. These findings suggest the involvement of a cortico-subcortical brain network involving the hippocampus for auditory recognition of tonal musical sounds and support the idea that stimulus complexity qualitatively alters the neural pathways of recognition memory ((Wiltgen et al., 2004)en et al., 2004). Converging evidence points at the hippocampus as the headquarter of memory encoding (Bird and Burgess, 2008), whereas subsequent levels of memory recognition are orchestrated by functional networks located in the temporal lobe, including the insula and the inferior temporal cortex (Eichenbaum et al., 2007).

Within the perceptual domain of music, until our recent MEG studies, only few previous fMRI investigations (e.g., (Burunat et al., 2014) attempted to examine how and where musical sounds are stored and consolidated in the brain, although focusing on tonal music with very rare studies using non-tonal sounds (for reviews, see Billig et al., 2022; Campo and Brattico, 2022; Freitas et al., 2018). One of such fMRI studies was conducted by Tsougli et al. (2022), using no-tonal sound triplets built according to artificial statistical rule. Errors in those artificial local rules activated not only auditory but also frontal regions in the right hemisphere, such as the orbitofrontal cortex, the frontal operculum and premotor cortex, similarly to brain activity related to violations of local syntactic predictions in language.

Overall, the findings seem to initially confirm what has been observed in other domains, namely the involvement of specific neocortical regions in the storage of information initially processed in the hippocampus: areas of the prefrontal cortex, including the anterior cingulate and prelimbic cortices, and the temporal cortex are recruited during remote memory retrieval, whereas damage to or inactivation of these areas produces selective musical memory and perceptual deficits, i.e., acquired amusia (Peretz, 2002; Peretz et al., 1997). More research, though, needs to be done to provide a definite answer on the brain mechanisms for formation and storing of musical memories, especially in presence of complex, unpredictable sounds and on connecting the findings on the brain structures responsible for prediction and memory of sounds with understanding whether and how those processes of auditory model formation and prediction are linked with emotional and aesthetic responses, to finally reach a comprehensive picture of the processes related to meaning making for the aesthetic experience of music (E. Brattico et al., 2013).

5. From activations to connections for music prediction

The neurophysiological studies reviewed have been able to track the neural dynamics of sound encoding and memorisation both at the auditory cortex and cortico-hippocampal level but they have not yet investigated the neural connections that are put in place for those processes (for a review, see Campo & Brattico, 2022). Knowledge on functional connectivity for musical memory formation, in fact, relies on inferences from studies conducted in other domains (e.g., speech or visual images) or in animals (cf. (Billig et al., 2022)), apart from sparse fMRI studies on task-free (tonal) music listening ((Alluri et al., 2015); Burunat et al., 2014).

An exception to this state of affairs is represented by the MEG (combined with MRI) study by Bonetti et al. (2021), focusing on the rapid encoding of tonal sounds forming a complex temporal sequence. MEG was used to record the brain activity of 68 participants while they listened attentively to a prelude by J.S. Bach during an encoding phase which they knew would be followed by a memory recognition phase. Functional connectivity analyses, performed using phase synchronisation and graph theoretical measures, showed a large network of brain areas recruited during attentive encoding of sounds (towards memory formation), comprising primary and secondary auditory cortices, frontal operculum, insula, hippocampus, and basal ganglia. These results highlighted the rapid transition of brain activity from primary auditory cortex to higher order association areas including insula and superior temporal pole within a whole-brain network occurring during the first 220 ms of the encoding process. Further, the authors found that individual differences in cognitive abilities and in musical expertise modulated the degree centrality of the brain areas implicated in the encoding process: participants with higher musical expertise presented a stronger centrality of superior temporal gyrus and insula, while individuals with high working memory abilities showed a stronger centrality of frontal operculum (Bonetti et al., 2021).

These findings provide insights into a dynamic view of the brain networks responsible for encoding sounds and their relationship to individual differences, showing a complex picture that goes beyond the known involvement of auditory areas. Moreover, the adopted approach opens a glimmer towards integration between neural activity and functional connectivity towards a complete picture of the brain networks involved in the listening process, networks that the sole brain activity missed to reveal: the brain activity was largely reconstructed on the primary auditory cortex and insula, whereas the large-scale whole-brain connectivity analysis revealed a wide set of higher-order brain areas that were highly synchronised between each other and central within the whole-brain network (Bonetti et al., 2021). These brain regions are not classically implicated in auditory processing, suggesting that the process of making sense of music during listening requires the collaboration of several brain structures for the integration and storing of the information carried by the sounds. From this perspective, it could be hypothesised that the primary auditory cortex is involved in the first processing of the incoming sound, whereas the integration between insula and superior temporal pole with the rest of the brain may play a crucial role for a more fine-grained elaboration of the sounds to be encoded.

Moreover, functional connectivity analyses in the source space revealed the emergence of cortico-hippocampal interactions during the formation of auditory memories for more predictable vs. less predictable sounds (Bonetti et al., 2021). These findings extend previous knowledge obtained with fMRI on the superior hippocampal connectivity in association to listening to familiar music in musicians as opposed to non-musicians (Burunat et al., 2018; Gagnepain et al., 2017). Further studies on continuous listening to either tonal or atonal music could enhance the knowledge on the general mechanisms underlying the encoding and predictive processes for individual objects (e.g., sounds) of a sequence (e.g., a piece of music) in the human brain, moving towards greater awareness on the neural dynamics under naturalistic listening conditions.

6. Conclusions

The above-described data converges in showing that music perception involves the constant prediction of future sound events by the brain, based on the continuous extraction of feature regularities from the sound environment. The neural hierarchical mechanisms for predictive processes in perception and memory, previously studied in relation to simple acoustic features or sound patterns inserted in highly certain contexts, have lately been investigated also in relation to highly complex sounds creating uncertain, confusing contexts. In real life, listening situations where uncertainty prevails are not uncommon: think of an urban auditory scene such as when taking the metro, we try to make sense of the deafening sounds around us.

In recent MEG/MRI and EEG studies, atonal music has been used as a model for the unpredictability of naturalistic listening conditions. A first set of findings related to the preattentive predictive processes indexed by the MMN error signal point at similar mechanisms for auditory-cortex predictions for basic acoustic features when inserted in certain or highly uncertain musical context (Mencke et al., 2021), although a decrease in model precision affects the MMN when the context lacks the anchor points of tonality (Quiroga-Martinez et al., 2019). Moreover, MMN results also highlight the role of listening biography and expertise in defining the predictive models by increasing their precision (Quiroga-Martinez et al., 2021; (D.R. Quiroga-Martinez et al., 2020)). Another set of MEG/MRI findings examines conscious memory predictive processes, namely encoding and recognition for tonal (Bonetti, Brattico, et al., 2022) and atonal music (Fernández-Rubio et al., 2022), evidencing qualitatively distinct neural activations for making sense of familiar, tonal melodies versus unfamiliar, atonal ones. Furthermore, functional connectivity analyses in source space revealed cortico-hippocampal interactions during the formation of auditory memories for more predictable versus less predictable tonal patterns, modulated by the individual level of cognitive abilities and musical expertise (Bonetti et al., 2021).

In the perspective of a deeper understanding of the neural mechanisms underlying the conscious predictions of auditory uncertainty, future studies could focus on recording the brain responses of a special and rare category of listeners, namely experts of contemporary classical music, a restricted group of aficionados for this niche musical style (Mencke et al., 2018, 2023). Functional connectivity analyses would verify whether the cortico-hippocampal dynamical interactions seen during recognising learned musical motifs of tonal music in musically non-expert listeners could be seen also for atonal music in contemporary classical music experts. The findings might elucidate whether frontal-mesotemporal connections and their bidirectional predictive loops are indeed the necessary and sufficient mechanisms for making sense of highly complex sounds. Fig. 1

CRediT authorship contribution statement

Elvira Brattico: Conceptualization, Writing – original draft, Writing – review & editing. **Marianna Delussi:** Writing – original draft, Writing – review & editing.

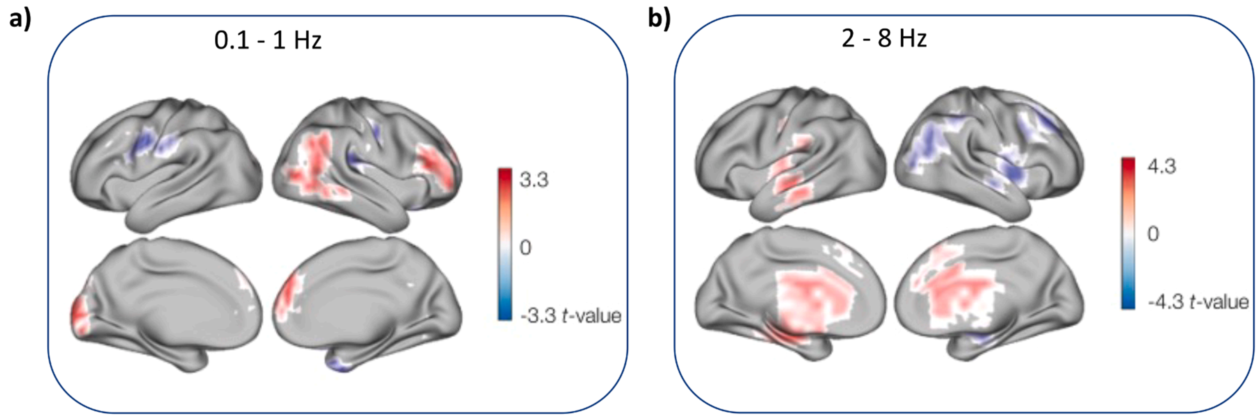

Fig. 1. Tonal vs. atonal musical recognition. Reconstructed magnetoencephalography activity to recognition of the memorized last tone of tonal vs. atonal musical motifs. For both frequency bands (1A and 1B) the brain activity was localized in memory processing areas for tonal sequences (in red) and in auditory processing areas for atonal sequences (in blue) for all tones. For the lowest frequency band (0.1–1 Hz) hippocampal activity is visible only in association with recognition of tonal motifs. Modified from (Fernández-Rubio et al. 2022) and reproduced with permission.

Data availability

No data was used for the research described in the article.

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