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Understanding music and aging through the lens of Bayesian inference

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ABSTRACT

Bayesian inference has recently gained momentum in explaining music perception and aging. A fundamental mechanism underlying Bayesian inference is the notion of *prediction*. This framework could explain how predictions pertaining to musical (melodic, rhythmic, harmonic) structures engender action, emotion, and learning, expanding related concepts of music research, such as musical expectancies, groove, pleasure, and tension. Moreover, a Bayesian perspective of music perception may shed new insights on the beneficial effects of music in aging. Aging could be framed as an optimization process of Bayesian inference. As predictive inferences refine over time, the reliance on consolidated priors increases, while the updating of prior models through Bayesian inference attenuates. This may affect the ability of older adults to estimate uncertainties in their environment, limiting their cognitive and behavioral repertoire. With Bayesian inference as an overarching framework, this review synthesizes the literature on predictive inferences in music and aging, and details how music could be a promising tool in preventive and rehabilitative interventions for older adults through the lens of Bayesian inference.

1. Introduction

Music is present in almost every culture and society. Its integral role in human civilization spans from societal and social functions (Koelsch, 2013) to emotion regulation (Moore, 2013). Indeed, music relates to key aspects of human perception and action including auditory perception, emotional perception and motor outputs, and offers therefore a unique opportunity to better understand the organization of the human brain (Abdul-Kareem et al., 2011; Münte et al., 2002; Schlaug, 2001).

Intrinsic in the discourse of human brain organization is the field of theoretical neuroscience. In the past few decades, this field of research has been marked by the development of a Bayesian modeling framework for human cognition (Friston et al., 2012; Knill and Pouget, 2004; Lin and Garrido, 2022; Vilares and Kording, 2011). Instead of characterizing the brain as a passive filter of the sensorium, this paradigm shift posits that the brain is akin to a statistical machine that holds beliefs and **predictions*** about its environment, and actively tests these predictions against incoming sensory evidence through a process known as active Bayesian inference. The main computational imperative of the brain is thus two-fold: (1) to encode predictions about the causes of sensory

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events, and (2) to minimize the prediction errors such that our actions are adaptive to the environment that generated these sensory events (Friston, 2010).

Bayesian inference could also underlie music perception (Koelsch et al., 2019; Vuust et al., 2009, 2022). During music listening, the individual is likely to engage in real-time perceptual inference and predictive processing in order to form expectations and understanding of the current musical context. Over multiple experiences, these inferences consolidate into an internal model that generates the appreciation of different musical patterns. Hence, an individual's musical taste and competency accumulate over the lifespan and is highly dependent on his/her cultural background (Balkwill and Thompson, 1999; Heng et al., 2021; Laukka et al., 2013; Li et al., 2014; Stevens, 2012).

In parallel, normative aging could be framed as an optimization process of Bayesian inference. As the internal model is continuously optimized over the course of a lifetime, it becomes more efficient in learning frequented variables in its ecological niche as compared to less-frequented ones in the larger environment (Friston et al., 2010; Moran et al., 2014). This is intuitively expressed as getting "stuck in our ways" as one ages, and can be computationally seen as a trade-off between model accuracy and complexity. To maintain model complexity in the face of biological limitations, the aging brain no longer learns the nuances in its environment through sensory evidence (Moran et al., 2014). This may explain the phenomenon of cognitive decline in aging.

Currently, predictive coding frameworks based on Bayesian inference have been developed to explain disorders such as dementia, autism,

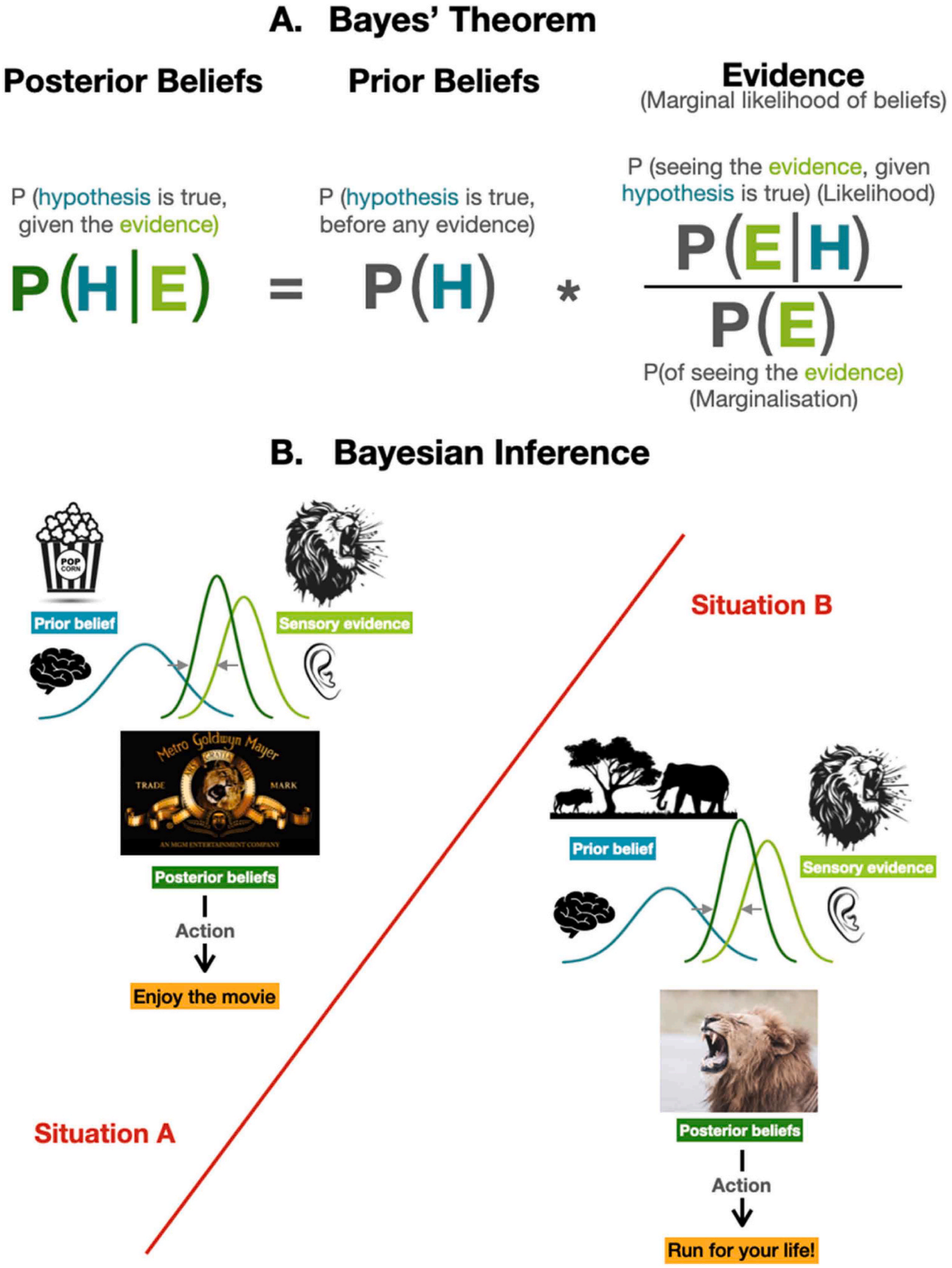


Fig. 1. *Bayesian Brain Hypothesis. Note.* A Bayesian Inference is a statistical theory that describes the update of the probabilities of a hypothesis being true based on prior beliefs and current evidence for the said hypothesis. The evidence for the hypothesis is marginalized by the probability of observing the evidence without any assumption. B Bayesian inference applied to neuroscience (Parr et al., 2018) posits that the brain not only perceives sensory events, but also concurrently makes hypotheses for the cause of sensory events based on prior understanding about the environment that it is in. The difference between a prior hypothesis or a prediction and the incoming sensory evidence will contribute to the optimization of the beliefs of the environment.

schizophrenia (Friston et al., 2016; Kocagoncu et al., 2021; Van de Cruys et al., 2014; Yao and Thakkar, 2022), and have extended its discourse from explaining disorders to discussing implications for treatments (Putica et al., 2022). However, an outline illustrating how active inference can be considered as an overarching framework underlying music, aging and the effects of music on aging is outstanding. Therefore, the current review seeks to bridge the gap among these aforementioned research fields. Firstly, we outline how Bayesian inference underlies the appreciation and learning of music in the brain. Next, we discuss how Bayesian inference can be used to explain age-related decline in cognition and the brain (including functional, structural and metabolic changes). Lastly, we will look at how, according to Bayesian inference, music can be a unique opportunity to understand age-related changes and how it may be an optimal way to retard the effects of aging in the brain.

2. Music in the Bayesian brain

2.1. The Brain computes music through Bayesian Inference

Music is a uniquely neurological phenomenon. Fundamentally, sound waves are produced when an individual plays a musical instrument. These sound waves consist of simple and complex frequencies, and create small vibrations that are passed along the air particles. These vibrations are translated in the brain into something that holds meaning and beauty, something that engenders emotions and movements, and brings about social bonding within and across different cultures. The brain accomplishes this just like how it engages in all the other wonderful marvels that it does - by making Bayesian inferences.

2.1.1. What is Bayesian inference in the brain?

Bayesian Inference* is a statistical theory that outlines the update of a **prior model*** to a **posterior model*** with new information gathered (Fig. 1A; see Glossary) (Jaynes, 2003; van de Schoot et al., 2021). Consequently, applied to the brain (Knill and Pouget, 2004), it argues that the brain makes inferences about the environment based on prior knowledge; it forms an internal model of the probabilistic distribution of environmental states to understand the uncertainties associated with its surroundings. This model is optimized by the evidence collected through interaction with the immediate environment (Fig. 1B; Friston et al., 2012; Knill and Pouget, 2004; Vilares and Kording, 2011).

Music is a type of internal model (a.k.a., **generative or world model***) that is formed in the brain. It holds the probabilistic distribution of different sounds in a musical piece. These probabilistic distributions are then associated with different situations and surroundings. Indeed, Pearce (2018) showed that a broad range of psychological processes involved in music perception (e.g., expectation, emotion, memory, similarity, segmentation and meter) can be understood in terms of a single underlying process of probabilistic prediction using learned statistical regularities, termed the Information Dynamics of Music (IDyOM; Pearce, 2005). Using probabilistic predictions and **statistical learning*** (see Glossary), IDyOM could effectively simulate and generate predictions about individual differences in music perception and experience, which occur as a result of enculturation in different musical styles. This parallels the central tenet in Bayesian inference; our understanding of the environment around us, which includes music, is built upon our internal generative or probabilistic model. As this model gets optimized by different encounters, our understanding of the world also consolidates around these experiences accumulated throughout our life. Thus, Bayesian inference can be conceptualized as the fundamental mechanism underlying perception and emotional experience of music, instead of other distinct psychological and cognitive mechanisms (see BRECVEM model; Juslin and Västfjäll, 2008).

Bayesian belief updating in the setting of active inference constitutes two processes: (1) to encode predictions about the causes of sensory events, i.e., **perceptual inference***, and (2) to minimize the prediction errors such that our actions are adaptive to the environment that generated these sensory events, i.e., **active inference*** (Friston, 2010, and see Glossary). This is a recurrent process that ultimately leads to individualized experiences and musical tastes. Perception engenders action, and actions refine perceptions. In the case of music listening, at one end of the hierarchy, sensory learning occurs during music perception as state-to-state musical changes accumulate as a model of expectancy of the upcoming tonal and rhythmic context and its volatility. At the other end, actions are generated that are congruent with this expectancy, for instance in the form of finger-tapping to the rhythm of the song, that reflects the learnt model of context and volatility. This finger tapping is satisfying because it is based on internal models that are congruent to the incoming sensory data, and it further contributes to the expectation of upcoming rhythmic context. This may explain why a mismatch between prior expectations (i.e., the finger tapping) and the incoming data (i.e., music) results in a **prediction error*** (see Glossary) that evokes a sensation of surprise. Following this error, is a strong impulse to tap to the new beat, where adjustments are made based on the prediction error, and the prior expectation is updated to a posterior belief to accommodate the new incoming data.

2.1.2. How does the brain create an internal model?

As individuals gain an understanding of the statistical regularities of sensory information in the world, an internal model of these environmental phenomena, including music, is formed (Friston, 2010). This is achieved through interactions and predictive inferences with that phenomenon (Friston, 2010). Predictive inferences refer to the process whereby the brain actively predicts incoming sensations and their causes based on the likelihood of sensations, given their external causes. When listening to music, the listener develops an expectation of the upcoming musical sequences based on a learnt internal model of the probabilistic fluctuations in the melodic, rhythmic and harmonic structure of the music (for a review of predictive processing of melody, see Basiński et al., 2023). This understanding of the dynamic formation of expectations (along with their realization or denial) during music listening builds upon seminal works such as Meyer (1956), Narmour (1992), and Huron (2006) among others.

Recently, Vuust and colleagues (2022) formulated the predictive coding of music (PCM) model (see also see previous works from Koelsch et al., 2019; Vuust et al., 2009), which inherits largely from the Bayesian inference perspective. Essentially, the PCM model posits that recursive Bayesian processes between perceptual and active inference are the fundamental underlying principles resulting in music perception (which encompasses melodic, harmonic and rhythmic processing), action, emotion and learning.

The brain actively goes through Bayesian inference as we listen to music. It deploys an internal predictive model that is based on consolidated past musical experiences to guide our perception of the current piece of music. The internal model is built upon the incoming sensory evidence (μ). The likelihood of musical progressions (λ) can be inferred to track the statistical regularities (X) underlying dynamic sensory changes when listening to music. This is what the brain uses to actively predict the upcoming musical notes and set up an expectation of the musical motif. This expectation creates actions (α) that are consistent with it, such as tapping or dancing to keep with the rhythm (Fig. 2). As expectations are realized or violated, brain regions responsible for the release of neurochemicals that engenders emotions are also activated (e.g., Blood and Zatorre, 2001; Gold et al., 2019).

Individuals navigate the environment via actions based on predictions that are consistent with their current internal understanding of the surrounding. When there is a mis-match between the prediction and the actual incoming sensory experience, a prediction error is generated. This prediction error is used to update the prior expectations we have about the current sensory context, for instance a particular piece of music, and the updated expectations will generate actions that reduce the prediction error between current expectations and the music (Vuust

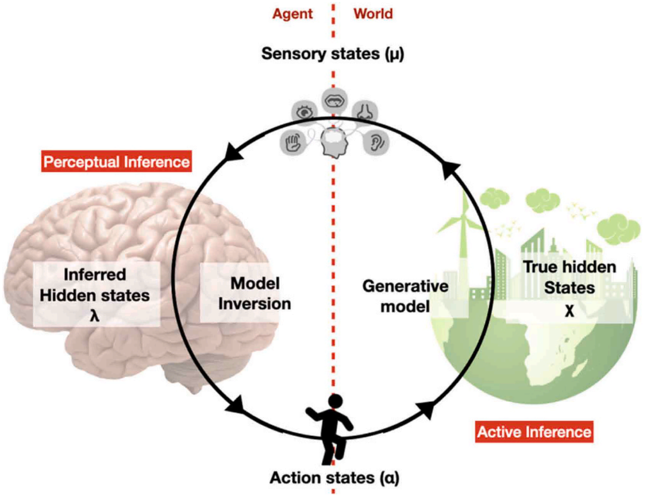


Fig. 2. *Interaction between Agent and Environment. Note*. Hidden causes of environmental changes (X) generates sensory stimuli (μ) observed by an agent. The likelihood of environmental events (λ) can be inferred from probabilistic fluctuations of the hidden environmental states computed from the incoming sensory evidence. This internal model of inferred states guides the agent's actions (α) in response to the environmental stimulus. The actions of the agent are consistent with the internal model of its environment. The internal model is also used to actively predict incoming sensations and their causes. The update and optimization of the internal model depend on the difference (prediction error) between an agent's prior beliefs and the sensory stimulations received. Perceptual inference is the process of making sense of environmental stimulus via optimization of the internal model, while active inference is the process of embodied perception, where the agent interacts with the environment according to what he believed to have perceived to test these perceptual beliefs.

and Frith, 2008).

Notably, prediction errors have two important properties: firstly, prediction errors are weighted by their expected **precision***. At any instance, the brain is experiencing an influx of sensations; yet, it has limited resources to process all this information. Within the mass of information, the brain needs to select the most relevant, precise and important data to the current context. Therefore, the brain does not treat all prediction errors equally (see Herff et al., 2020), but instead assigns more weight to prediction errors that were expected to be more precise or reliable in updating Bayesian beliefs under the generative model. Activation of these errors will be amplified while errors that are deemed less accurate will be inhibited. In this regard, studies have shown that the precision of a prediction error correlates with the synaptic gain of the error units, and is modulated by long-range neuromodulators such as dopamine, acetylcholine and norepinephrine (Friston et al., 2010, 2016; Iglesias et al., 2021; Moran et al., 2013; Newman et al., 2012; Powers et al., 2017; Vossel et al., 2014; Yu and Dayan, 2005). This process also accounts for the release of aforementioned neuromodulators (particularly dopamine) while individuals internalize the statistical regularities within a new piece of music.

Secondly, prediction errors are hierarchical. Sensory events in the environment, such as music, can often be a result of a hierarchical structure of causal latent levels (see Box 1). Recent studies showed that the brain does perform Bayesian inference on multisensory information across different levels of the cortical hierarchy (Gordon et al., 2017; Rohe and Noppeney, 2015; Chao et al., 2022), and that distinct neurological signals for different levels of prediction errors could be (Stephan et al., 2019), and indeed have been (Koelsch et al., 2019) captured in experiments. Further, the hierarchy of expectations that the listener forms and draws from during music listening has explicitly been captured in Pearce's IDyOM model (2005), which includes a short-term and long-term model (reflecting the expectations stemming from the local context, as well as those resulting from long-term musical knowledge, respectively). The next section will outline features of the brain that allow for such hierarchical Bayesian inference.

3. Neuronal implementation of Bayesian inference in the musical brain

Hierarchical levels are evident across Bayesian inference, musical and neural structures. Different brain regions and networks formulate expectations at different levels in the latent hierarchical structure of sensory events. Violations to these expectations produce prediction errors at different levels (see Siman-Tov et al., 2019 for a recent meta-analysis of prediction networks in the brain). Synaptic gain as a function of precision of prediction errors determines the fecundity of the signal to subsequent processing and is proposed to be mediated by attentional mechanism and neuromodulators that control the post-synaptic excitability of neuronal populations encoding sensory information, thereby making the chosen signals more influential in driving belief updating in the hierarchical brain.

3.1. Neuroarchitecture

The cortical architecture of the brain allows the estimation of these uncertainties through a process known as **predictive coding**^ (Clark, 2015; Shipp, 2016). Predictive coding is a computational framework that describes perceptual inference in the brain (for a review of the empirical status of predictive coding, see Hodson et al., 2024). It posits that the brain generates top-down predictions to explain bottom-up sensory input by minimizing prediction errors at various levels of the cortical hierarchy (Arnal and Giraud, 2012). The top of the cortical laminar (Fig. 3A within the orange band) consists of mostly excitatory neurons with a spectral activity that accumulates at higher frequencies in the beta (12–30 Hz) and gamma (30–100 Hz) oscillatory bands (Maier et al., 2010). From the bottom (Fig. 3A within the green band), the deep layers mostly comprise inhibitory neurons that have low spectral frequencies in the theta (4–8 Hz) and alpha (8–12 Hz) oscillatory bands (Buffalo et al., 2011; Roopun et al., 2006, 2008).

Gamma band oscillations have been proposed to encode low level (sensory) prediction errors, as evinced by both auditory and prediction error research (Bastos et al., 2012, Chao et al., 2022, Fujioka et al., 2009). This is coherent with findings in music studies that reported correlations between gamma oscillations and musical meter (Snyder and Large, 2005), whereby musical meter can be considered as a type of probabilistic context that describes the temporal occurrence of rapid sensory activations. This is in line with the concept of Bayesian filtering, whereby accumulation of mass evidence is required to produce one probabilistic distribution that accounts for these evidence (Bastos et al., 2012).

Furthermore, neural synchrony between gamma and beta band oscillations have been reported (Fujioka et al., 2009). Specifically, Fujioka and colleagues (2009) found that pre-stimulus beta power in the parietal region was correlated with post-stimulus prediction error and gamma power in the auditory cortices. This observed coupling is posited to reflect the role of beta band oscillations in signaling predictive expectancies according to top-down modulation (Arnal and Giraud, 2012), suggesting that beta band oscillations could be a measure of precision for lower-level sensory data.

Gamma oscillations in the lower sensory regions have also been reported to be associated with alpha and theta oscillations in the central to anterior brain regions (Kosciessa et al., 2021). To utilize limited neural resources optimally, the brain lowers internal inhibition by shifting attentional gain to sensory learning. The lowering of internal inhibition is represented by decreased alpha activity, given that alpha power reflects internal cognitive control; i.e., top-down predictions (Cona et al., 2020; Klimesch, 2012; Kosciessa et al., 2021; Sadaghiani and Kleinschmidt, 2016). The shift of attentional gain to sensory learning is represented by increased lower sensory gamma oscillations. From a

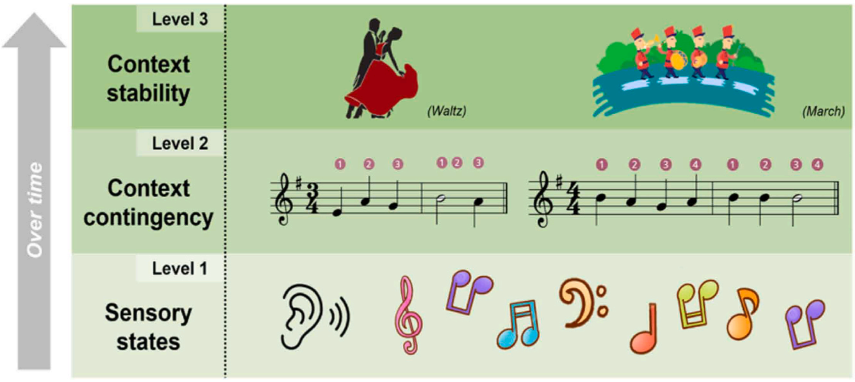
Bayesian inference perspective, musical tension can be considered as the degree of uncertainty within the music, whereby increased tension represents increased uncertainty. In this regard, increased musical tension is observed to be associated with decreased alpha power in the central-frontal regions (Sun et al.,2020).

The top layers of the cortical laminar extend in a **forwardˆ manner** to the deep layers of the columns in the front, i.e., anterior direction (Fig. 3B, blue to red region), where information from the sensory regions are gradually propagated towards executive centers and serve as evidence that will be checked against the current predictions and context (Buschman and Miller, 2007). On the other hand, predictions are propagated by the deep layers in the opposite direction; the deep layers extend in a **backwardˆ manner** to the top layers of the columns at the back, i.e., posterior direction (Fig. 3B; red to blue region).

This pattern of forward and backward neural organization has also been reported in neuroimaging studies of music listening and music recall (Ding et al., 2019; Lumaca et al., 2021). Specifically, Lumaca and colleagues (2021) employed a complex oddball paradigm based on tone patterns, and found increased excitation within the left Helsch's gyrus, coupled with a forward connectivity from this region to the left planum temporale during deviant responses. Electrophysiology recordings in epilepsy patients showed that in the early onset of music listening, brain activity was first observed in the gamma frequency band in the temporal lobe, followed by the prefrontal region (Ding et al., 2019). In other words, activity in the prefrontal region lagged behind the temporal regions. The reverse was observed during music recall: prefrontal activity preceded activity in the temporal regions. This provides support for the notion that while sensory evidence is propagated in a bottom-up fashion,

Box 1

The hierarchical nature of uncertainties in a musical context.



The stochastic fluctuations in sensory states are the result of a latent hierarchy of hidden causes that are often unknown to the brain. Music is a prime example of such a dynamic sensory phenomenon that is generated by a latent hierarchy of musical form and groupings (see Generative Theory of Tonal Music (GTTM); Lerdahl and Jackendoff, 1983). At the sensory level (Level 1), the listener receives a wide range of auditory and acoustic information, including but not limited to pitch, timbre, loudness, and rhythm. As the listener continuously collects these data, he/she builds toward an internal model of his/her understanding of a specific musical pattern, such as the meter (Level 2). In this instance, the perception of meter is only formulated when there exists an internal understanding of notes grouped into "strong" or "weak" beats. This means that the listener must have formed an expectation about the statistical regularity (i.e., a context) of the beats. The regularity and the context of the beats may be constant throughout a piece of music (e.g., for 'Waltz' and 'March'), or it may change across time (e.g., for Jazz). With repeated exposure, the listener learns the stability of the context (Level 3) (Koelsch et al., 2019). Thus, in order to generate predictive inferences about the type of music, one must form expectations of the musical context, whereby the rate of change in the musical context is based on the organization within a meter and the frequency of meter changes across the musical piece.

This example shows that dynamic changes in the musical context (i.e., causal model of the world) can be inferred from a temporal hierarchical structure of recurrent causal levels (i.e., inference model of the listener). The levels are recurrent because the update of one level depends on its neighboring levels, and changes on one level bring about changes in other levels. At the highest level (Level 3), volatility of the larger musical context determines the stability of contextual contingencies at the lower level (Level 2). Contextual contingencies at the second level in turn determine the probability distribution of state-to-state sensory stimulation at the lowest level (Level 1). To generate accurate predictions about future musical contexts, the listener must implicitly learn the contextual contingencies that underline the uncertainties of predicting the sensory stimulation in the next context. He/she must also form a belief of the uncertainties associated with these contextual contingencies across time.

Literature supports the computation of Bayesian inference in the brain in terms of hierarchical recurrent levels (Bach and Dolan, 2012; Marshall et al., 2016; Yu and Dayan, 2005). Accordingly, higher uncertainty estimates (i.e., lower precision), are associated with different outcomes at different levels of the hierarchy. Higher uncertainty estimates in the current contingencies promote re-learning about the current context through evidence from state-to-state sensory perceptions, while higher uncertainty estimates associated with state-to-state perceptions increase the reliance on prior estimates of contextual contingency and their volatility (Dayan and Yu, 2003; Yu and Dayan, 2005). As such, sandwiched between two layers of the hierarchy of uncertainty estimates is the precision between evidence input from the lower level and prediction of the higher level. This precision weight gives rise to attentional and sensory gain tuning as individuals attempt to sharpen relevant information that would result in a self-perceived reduction in uncertainty. At lower levels of the functional hierarchy, these recurrent pairs may simply be involved in sensory processes such as listening and moving. At higher levels of functional hierarchy, however, these recurrent pairs may be involved in more complex roles such as decision-making (e.g., a marching band conductor deciding a certain piece of March is more suitable for a specific performance), and epistemic affordance (e.g., re-mixing a piece of music for a DJ set at a musical festival). Thus, the unique hierarchical structure of human neuronal circuitry is crucial to the physical feasibility of implementing the computations of hierarchical uncertainties in the environment via Bayesian inference (see Figure 3).

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Glossary

Bayesian inference*: A statistical theory that furnishes the optimal updates of a prior belief to a posterior belief, given new information or evidence.

Generative model*: A probabilistic mapping from causes to observed consequences (data). It is usually specified in terms of the likelihood of obtaining some data given their causes (parameters of a model) and prior on the parameters.

Prior model / belief*: The initial belief about an uncertain parameter before new information/evidence is considered.

Posterior model / belief*: The updated belief following the assimilation of new information or evidence.

Statistical learning*: The process by which recurring patterns of sensory input across time and space are extracted from the sensory environment (Frost et al., 2019; Schapiro & Turk-Browne, 2015).

Perceptual inference*: The process of making sense (or encoding predictions) of environmental sensory stimulus via optimization of the internal model.

Active inference*: The process of embodied perception or active sensing and learning, where the agent interacts with the sensory environment to test posterior beliefs and realize predictions under these beliefs.

Precision*: The inverse variance of a random variable, which quantifies the degree of certainty about the variable. Precision corresponds to a second-order statistic of the probability distribution or density of the variable. This can be contrasted with expectation (i.e., the mean or average of a probability distribution or density of the variable, a.k.a. first-order statistic).

Predictions*: The output of a model generating outcomes from their causes. Prediction is generated from expected states of the world and compared with observed outcomes to form a prediction error.

Prediction error*: The difference between predictions furnished by posterior beliefs and the information or evidence (i.e., sensory stimulations) observed.

Predictive coding^: The framework in which the brain is organized in hierarchical layers that make predictions about the representations in lower levels. Prediction errors are then propagated forward to update representations in higher cortical level.

Forward^: The bottom-up flow of information from sensory input regions towards executive centres.

Backward^: The top-down flow of information from deeper layers (i.e. executive centres) towards sensory regions.

Entrainment^: The concept that two oscillating bodies, each moving in its individual frequency or movement period, become locked in a common period when they interact.

*Note: Terms marked with * are mostly discussed under the basics of Bayesian Inference (see Introduction, Sections 2.1.1. and 2.1.2.). Terms marked with ^ are mostly discussed in the context of neuronal implementation of Bayesian inference in the brain (see Sections 3.1. and 3.3.)* (Frost et al., 2019; Schapiro and Turk-Browne, 2015).

the predictions are propagated by the deep layers in the opposite direction - i.e., away from the prefrontal regions and towards the sensory regions in a top-down fashion. This hierarchical and recurrent organization of the cortex is proposed to account for music listening amongst many other sensory phenomenon (Huang et al., 2023; Lakatos et al., 2005; Rohe and Noppeney, 2015; Siman-Tov et al., 2019; Wang, 2013) and fits perfectly with the computation of hierarchical uncertainty estimates via Bayesian inference (Bastos et al., 2012).

3.2. *Bayesian predictive coding in auditory processing*

The Bayesian brain, guided by the recursive hierarchical minimization of prediction errors, also provides a framework for understanding various electrophysiological phenomena observed in auditory perception studies. Specifically, the phenomenon of repetition suppression (RS), omission response (OR), mismatch negativity (MMN), and early right anterior negativity (ERAN) can be explained through the lens of Bayesian inference.

3.2.1. *Predictive coding and auditory event-related potentials/fields (ERP/Fs)*

Repetitive stimuli contribute to the formation of prior expectations, with RS and OR manifesting as a result. RS signifies a gradual decrease in evoked responses over repeated stimuli, attributed to the suppression of sensory excitations congruent with top-down inhibitory expectations (Auksztulewicz and Friston, 2016). This effect is thought to be similar to the gradual attenuation of the N1 event-related component during repetitive stimuli (Bendixen et al., 2012; Grill-Spector et al., 2006), where N1 reflects auditory evoked-response to unpredictable changes in auditory stimuli in the absence of task demands (Joos et al., 2014). OR occurs when an expected stimulus is unexpectedly omitted, leaving an imprint of the anticipated sensory response (Kok et al., 2014, 2017).

The role of expectation becomes even more apparent when examining MMN, which emerges as a consequence of expectation violations. In particular, MMN is automatically elicited by deviant stimuli introduced within a sequence of standards. Here, MMN reflects an automatic prediction error, providing a neurophysiological marker for the conflict between incoming sensory input and prior expectations (Baldeweg, 2006; Friston, 2005). MMN studies in both auditory and musical

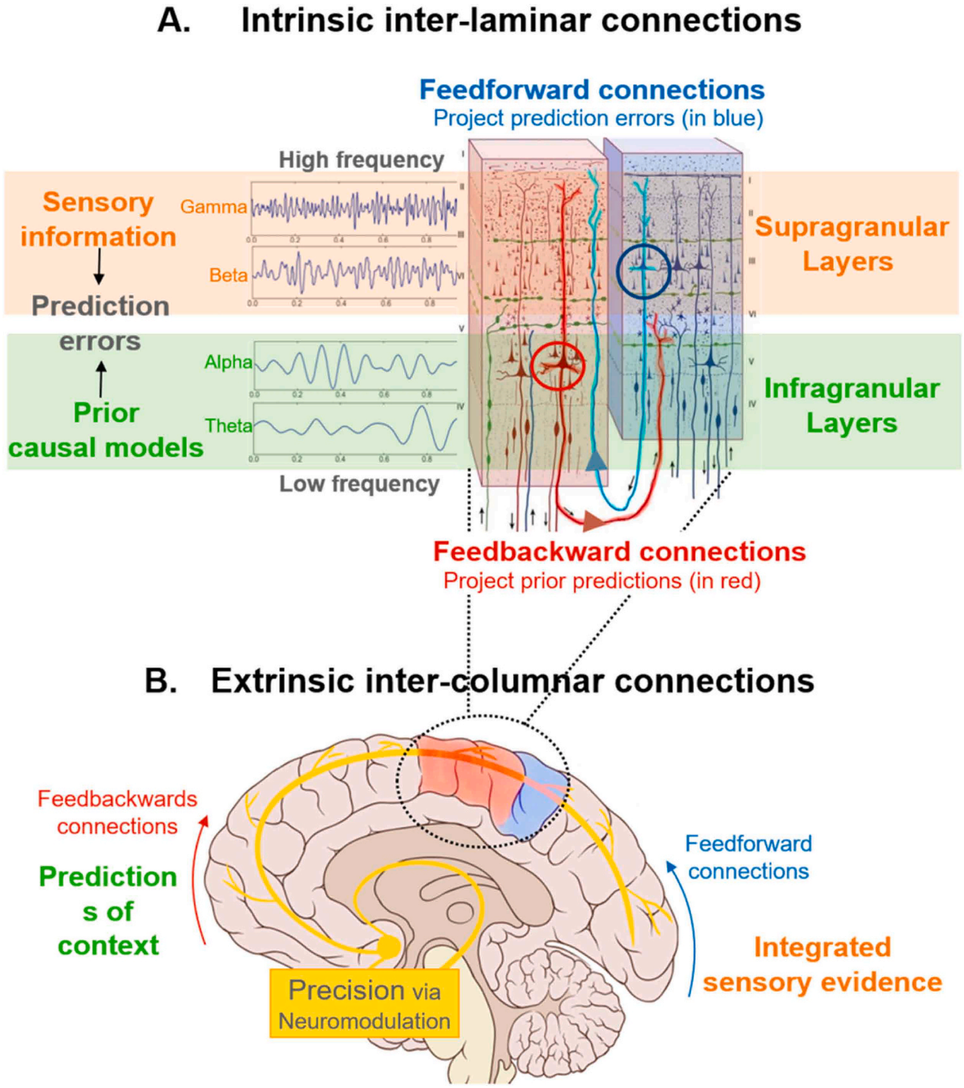

Fig. 3. *Schematic illustration of the hierarchical organization of the brainNote:* A. graded potential across the cortical layers in one single cortical column. High-frequency oscillations originate from the superficial layers that represent prediction errors, while low-frequency oscillations originate from the deep layers that represent predictions. Differences between sensory information and predictions are propagated forward to the neighboring column as information across these columns is gradually integrated at the prefrontal regions. B. A simplified representation of sensory information integration across the anterior-posterior axis. Long-range neuromodulation (yellow, in this example, the acetylcholine pathway from the basal forebrain constellation, illustrated roughly) helps to integrate incoming sensory information into the predicted context by modulating the gains of the synaptic connections based on the precision of this information. This causes a distributed pattern of response across the brain that forms the functional correlates of hierarchical Bayesian inference.

contexts highlight its sensitivity to predictability: smaller MMN have consistently been observed in less predictable contexts, such as sequences of high-entropy stimuli characterized by either non-repetitive melodies (Quiroga-Martinez et al., 2019) or increased temporal complexity (Lumaca et al., 2019). Collectively, these studies show that more complex auditory contexts pose greater challenges for the brain in terms of predictive coding, and may lead to less confident predictions and smaller prediction errors for deviant sounds.

Environmental factors exemplified by the impact of musical training (Bonetti et al., 2022; Vuust et al., 2012), and psychological variables including depression (Bonetti et al., 2017) and working memory capacity (Bonetti et al., 2018) affect MMN responses. In addition, quantitative evidence of hierarchical brain processing in the context of MMN has been provided by Garrido et al. (2009). The authors used dynamic causal modeling (DCM) to test the information flow in the brain during a passive oddball task which elicited MMNs, and revealed effective connectivity in the brain from the primary auditory cortex to the superior temporal gyrus and inferior frontal gyrus, suggesting that MMN might be an error signal which assists the brain in fine-tuning its internal predictive model.

Beyond MMN, ERAN is a brain response which plays a pivotal role in the context of predictions for auditory and musical stimuli (Arnal et al., 2011; Koelsch et al., 2002; Koelsch, et al., 2002). ERAN, a distinct electrophysiological marker associated with selective attention, signifies the entrainment of sensory evidence (represented by high-frequency cortical oscillations) with prior expectations (represented by low-frequency cortical oscillations). In other words, the ERAN attests to the brain's ability to selectively attend to auditory features based on knowledge about impending irregularity, which will resolve uncertainty about the upcoming sensory sequence (Rohrmeier and Koelsch, 2012). The ERAN is most apparent in response to irregularities during syntactic processing in music, particularly in detecting irregularities and violations within musical syntax (Koelsch et al., 2019; Lindsen, 2012).

The persistence of ERAN over repeated exposure to syntactical irregularities contrasts with MMN, which typically attenuates with continued exposure to acoustical irregularities (Koelsch et al., 2001).

This temporal distinction suggests that ERAN is not merely reactive but is actively engaged in ongoing predictive processes associated with musical syntax. Moreover, while the MMN is mainly source-localized in the primary and secondary auditory cortex (with contribution from hippocampus and medial cingulate) (Alho, 1995; Bonetti et al., 2022; Naatanen et al., 2005), ERAN mainly originates in the right inferior frontal gyrus (Koelsch, 2011; Maess et al., 2001), highlighting the specific neural circuitry involved in processing musical syntax and actively detecting syntactic errors. This fits with the nature of the anterior- and posterior-axis of predictive coding, where MMN as a sensory error signal is found posterior to ERAN, which signals context and predictions in the prefrontal region.

Furthermore, the magnitude of ERAN has been observed to vary based on the level of attention directed toward the musical stimulus, with reduced ERAN amplitudes noted in individuals not primarily attending to the music (Loui, 2005). This implies that focused attention plays a crucial role in modulating ERAN responses, underscoring the interactive nature of attention and expectation in shaping neural responses to complex auditory stimuli (Maidhof and Koelsch, 2011; Vuust et al., 2022). Attention increases neuronal activity associated with the attended stimulus, while expectation, grounded in previously learned probabilities, reduces neuronal activity linked to the expected stimulus (Arnal and Giraud, 2012). Thus, attention is a function of the precision of sensory information, while expectation is the prior model in predictive coding. This interplay also extends across different hierarchical levels of auditory prediction and involves some of the ERP/Fs discussed above. For instance, MMN is enhanced by attentional precision but attenuated by explicit top-down expectations (Chennu et al., 2013; Paquette et al., 2013). As further evidenced by the P300 responses subsequent to MMN, automatic prediction error is highly dependent on attentional engagement, with explicit top-down expectations sharpening neural responses (Schwartze et al., 2011). Notably, attention not only supports goal-directed behavior but also minimizes internal noise by sharpening the amplitude of neuronal activity.

While temporal fluctuations of attention influence predictive processes, a detailed exploration of temporal attending theories (see Palmer and Demos, 2022) goes beyond the current scope. In conclusion, it is essential to recognize the dynamic interplay between expectation and attention, shaping neural responses across different hierarchical levels of auditory processing and providing a nuanced understanding of the Bayesian predictive coding framework in auditory perception.

3.2.2. Optimal levels of complexity in sensory information: musical reward & Groove

When a specific musical feature violates, delays, or confirms the listeners' expectations about the continuation of the music, emotions may be elicited (Meyer, 1956). These expectations are based on the listeners' prior exposure and experience of the same musical style (Krumhansl et al., 1999). In general, musical emotions related to violation of expectancies include awe, surprise (Huron, 2006) and anxiety (Meyer, 1956). Violation of musical expectancies can also bring about psychogenic responses (e.g., chills) and increased physiological responses (e.g., increased heart rate and perspiration) (Rickard, 2004).

Higher levels of the cortical hierarchy encode expectations in the form of prior models through repeated sensory stimulation. The complexity of these models varies with the statistical structure of the sensory stimulus. Intermediate levels of complexity have been reported to optimize reward-related responses in music (Agres et al., 2017; Witek et al., 2014), as they maximize both reducible uncertainty and learnable information (Gold et al., 2019). Reducing uncertainty and seeking information are critical components of learning, which have been reported to elicit dopamine transmission and involve activation of the nucleus accumbens (NAcc; a reward-related brain area) (Gold et al., 2019). In a similar vein, Cheung and colleagues (2019) showed that chords with low uncertainty and high surprise (and vice versa), evoked high musical pleasure. In sum, these studies are reminiscent of the inverted U-shaped "Wundt" effect (Berlyne, 1974; Wundt, 1874), which suggests that intermediate levels of complexity are the most optimal for learning and liking.

Relatedly, pleasure can also be derived from musical groove - known as the pleasurable urge to move (Stupacher et al., 2016; Vander Elst et al., 2021). Music that elicits the strongest sensations of groove often has a repetitive rhythmic pattern (Butler, 2006; Madison et al., 2011; Pressing, 2002) which is characterized by syncopated notes with short durations (Madison and Sioros, 2014). Here, syncopation refers to the phenomenon whereby notes occur on weak metrical positions (as opposed to strong metrical positions), and are followed by silences on stronger metrical positions (Longuet-Higgins and Lee, 1984). Moderate amounts of syncopation are especially effective in eliciting musical groove, forming an inverted U-shaped function between syncopation and groove (Sioros et al., 2014; Witek et al., 2014). Moderately syncopated rhythms may engender the highest number of strongly weighted prediction errors, and thus provide the most optimal opportunity for active resolution of uncertainty via movement, resulting in the experience of pleasure associated with groove (Vuust et al., 2022). Besides musical features that elicit the sensations of groove, entrainment is also an important mechanism that subserves musical groove, and more broadly the phenomena that associates auditory-motor movements.

3.3. Oscillatory and rhythmic entrainment

In Bayesian inference, prediction errors reflect the extent to which a stimulus differs from the prediction (Vuust and Frith, 2008). Thus, when prediction errors are low, the deviation between sensory evidence (as encoded by high-frequency neural activity) and predictions as propagated by low-frequency activity is minimized. Consequently, neural entrainment across frequency bands occurs. In this regard, **neural entrainmentˆ** (see Glossary) refers to the synchrony between the periodicity of an external stimulus, such as rhythmic sensory input, and the timing of neural oscillations. This coherence allows the brain to encode the temporal signature of sensory stimulus and improve processing efficiency.

In the musical context, when the neural activity of the brain is entrained to the rhythm of the beat, it often further acts in accordance to the updated internal model by interacting with the external environment according to the rhythm, and thereby engaging in active inference. The moving of the body to the pace of regular auditory cues (e.g., metronome or music) without specifically synchronizing each motor element to a discrete beat, thus reflecting the process of rhythmic entrainment (Merker et al., 2009; Thaut et al., 2015). Rhythmic entrainment plays a key role in music's ability to create movement and groove (Vander Elst et al., 2021). Inherent in music is the rhythmic structure, which creates stable anticipatory time scales or templates. Given that anticipation is a critical element in improving movement quality, the rhythmic structure in music provides precise anticipatory time cues to prime the brain to plan ahead and be ready.

Musical rhythms thus act as a sensory feedback to the brain's internal timekeeper, providing it with additional supporting evidences about how much time has elapsed and how much time is left in a movement. As the brain accumulates sensory priors of the time duration of the cue period, it is able to update its internal predictive model, reduce prediction errors, and make accurate active inferences of forthcoming movements. Rhythmic cues thus provide rich and comprehensive temporal information for the brain to optimize movement with respect to the auditory input. Over time, synchronization occurs between neural oscillations in the brain and music. This leads to further synchrony between the body's physiological processes and environments external to the body, such as dance and even social interactions, thus enhancing both intra- and inter-brain synchrony (Basso et al., 2021; Ross and Balasubramaniam, 2014).

Indeed, recent studies have reported inter-brain neural synchronization while people listened to music as a group (Chabin et al., 2022;

Khalil et al., 2022; Müller and Lindenberger, 2023; Samadani et al., 2021), and this synchrony can be maintained beyond the period of interaction. Likewise, brain coupling has also been observed for individuals improvising music during a music therapy session (Maidhof et al., 2023). These findings provide some evidence for the neuroplastic effects of music, and the long-term benefits of listening to or playing music, for building and maintaining social relationships, emotionality, and supporting brain health in general. In sum, music not only elicits synchronized activity in the brain, but also triggers a cascade of neurological, physical, and social phenomena that promote the active exploration of one's environment according to these musical inferences. These phenomena might provide an ideal chemical milieu in the brain that potentially facilitates structural and functional changes in the brain (Reybrouck et al., 2018).

3.4. Neural substrates of music in the Bayesian brain

Musical processes, including music perception and music making, activate a widely-distributed network of brain regions and involve multiple neurochemical processes (Bonetti et al., 2021a,b; 2023a,b; Chan and Han, 2022; Fernandez-Rubio et al., 2022; Fernandez-Rubio et al., 2022; Koelsch, 2014; Gordon et al., 2018; Platel et al., 1997). Some of these neural mechanisms activated also intersect with Bayesian inference processes: for instance, the cerebellum, auditory-motor network, and dopaminergic system.

3.4.1. The cerebellum: role in rhythmic entrainment, synaptic plasticity, and an encoder of event-likelihood

The cerebellum is implicated in rhythmic entrainment and synaptic plasticity. It is postulated to be the foundation of instantaneous entrainment between the period of a rhythmic stimulus and the body (Thaut et al., 1998), of which rhythmic entrainment is mediated through the auditory-motor networks (i.e., auditory cortex, sensorimotor cortex, supplementary motor area; Fujioka et al., 2012). Controlling the motor neurons in the body, the cerebellum is the gateway for active inference. It serves as the bridge between inference and intentions in the brain, and actions via the body. The complex activation pattern of the Purkinje cells in the cerebellum may directly encode likelihood of probabilistic distributions of temporal events through synaptic plasticity by changing the variability of postsynaptic potentials (Aitchison et al., 2021; Blackwood et al., 2004; Popa and Ebner, 2019).

Synaptic plasticity in the cerebellum, particularly at the Purkinje cells, can encode prior knowledge for Bayesian inference through mechanisms like long-term depression (LTD) and long-term potentiation (LTP) occurring at the confluence of parallel or climbing fiber inputs. These synaptic changes influence the synaptic weights, which embody the prior knowledge and likelihood estimates that are used to transform incoming measurements through parallel fibers into Bayesian estimates (Friston and Herreros, 2016). Similarly, in music, besides rhythmic entrainment, the cerebellum may also be an important locus of context and likelihood estimator. This may explain why cerebellar disorders could affect musical perception, particularly in metrical tasks (Evers and Tölgyesi, 2022).

3.4.2. Coupling between auditory and motor cortices

Besides the cerebellum, the ability of the motor system to couple with the auditory system (also referred to as auditory-motor coupling) and engage in error-prediction correction, has also been proposed to be essential in driving active inference through music exposure (Thaut and Hoemberg, 2014). In this perspective, the sensory input provided by auditory rhythm functions as a bottom-up driving force in optimizing all aspects of motor control via physiological rhythmic entrainment of the motor system. The involvement of the motor system necessitates higher precision of auditory predictions as hypothesized by internal predictive models (i.e., top-down processes) (Morillon and Baillet, 2017; Vuust et al., 2022).

The ability of the auditory system to rapidly construct stable temporal models has been well-established (for a review, see Thaut and Kenyon, 2003). The auditory system is able to detect temporal patterns in auditory stimuli with extreme precision and speed, as required by the nature of sound, which exists only in temporal vibration patterns (Moore, 2003). In addition, the auditory system has richly distributed fiber connections to motor centers from the spinal cord upward to the brain stem, subcortical and cortical levels (Felix et al., 2011; Schmahmann and Pandya, 2009), thus allowing efficient neuronal processing between auditory sensory input and motor control. Besides, the ability of sound signals and rhythmic music to prime and time muscle activation was thought to be modulated via reticulospinal pathways (Takakusaki, 2017) - with supporting evidence reported as early as 1967 by Paltsev and Elner. In sum, movements can instantaneously entrain to the period of a rhythmic stimulus (e.g., metronome beat), and stay locked to the metronome frequency even when subtle tempo changes (that are not consciously perceived) are induced (Thaut et al., 1998). This suggests that auditory stimulation could induce short-term plastic changes in the firing of the motor neurons.

3.4.3. Neuro-endocrine effects of music

In music, dopamine is imperative in the experience of reward, pleasure and movement, is dopamine. A plethora of studies have reported that the experience of musical chills is correlated with release of dopamine in the striatal system and musical reward (Blood and Zatorre, 2001, Salimpoor et al., 2009, 2011, 2013). More specifically, the anticipation phase is reflected in neural activity in the caudate, and the experience of reward and emotional arousal is reflected in neural activity in the nucleus accumbens (NAcc).

Furthermore, dopamine is crucial in maintaining brain plasticity through its effects on long-term potentiation and depression across cortical and subcortical regions. It has been well-established that dopaminergic striatum modulates prediction errors (Chowdhury et al., 2013; Friston et al., 2012; Schwartenbeck et al., 2015; Stalnaker et al., 2019). Depending on the level of prediction error, dopamine can either favor the stabilization of prior predictive models, or create lower inhibitions to favor fast flexible switching between different models (i.e., belief updating) (Durstewitz and Seamans, 2008). The precision of prediction errors, as signaled by dopamine, engender actions to optimize inferences about our environment (Friston et al., 2012; Marshall et al., 2016). Thus, it is no surprise that dopamine is central to movement. The dorsal striatum, wherein dopamine is released, is also suggested to support hierarchical metrical structure (Cannon and Patel, 2021; Palmer and Krumhansl, 1990). The dorsal striatum works in conjunction with the supplementary motor area (SMA) to facilitate beat perception whereby activity in both of these regions repeats with the metrical cycle as well as with the musical beat (Cannon and Patel, 2021; Li et al., 2019). Integrating existing evidence of dopamine on both musical reward and movement, Pando-Naude and colleagues (2023) recently showed that dopamine is indeed a crucial factor related to the rewarding experience during musical movements, also referred to as the pleasurable urge to move.

Besides dopamine, studies have also investigated the role of norepinephrine in music perception, albeit to a lesser extent. These studies showed that listening to fast-paced music increases serum levels of norepinephrine as compared to slow-paced music (Gerra et al., 1998; Hirokawa and Ohira, 2003; Yamamoto et al., 2003). This is coherent with the suggested function of norepinephrine as a modulator of attention and salience in Bayesian Inference (Yu and Dayan, 2005). Norepinephrine has been hypothesized to enhance detection of salient stimulus during situations where the changes of probabilistic context is very frequent (i.e., high unexpected uncertainty). As such, music with faster pace might have a stimulating effect on its production in the body. Indeed, in animal studies, norepinephrine has been found to modulate the coding of complex vocalizations in the songbird auditory cortex, enhancing signal detection and information encoding (Ikeda et al., 2015). However, this effect has yet to be repeated in human studies.

In sum, neuromodulators such as dopamine, and norepinephrine modulate the synaptic gains of forward and backward connections under the context of uncertainty (Bauer et al., 2012; Thiele and Bellgrove, 2018; Yu and Dayan, 2005; Fig. 3B). It also allows the selective activation of different neuronal populations to produce specific temporal and spatial patterns of cortical oscillations that facilitates Bayesian inference by sharpening the sensory contour and redirecting attention to information with higher precisions. Overall, different brain networks and neurotransmitters work synergistically to compute Bayesian inference processes (such as signaling expectations, precision of prediction and prediction errors) in music processing, which gives rise to rewarding experience and movement while engaging with music.

These processes change as we mature into the golden years. As we age, our experience with music increases and crystallizes into a robust internal model of musical perception. Yet, at the same time, many of these neuroarchitectures subserving Bayesian Inference deteriorate. In the next section, literature on music in the aging Bayesian brain will be outlined and discussed.

4. The aging bayesian brain

Aging stands as a profound biological and societal phenomenon, presenting substantial challenges and economic implications (Lenox-Smith et al., 2018). For these reasons, a wealth of research has investigated aging, focusing both on healthy aging and pathological conditions such as dementia. This multidisciplinary exploration, spanning from psychology (Bartrés-Faz et al., 2023; Pione et al., 2021), biology (Cipolla and Alkayed, 2023), to pharmacology (Watts et al., 2023), consistently revealing a primary concern - the decline in cognitive functions, especially affecting processing speed, memory and predictive processes (Darby and Dickerson, 2017; El Haj et al., 2015; Fabiani, 2012; Grady, 2012). Predictive processes, as discussed earlier, are essential to music perception and experience. In this regard, music thus offers a unique opportunity to elucidate the relationship between aging and aforementioned cognitive processes, including prediction.

4.1. The paradox of Bayesian aging: cognitive decline despite optimization of Bayesian Inference processes with age

Consolidated priors, which get refined over the course of our lives and determine our understanding and interaction with the world, is fundamental to Bayesian Inference. As we keep testing our beliefs about the environment, we use prediction errors to update our model about the world and consolidate it into precise and adaptive understanding of our ecological niche. Therefore, aging can be seen as an optimization process of Bayesian inference; as we age, we get better at predicting environmental outcomes. However, this raises an obvious question: why do our cognitive faculties start to decline as we step into our golden years?

The information processing speed theory of aging (Salthouse, 1996) proposed that one of the main factors of aging is the global decline of cognitive functions due to reduction in processing speed (Charlton et al., 2008; Park et al., 2002). The decrease in processing speed is correlated with the ability to inhibit irrelevant information and afford attention to processes that are relevant to the task at hand. From the Bayesian perspective, this can be seen as the inability to determine the precisions of different information during task performances. This may seem contradictory to the Bayesian hypothesis that precision of prior models and sensory evidence are continuously refined through life experiences.

One important consideration that might disentangle this contradiction, is that an individual's priors are consolidated based on biased sensory experiences over the course of life that is unique to him/her (Friston, 2010). As we learn more about the beneficial states of the environment, we afford actions that we perceive to allow us to experience more of these adaptive environments. Thus, while the internal model is continuously optimized over the course of a lifetime, it gets better at encapsulating a small set of frequented variables in its ecological niche as compared to less-frequented variables in the larger environment (Moran et al., 2014). This explains the observation that older adults retain a significant amount of crystalized intelligence (Park and Reuter-Lorenz, 2009; Zec, 1995), such as verbal skills, despite decline in fluid intelligence (including information processing speed, working memory, executive control; Grady, 2012), which are commonly tested in experimental scenarios (Li et al., 2001). This also explains why older adults seem to update their predictions (after an incorrect prediction) of the forthcoming auditory information more slowly and cautiously than younger adults (Herff et al., 2020).

Moreover, the increased reliance of consolidated models is accompanied by a relative decrease in precision of sensory prediction errors. Older adults might have difficulty learning the nuances in the environment through sensory evidence (Moran et al., 2014), although some research suggests that over time, they eventually arrive at an accurate and stable model (Herff et al., 2020). Generally, reliance on consolidated priors mediated by top-down control increases, and Bayesian model updating through bottom-up sensory learning attenuates (Bruckner et al., 2022; DeDe, 2014; Nassar et al., 2016). This shift in balance helps to prioritize limited functional resources in the aging brain and is also collaray to the natural decline of functional specialization, particularly in the sensory regions (see neural dedifferentiation; Li and Lindenberger, 1999). Computationally, it can be seen as a trade-off between model accuracy and complexity under the context of limited brain resources.

Neural complexity can be indexed by brain entropy, which sees marked decline in older adults (Cieri et al., 2021). This decline reflects the decrease in the dynamic balance between order and chaos in the older brain. The decline in sensory ability to receive stimuli in a bottom-up fashion also affects the cognitive capability to process, interpret, and integrate these stimuli in a top-down manner. Indeed, early large cross-sectional studies (Baltes and Lindenberger, 1997; Lindenberger and Baltes, 1994; Valentijn et al., 2005) have found strong correlation between sensory and cognitive decline in older adults. Specifically, decreased acuity of sensory faculties is likely to result in poor recognition of task stimulus, which leads to slower processing speed, reduced working memory and episodic memory encoding, and poorer task performance (Park et al., 2004). In the auditory domain, decline in auditory perception has been proposed to be related to the observation of reduced musical perceptual abilities in older adults (Bones and Plack, 2015; Halpern et al., 1995; Peelle, 2019).

4.1.1. Increased reliance on consolidated priors with age: Evidence from functional and structural studies

The notion of an increased age-related bias towards consolidated internal models is further supported by neuroimaging literature (e.g., Chan et al., 2021). Functional imaging literature shows that older adults display a stronger preference for frontal activation during cognitive task performances as compared to younger adults (Cabeza, 2002; Heng et al., 2018; Park and Reuter-Lorenz, 2009; Reuter-Lorenz et al., 2000). Relatedly, Sikka and colleagues (2015) showed that age-related effects on musical semantic memory follows a similar pattern: greater frontal activation (specifically the left superior frontal region) was observed only in older adults while young adults showed greater activation in the left superior temporal gyrus. According to hierarchical Bayesian inference, consolidated priors are mediated by prefrontal activity, and therefore an increase in the reliance on prior beliefs would be reflected as a preference for frontal activation. This has been observed alongside a general shift of posterior to anterior activation during task, also known as the Posterior to Anterior Shift in Aging (PASA, Davis et al., 2008; first observed by Grady and colleagues (1994) with Positron Emission Tomography (PET)). Aging was also associated with a diminished occurrence of lower-order and an augmented occurrence of higher-order brain networks (Tibon et al., 2021).

Furthermore, as prior models solidify, connections servicing unused models in the prefrontal regions might also be consolidated into those that subserve the crystalized cognitive models. This is reminiscent of the common observation of structural frontal atrophy in older adults, despite high activation of these areas during task performances (Kennedy and Raz, 2009). While this process enables the aging brain to solve simpler and common problems with higher accuracy, it also limits the brain's ability to tackle novel and uncommon problems due to its reduced complexity and flexibility. In support of this view, existing studies have reported correlations between prefrontal atrophy and reduced working memory capacity and processing speed (Head et al., 2004). Structural atrophy is commonly a result of neuronal loss in dendritic spines and synapses, which also affects the neurochemical balance of the aging brain (Webb et al., 2019). Neurochemicals, including but not limited to dopamine and norepinephrine, are crucial encoders of precision and uncertainty in the brain, which also see marked decline with age.

4.1.2. Shift in precision of sensory learning with age: Evidence from studies on neuromodulation

Multiple neurotransmitter systems work synergistically to encode the precision of the dynamic sensory environment, thereby enabling the individual to selectively allocate precious attentional resources to relevant and salient stimuli. Dopamine, which is thought to encode the precision of certain prediction errors pertaining to action, is a crucial neurotransmitter in this process (Friston et al., 2012; Marshall et al., 2016; Schultz, 2016) that is vulnerable to aging (Bäckman et al., 2006; Li et al., 2010; Tomasi and Volkow, 2012). Age-related reduction in dopamine receptors and transporters (Bäckman et al., 2011) is correlated with deficits in working memory (Abdulrahman et al., 2017; Bäckman et al., 2011) and predictive processes in older adults (de Boer et al., 2017). Specifically, dopamine precursor levodopa (L-DOPA) has been shown to restore prediction error during task performances and improve task learning in older adults (Chowdhury et al., 2013).

Sensory prediction errors, which are modulated by dopamine, provide the bottom-up representations of external stimuli during Bayesian inference. These representations guide the choice of prior predictive models and sharpen top-down executive control over posterior areas (Li et al., 2001; Noudoost and Moore, 2011). The modulation of dopamine on frontal brain regions contributes to the complexity, sensitivity and variability in signals that is important for cognitive flexibility and precise representation of sensory prediction errors (Klanker et al., 2013). Consequently, as older adults prioritize prior beliefs (also observed in the auditory domain - see Herff et al., 2020), representation of sensory prediction errors in the brain declines. Studies have reported attenuated prediction error responses (as indexed by MMN and subsequent P300 during auditory oddball tasks) in older adults as compared to their younger counterparts (Cheng et al., 2013; Pekkonen, 2000). This decline in prediction error signaling corresponds to a metabolic decline of dopamine in the prefrontal regions and may explain older adults' difficulty in affording selective attention and encoding the precision of sensory prediction errors during task.

Beyond the involvement in cognitive flexibility, dopamine also has a crucial role in affect regulation and networks subserving motoric movements, particularly the basal ganglia. In this regard, dopamine dysregulation in patients with Parkinson's Disease (PD) was found to be associated with flatten responses to musical groove (i.e., the pleasurable urge to move to musical rhythms) (Pando-Naude et al., 2023). Specifically, older adults in this study showed less preference and sensitivity to the complexity of musical rhythms, suggesting a reduced ability to register and process the precision of sensory evidence, amidst biases for top-down consolidated prior models and preferences acquired through lifelong musical experiences.

4.1.3. Age-related changes in hierarchy and uncertainty estimate

Flexible response to a stochastic environment is crucial to survival (Friston, 2010). This adaptive behavior requires the internalization of the uncertainties and inherent statistical structures present in the environment (Bach et al., 2011; Bach and Dolan, 2012; Pearce, 2005; Pearce and Wiggins, 2006). However, aging is associated with poorer performance under uncertainty (Herff et al., 2020; Nassar et al., 2016; Palmer and Mattys, 2016). Specifically, older adults utilize uncertainty of information to a lesser extent than younger adults, and also show smaller behavioral adjustments to prediction errors (Herff et al., 2020). This suggests that older adults may employ different strategies for learning and decision-making, potentially favoring more stable, and less flexible information integration compared to younger adults. In contrast, younger adults adjust their behavior significantly in response to minor prediction errors, indicating a strategy that allows for rapid adaptation.

Other explanations to account for age-related decline in efficacy of hierarchical uncertainty estimation include: (1) poorer estimate of probabilistic context due to insensitivity to prediction errors (Nassar et al., 2016), (2) higher variance in the estimate of probabilistic context (Mata et al., 2010), and a slower rate in updating information weights (Herff et al., 2020). For instance, in studies that utilized probabilistic tasks to probe age-related differences in ability to estimate probabilistic contexts, it was found that older adults tend to favor a Win-stay, Lose-shift mentality (Mata et al., 2010). In this strategy, the current decision is inherited from the outcome of the last response. This may reflect an incomplete understanding of the hierarchical structure of hidden statistical regularities that is necessary to deduce the state-to-state transitions of sensory stimulus, which result in an unstable understanding of the statistical context with large variances. Furthermore, Herff and colleagues (2020) applied Bayesian modeling to auditory tone sequence learning, and found that older adults update their information weights more slowly than younger adults (who are biased to react more strongly to negative information).

In essence, the aging brain is optimized to explain common sensory phenomena that are necessary for survival (Friston, 2010; Bonetti et al., 2024), but may not perform as well in less common and cognitively-challenging tasks. This presents a paradox as Bayesian inference is optimized through aging. To maintain efficient neural resource allocation, the aging brain increases reliance on consolidated inferences while decreasing reliance on computational resources of sensory learning. This shift in the brain's neural milieu allows older adults to encode simpler yet accurate explanations for common sensory events, but it also limits cognitive flexibility and affects fluid intelligence.

Despite these neural challenges, some older adults appear to maintain cognitive abilities as they age, showing relatively lesser decline as compared to others in their age cohort. These individuals, or 'super-agers', who can achieve successful cognitive aging trajectories through the maintenance of one's cognition and flexibility (i.e., 'optimal aging'), experience less pathological atrophy in their brains (Borelli et al., 2018; Zhou et al., 2023) and show maintenance of neurotransmitter systems (e.g., dopamine) (Ciampa et al., 2022; Nordin et al., 2022; Rieckmann et al., 2011). This attests to the efficacy of neuroplasticity, even in old age, where the organization of the brain can still change substantially as a result of continuous practice and experience in enriched sensory environments, such as active engagement with music (Shaffer, 2016).

4.2. Not all is lost: drawing insight from the musician's brain

Indeed, Bayesian inference is a process that can be fine-tuned through practice. A plethora of studies have examined the effects of musical training on non-musical cognitive domains, and mostly reported differential transfer effects of musical learning on cognition, behavior and the brain (e.g., Chaddock-Heyman et al., 2021; Hansen et al., 2013; Neves et al., 2022; Talamini et al., 2017, see Sala and Gobet, 2017, 2020 for null effects). This parallels the notion of neuroplasticity, wherein the brain reorganizes into more efficient neural networks as a result of continuous practice in a particular domain (Pascual-Leone, 2001).

4.2.1. *Structural differences in musicians*

At the neural level, learning to play music has been shown to have significant structural and functional effects on the brain (Criscuolo et al., 2022; Münte et al., 2002; Pascual-Leone, 2001; Schlaug, 2001). Several brain regions that show structural differences in musicians are also implicated in processes related to Bayesian inference, particularly the cerebellum and corpus callosum. Studies have reported that the cerebellar volume is about five percent larger in musicians than in non-musicians (Hutchinson et al., 2003; Wieser, 2003). Increased cerebellar volume was posited to be a result of extensive musical training - which involves movement coordination, timing of sequential movements and prediction error driven motor updating, i.e., active inference and cognitive skill learning (Hutchinson et al., 2003). This observation parallels studies that showed microstructural changes after intense and prolonged motoric activity, which creates an ideal neurochemical milieu for microstructural plasticity (e.g., Schlaug, 2001; Wieser, 2003).

Movement provides the brain the agency to evince its predictions through data collection. Complex synaptic mechanisms within the cerebellum allows the brain to encode the likelihood of such data collected through neuroplasticity. As such, cerebellar changes associated with musical expertise may provide musicians with more robust likelihood estimators that allow rapid adaptations of motor movements in order to minimize prediction errors. This results in a more effective foundation for predictive processes and statistical learning. (Daikoku and Yumoto, 2020; Pesnot Lerousseau and Schön, 2021).

The ability of the cerebellum to make successful active inference is facilitated by the corpus callosum. The corpus callosum plays a crucial role in the transfer of motor, sensory and cognitive information between the two hemispheres, leading to integration of functions and coordinated inferences and actions across the brain and body respectively (Shillcock et al., 2019; although note that Bayesian inference is not limited to interactions across the hemispheres). This integral member of the predictive processing network was found to be significantly larger in musicians who commenced musical training before the age of seven as compared to non-musicians. The structural difference in callosal anatomy between musicians and non-musicians was argued to be a result of intensive musical training, of which increased efficiency in interhemispheric exchange is necessary to perform bimanual complex motor sequences (Schlaug, 2001).

Furthermore, the functional importance of the corpus callosum as a neural hub for long-distance neuromodulators may facilitate the transfer of motor skills to other sensory domains and scenarios (e.g., interlimb transfer; Gooijers and Swinnen, 2014). Long-distance neuromodulators, such as acetylcholine, are crucially involved in neuroplasticity and computing precision of prediction errors in Bayesian inference (Chandler, 2016; Khasawneh et al., 2022). The concentration of acetylcholine affects the integrity and anatomy of the corpus callosum in aging. Therefore, evidence of larger corpus callosum as a result of musical training provides motivation for the use of music in preventive or rehabilitative measures in aging.

4.2.2. *Electrophysiological differences in musicians*

Besides structural changes, differences in electrophysiological markers that encode predictive inferences in auditory information (e.g., ERAN, MMN and P3a components) have also been consistently reported between musicians and non-musicians (Geiser et al., 2010; Jentschke and Koelsch, 2009; Koelsch et al., 2002; Marie et al., 2012; Tervaniemi et al., 2006; Vuust et al., 2012). Studies have documented enhanced ERAN amplitude at early stages of music processing in musicians, and not non-musicians (Centanni et al., 2020; Jentschke and Koelsch, 2009; Müller et al., 2010; Steinbeis et al., 2006). Two plausible mechanisms from the perspective of Bayesian inference could explain this finding: Firstly, heightened musical expectancies could be a result of reinforced statistical learning in musicians, leading to the development of more specific representations of musical regularities (for instance, chord sequences). Secondly, as ERAN represents neural entrainment between sensory evidence and prior expectations, enhanced ERAN thus suggests increased entrainment between these two bodies of information. This increased neural entrainment could possibly be a result of sharpened selective attention and improved ability in rapidly resolving prediction errors necessitated by the multisensory stimulation over the course of musical training.

Studies that found musicians to show increased P300 amplitudes to the first critical note in minor melodies support a similar idea that the musician's brain appears to assign greater saliency to critical sensory evidence that help to reduce uncertainty within the current musical context, while non-musicians may yet to have developed such specific sensitivity to the musical context (Centanni et al., 2020; Halpern et al., 2008; Steinbeis et al., 2006). In addition, musicians repeatedly show enhanced MMN responses (i.e., better abilities at encoding and discriminating auditory information), in a wide variety of musical tasks such as the detection of melodic (Pantev et al., 2003) and location (Tervaniemi et al., 2006, 2009) changes, and rhythmic tasks that involve detecting anticipated and upcoming beats (Munte et al., 2003; Vuust et al., 2009). From the predictive coding framework, MMN and P300 components correspond to prediction errors subsequent to the evaluation of sensory evidence. In this regard, enhanced MMN and P300 responses observed in musicians could be interpreted as a functional adaptation and/or a genetic predisposition, allowing for higher sensitivity to prediction errors that eventually leads to more sophisticated internal models of music.

In favor of functional adaptation as a result of musical training, enhanced MMN responses were also reported in non-musicians who were trained to play a musical sequence on the piano (Lappe et al., 2008). This enhanced sensory response could be attributed to the involvement of auditory-motor coupling and multisensory integration (e.g. looking at hand and finger positions and reading musical notation) necessitated by learning to play a new musical instrument. Indeed, learning to play a new musical instrument is a multimodal task that requires neural communication between multiple brain regions across both hemispheres (Herholz and Zatorre, 2012; Moreno and Bidelman, 2014). Improvements in sensory integration could thus afford more precise representation of sensory evidence in Bayesian inference, and ultimately lead to more accurate priors and understanding of the context (e.g., task requirements during an experiment).

Collectively, these studies provide support for structural and electrophysiological advantages in Bayesian inferences of auditory information associated with musical training. Musicians show greater sensitivity to the fluctuations and probabilistic distributions within a musical piece, resulting in better encoding abilities of the precision of priors and prediction errors. Larger prediction errors generate more sensory learning so as to reduce the discrepancies between incoming sensory information and the internal predictive model. In addition, musical training also necessitates heightened demands on auditory-motor coupling mechanisms that results in improved sensory learning. The combination of top-down (musical expectancy) and bottom-up (sensory stimulation) processes shapes brain structure and the ability to form music-related predictions with high precision (Tervaniemi et al., 2009; Vuust et al., 2022).

Coupled with the brain's propensity for neuroplasticity even in old age, evidence from enhanced cognitive and neural processes involved in Bayesian inference as a result of musical training provides strong motivation for music to be a prime candidate for cognitive maintenance and interventions to support aging.

4.3. *Mitigating age-related decline in the Bayesian brain: Use of music in interventions for older adults*

Aging is an increasingly important concern around the globe (Bloom et al., 2015; Lenox-Smith et al., 2018), and is accompanied by a combination of cognitive decline (mentioned earlier in this review) and various age-related neurodegenerative disorders and cardiovascular health issues (e.g., Brookmeyer et al., 2007). Therefore, it is critical to invest resources in developing effective non-pharmacological interventions (e.g., Ng et al., 2022) to either help mitigate the rate of cognitive decline or promote cognitive maintenance, so as to reduce economic burdens on society and healthcare institutions. As music is highly accessible and widely available, music-based interventions or music therapy, could be considered as one of the most ideal candidates among current forms of non-pharmacological interventions (Agres et al., 2021). Indeed, existing studies have highlighted the therapeutic effects of music on cognition, mood and emotion in healthy older adults (Marie et al., 2023; Sajnani et al., 2021; Sheppard and Broughton, 2020) as well as in clinical populations such as stroke (Särkämö, 2018, 2014) and Parkinson's disease (PD) (Rose et al., 2019).

In this regard, two common themes in the aging literature have emerged. Firstly, active music engagement, such as short-term musical interventions of piano playing (Bugos, 2019; Bugos and Kochar, 2017), music making (Jäncke, 2013), and singing (for a review, see Clements-Cortés, 2015), have been associated with cognitive improvements or maintenance in older adults (Chaddock-Heyman et al., 2021; Jäncke, 2013). Secondly, studies have commonly highlighted the efficacy of using music as a form of auditory and rhythmic entrainment in improving gait ability (Ghai et al., 2018; Thaut et al., 2015; Thaut and Koshimori, 2020) and aiding preventive measures, such as reducing incidences of falls (Ghai et al., 2018; Rose et al., 2019; Särkämö, 2018).

Moreover, emerging research suggests that music perception may be less impacted by aging as compared to other domains of auditory processing like speech perception (Halpern et al., 2017; Lagrois et al., 2018). Clinical studies showed that musical memory (both implicit and explicit), musical engagement and music-seeking may be relatively preserved in dementia (Cuddy et al., 2015; Hailstone et al., 2009). As such, the ability of music to activate multiple neural networks, and the relatively low impairment of musical memories and experiences due to aging, position music as a promising tool in preventive and rehabilitative interventions for older adults.

4.3.1. *Reward experiences during music listening*

Music listening is a common, everyday leisure activity for older adults that is linked to positive emotions and contributes to psychological well-being (Ferreri et al., 2019; Laukka, 2007). Music has the capacity to dynamically manipulate interweaving melodic, rhythmic and harmonic structures to create an optimal level of uncertainty and predictability required for the experience of musical reward and pleasure (Gold et al., 2019).

Pleasurable experiences during music listening, as discussed earlier in this review, may be fundamentally rooted in Bayesian inference process: particularly the generation and successful minimization of prediction errors. Music listening could therefore potentially re-engage the aging brain in Bayesian inference and uncertainty estimation, which involves the concurrent release of neuromodulators such as dopamine, acetylcholine and norepinephrine. These neuromodulators are essential in signaling prediction errors (dopamine; Fiorillo et al., 2003) and encoding higher-order contextual uncertainty (acetylcholine and norepinephrine; Dayan and Yu, 2003). With the synergistic interactions of these neuromodulators, the rate of learning and neuroplasticity that commonly declines with age could thus be attenuated.

One important observation, as reviewed earlier, is that prediction error responses are attenuated in older adults as compared to young adults (Cheng et al., 2013; Pekkonen, 2000). However, studies have also found that dopamine restores reward prediction errors in old age (Chowdhury et al., 2013). On the basis that music activates the dopaminergic system (Ferreri, Mas-Herrero, et al., 2019), repeated pleasurable experiences during music listening could potentially assist older adults in recovering some of the ability to compute prediction errors by boosting the level of dopamine in their brains. Furthermore, as music has been demonstrated to be able to gain qualities of reward prediction error similar to rewards driven by biological needs such as food and monetary rewards (Gold et al., 2019), it thus has the potential to serve as a reward that could complement cognitive and motor interventions.

Individual differences in music experience and background highly influence the efficacy of music-based interventions. Thus, it is also necessary to take into consideration older adults' musical experiences and cultural background, given that their lifetime of experiences (musical and non-musical) has shaped their internal model and beliefs related to music, which forms the basis of their expectations (Savage and Fujii, 2022). In this regard, Quinci and colleagues (2022) recently found that when cognitively unimpaired older adults listened to self-selected and other-selected (including well-known and novel) music, an increase in activity and connectivity between and within auditory-reward networks was observed only during self-selected music, which are highly familiar and well-liked. From the Bayesian inference perspective, increased activity in the auditory areas indicate that stronger predictions for familiar music may have been previously formed (Freitas et al., 2018). Results from this study thus support the notion that music listening may be able to positively modulate auditory-reward connectivity, despite other studies observing decline in auditory perception and musical reward with age (Belfi et al., 2022).

In sum, music is powerful in its ability to introduce optimally complex environments ideal for sensory learning, and its ability to elicit reward prediction errors and activate the limbic network (particularly the amygdala) creates opportunities for learning and Bayesian model updating. This can potentially promote instances of musical pleasure and reward in older adults.

4.3.2. *Effects of rhythmic entrainment on motor rehabilitation*

Another important form of intervention for older adults is motor rehabilitation, which either aims to restore motor deficits as a result of neurodegenerative diseases, or to combat increasing prevalence of falls in this age group. The underlying mechanisms for attaining benefits in the motor domain are suggested to be multifactorial (Thaut, 2003), including but not limited to the activation of the dopaminergic system as a result of movement and pleasurable feelings elicited by music (Ferreri, Mas-Herrero, et al., 2019, albeit a reduced intensity in PD - see Pando-Naude et al., 2023), and endogenous mechanisms that help maintain the effect of entrainment when external pacing cues cease (Rose et al., 2019), and rhythmic entrainment mediated by auditory-motor coupling.

Rhythmic auditory cueing, a prime example of a motor intervention based on the principles of auditory-motor coupling and rhythmic entrainment (Yoo and Kim, 2016), has been reported to mediate cortical reorganization and neural plasticity (Luft et al., 2004), targets stride-to-stride fluctuations in gait (Rochester et al., 2011), and enhance motion perception (Effenberg et al., 2016) through the engagement of basal ganglia frontocortical network (Schmitz et al., 2013). The basal ganglia is a linchpin in the process of Bayesian inference. Not only does it produce dopamine (which signals sensory prediction errors) (Graybiel, 2000), it is also responsible for action affordance and is therefore a nexus in active inference (Friend and Kravitz, 2014; Grillner et al., 2013; Parr and Friston, 2018). The basal ganglia is proposed to reduce inhibition to the cortical network that instantiates the desired action plan and its associated sensory expectation (Colder, 2015). Beyond initiating actions, the basal ganglia also allows the propagation of the actions' associated sensory expectation down towards the primary sensory cortex, thus playing a role in biasing perception by selecting the expected sensation and initiating the top-down transmission of those expectations in predictive coding. Therefore, the activation of basal ganglia fronto-cortical network through rhythmic auditory cueing promotes the active use of these Bayesian inference processes in the aging brain, which may potentially help to counteract age-related declines.

Moreover, building on research and literature reviewed earlier about the musician's brain, it was found that patients with early-stage PD who were musically trained showed comparable rhythmic motor timing abilities as musically-trained healthy adults (Hsu et al., 2022). From the Bayesian inference perspective, repeated active music making requires the brain to refine motor abilities, and continue engaging sensory learning processes to minimize prediction error via auditory-motor coupling, such that the consolidated internal model becomes more precise. This could possibly explain the preserved rhythmic motor timing abilities found in musically-trained patients with early-stage PD.

Lastly, one of the most critical components in the context of motor rehabilitation is the finding that the injured brain can indeed access rhythmic entrainment mechanisms. Early studies of gait training in Parkinson's disease (PD) (McIntosh et al., 1997; Thaut et al., 1996) and traumatic brain injury (Hurt et al., 1998) confirmed behaviorally the existence of rhythmic entrainment processes in clinical populations, whereby patients are able to coordinate their movements to a common auditory rhythm. This effect was enhanced when the speed of the external pacing cue is of a moderate to fast tempo (Rose et al., 2019), reminiscent of the preference for sensory environments that are moderately challenging, which are optimal for initiating Bayesian inference processes. This positions rhythmic entrainment as a valuable mechanism for effective motor rehabilitation, particularly in the aging population where onset of degenerative diseases and neural injuries (due to undiagnosed stroke), could sometimes be undetected.

In sum, music-based interventions or activities based on the principles of rhythmic entrainment and auditory-motor coupling could provide a solid foundation in explaining the efficacy of these programmes through Bayesian inference processes. Music thus serves as a motivating and engaging stimulus to cause the individual to want to start and continue in these interventions. In the predictive coding perspective, entrainment at the neural level between the auditory and motor cortices as a result of music makes it easier for movement. In addition, the need to focus on these external cues could facilitate attention switching, and attention is an important component in the process of predictive coding.

4.3.3. Multisensory processes involved in music-making and learning music

Neuroimaging literature has documented better frontal lobe functioning as a result of musical training and better cognition in older adults. This has been attributed to the notion that such activities require new learning while placing demands on cognition (Hanna-Pladdy and MacKay, 2011). Indeed, learning a new musical instrument demands continuous Bayesian updating of prior musical understanding through sensory learning. This coupling of neural activity between the posterior brain regions (associated with sensory learning) and the anterior brain regions (associated with consolidated models) can potentially generate more neural resources (e.g., increased synaptic plasticity through increased modulatory effects of neurotransmitters) that further facilitates functional connectivity between the posterior and anterior brain regions. As a result, some of the effects outlined in the PASA model of aging (Davis et al., 2008; Grady et al., 1994) can potentially be mitigated.

Furthermore, studies that investigated effects of choir singing on aging have revealed similar results. As reviewed earlier (see *Section 3*), repeated stimulus generates an expectation for the future recurrence of the stimulus, resulting in the gradual attenuation of the N1 component (where N1 reflects auditory evoked-response to unpredictable changes in auditory stimuli in the absence of task demands; Joos et al., 2014). This effect is thought to be similar to that of repetition suppression (Bendixen et al., 2012; Grill-Spector et al., 2006). ERP studies have consistently reported that musical (Seppänen et al., 2012) or frequency discrimination (Brattico et al., 2003) training, and choir singing (Pentikäinen et al., 2022), are associated with increased N1 attenuation in auditory oddball tasks. For instance, older adults who are choral singers have shown reduced N1 responses to a simple oddball condition where only either the pitch or spatial location of the sounds was varied, as compared to non-singers (Pentikäinen et al., 2022). The finding of reduced N1 amplitude provides support that choral singing could be associated both with more enhanced encoding of complex auditory regularities and more effective adaptation to simple sound features (i.e., effective predictive auditory processing).

Essentially, learning a new musical instrument and singing necessitate effective multisensory integration (Perron et al., 2022; Sutcliffe et al., 2020), which declines in older adults (Koen and Rugg, 2019). The need for multisensory integration places neural demands that help to maintain brain health in older adults. For instance, Perron and colleagues (2022) showed that the number of hours of group singing positively moderated the relationship between age and speech-perception-in-noise capabilities through the thickness of the right dorsal precentral sulcus. This effect was further influenced by the number of singing languages, and is associated with structural changes of bilateral fronto-temporal regions, including the right pars opercularis of the inferior frontal gyrus. Therefore, it appears that the demands of the task may promote neural plasticity, thereby increasing resistance to age-related neurodegeneration. As the aging brain performs these processes repeatedly, brain networks involved in learning from sensory evidence with precision become stronger and thus are less susceptible to cognitive decline. Music-making or singing thus provide an ideal avenue to activate neural pathways that are associated with these predictive processing processes.

In addition, new learning that involves motor-related functions appears to be a crucial factor for inducing robust cognitive changes. This may be attributed to the engagement of the cerebellum, which is pivotal in cognition (Blackwood et al., 2004; Popa and Ebner, 2019; Schmahmann, 2019), but often implicated in age-related neurodegeneration (Bernard and Seidler, 2014). The cerebellum is the gateway of the brain to the body, and thus serves two important functions in Bayesian inference: it (1) actively seeks out evidence in accordance to the current prior models through efferent motor commands from the brain to the body (i.e., active inferences), and (2) updates the likelihood of environmental events through afferent sensations from the body to the brain. As such, engagement in musical activities that directly activates the cerebellum could help in enhancing active inference and the health of Purkinje cells. Purkinje cells are crucial in maintaining synaptic plasticity, which is vital for the encoding of probabilistic distributions of temporal stimulus under uncertainty.

In sum, the above evidence illustrates the ability of music learning to improve Bayesian inference in older adults by (1) improving the recurrent optimization of Bayesian inference through functional coupling between anterior and posterior brain regions, (2) increasing the precision of sensory evidence encoded through activating multisensory integration processes which allows for a more accurate internal predictive model, and (3) enhancing the encoding of probabilistic distributions of temporal stimulus under uncertainty in the cerebellum. These mechanisms of Bayesian inference impacts older adult's general cognitive capabilities. Therefore, it is no surprise that music learning also brings about marked improvements in processing speed, working memory and executive functions.

5. Discussion

In the current review, we demonstrated the potential and feasibility of utilizing Bayesian inference as an overarching framework to explain (1) how emotions, movement and learning are derived from music, and (2) how aging is conceptualized in terms of a breakdown of the brain's ability to optimize new sensory information and prior internal beliefs. With these, we sought to explain how mechanisms related to predictive coding in music, can help to reinstitute age-related cognitive, behavioral or physical declines as a result of less efficient predictive coding processes.

From the Bayesian inference perspective, human action and cognition can be defined by perceptual and active inferences of environmental uncertainties. In perceptual inference, we form hypotheses based on prior sensory experiences about the causes of current information; in active inference, we act to test out these hypotheses and collect new evidence in the process to refine our assumptions. Music, is one example where our appreciation and ability to engage with it is built upon our prior expectations of what is to come in the melody, harmony, or rhythm (Cheung et al., 2019; Gold et al., 2019; Huron, 2006; Meyer, 1956; Stupacher et al., 2022; Tervaniemi et al., 2009; Vuust et al., 2022; Vuust and Frith, 2008). This prior expectation is checked against the incoming multisensory evidence, and is continuously updated to form the basis of our musical experiences.

In addition, we further provided three perspectives on the importance of precision in this framework, namely (1) the encoding of reliability or confidence from point of view of Bayesian inference; (2) the notion of neuromodulators as encoding expected uncertainty; and (3) the role of dopamine in reward and motivated behavior.

Firstly, much of the foregoing account rests upon the precision of prediction errors in predictive coding accounts of Bayesian inference in the brain. In predictive processing generally, one can cast inference as the minimization of precision weighted prediction errors (Clark, 2013; Feldman and Friston, 2010; Hohwy, 2012); reflecting the fact that only precise prediction errors should be afforded the ability to update beliefs about states of affairs (see *Section 2.1.2*).

Secondly, as noted above, physiologically, this is thought to be mediated by increases and decreases in synaptic gain, of the sort associated with neuromodulators such as dopamine, acetylcholine and norepinephrine (see *Section 2.1.2*). Psychologically, precision weighting of this sort has been associated with selective attention (with increases in precision) and sensory attenuation (with decreases during the generation of self-made acts). Phenomenologically, this ability to select or ignore sources information actively, may translate into notions of mental action and the distinction between phenomenally transparent and opaque perception (i.e., experiencing music and knowing that I am listening to music) (Limanowski, 2017, 2022; Sandved-Smith et al., 2021) (see *Section 3.2.1*).

Lastly, we have referred to the role of neuromodulators as encoding expected uncertainty (Yu and Dayan, 2005). This expected uncertainty is the complement of expected precision (Parr and Friston, 2019); namely the confidence ascribed to various representations (e.g., prediction errors). We have also emphasized the role of dopamine in encoding the precision of certain prediction errors. This is usually associated with active inference about decisions, choices or plans. Dopamine may have a special role in encoding the precision or confidence in policies that underwrites the (mental or motor) actions to be selected at any particular time. In more expressive treatments of active inference, this rests upon the intrinsic motivation or epistemic affordance associated with certain policies (e.g., attending to music or rhythmic motor behavior) (Koelsch et al., 2019; Vuust et al., 2018). In short, the rewarding aspect of music perception and production can be cast as a particular aspect of resolving uncertainty about the actively sensed world.

Throughout the course of our life, we continue to refine our internal musical model and improve our abilities to understand and engage with it. As such, aging can be seen as an accumulation of life experiences, such as music, that get consolidated into adaptive models of the environment around us. Consolidated models allow a general and adaptive understanding of the world, and offer efficiency and security when we navigate our surroundings. At the same time, it takes away the cognitive and neural flexibility we have in the younger days. In this manner, Bayesian inference provides a parsimonious way of unifying both music and aging.

5.1. *Age-related improvements in movement and learning: Involvement of multisensory integration and sensory learning afforded by music*

As Bayesian inference is one of the main driving forces behind both music and aging, it stands to say that music may be a promising tool to reduce the effects of cognitive aging. Indeed, existing studies have provided support for the efficacy of music-based interventions (MBIs) in improving cognition in older adults (Coubard et al., 2011; Ferreri et al., 2019; Fu et al., 2018; Ghai et al., 2018; Pentikäinen et al., 2021; Sheppard and Broughton, 2020; Sutcliffe et al., 2020). Musical features such as rhythm, can be manipulated to elicit different degrees of predictability and uncertainty which challenge expectations built upon prior sensory evidence. This enriches the exposure of older adults and introduces new sets of statistical uncertainties that are not part of their prior musical experiences, thus increasing the complexity of their cognitive and behavioral repertoire and encourages them to engage in Bayesian model updating via sensory learning. We posit that the effects of engaging with music are not limited to auditory perceptual brain regions, but could extend to critical domains of cognition as well. Bayesian updating of prior models via sensory learning generates a series of neural and chemical milieu (e.g. increase in neurotransmitters), and increases activation of sensory regions in the brain that facilitates neuroplasticity.

We hypothesized that a particularly effective way to access these benefits of music in aging might be through pairing it with motor components such as learning and practicing musical instruments, or participating in dance programs. Such activities that integrate cognitive and physical components require action selection congruent to the cognitive implementations of a new motor routine that requires updates to previous implementation models via sensory learning. This necessitates the engagement of multisensory coordination and may potentially involve regions of the brain that are important in sensory coordination (e.g., thalamus), action planning and selection (e.g., basal ganglia, cerebellum and striatum), that may not be involved in passive music exposure.

In sum, active music engagement in the form of learning a musical instrument or dance, has been shown to result in positive cognitive and neurological outcomes in older adults. Improvements in these outcomes can be explained by the Bayesian framework of music perception and proficiency in terms of enhancement in Bayesian updating via sensory learning. Thus, the decline of these components of Bayesian inference in aging can be ameliorated through active music engagement, which stimulates multiple brain areas concurrently (Fig. 4).

5.2. *Bridging the gap among research disciplines*

5.2.1. *Relative lack of neurocognitive evidence to support common behavioral outcomes reported in music-based interventions*

The efficacy of MBIs in older adults in improving other aspects of cognition have received considerable support from behavioral studies (e.g., Bugos, 2019; Bugos and Kochar, 2017; Coubard et al., 2011; Feng et al., 2020; Fu et al., 2018; MacAulay et al., 2019). For instance, Coubard and colleagues (2011) reported an improvement in attention switching and cognitive flexibility in older adults. The authors conducted a study comparing the cognitive and physical benefits of older adults (age range: 65- to 83-year-old) in contemporary dance to tai chi and fall prevention classes. Following a 5.7 month period of participation, contemporary dance was the only activity that improved attention switching and cognitive flexibility in older adults. This effect was taken to reflect that contemporary dance improvisation was effective as a form of training for changing and inducing plasticity in flexible attention. In hierarchical Bayesian inference, attention is an important component as it sharpens the amplitude of neuronal activity to reduce internal noise in presenting external stimuli (see *Section 3.2.1* .). Therefore, the finding that dancing to music, can potentially counteract age-related declines in attentional allocation and resource by promoting plasticity in flexible attention, positions it as an effective form of intervention in older adults.

Besides, processing speed is reported to be significantly enhanced after a short-term intense piano training program (Bugos and Kochar, 2017) and only observed in older adults who participated in the instrument-only group as compared to the singing-only group (Mansens et al., 2018). Accordingly, the finding of enhanced processing speed as a result of active music-making could be reflective of better information processing abilities in older adults. Information processing can also be seen as the estimation of context uncertainties in order to engender accurate perception and fast adaptive actions. Thus, an improvement in information processing can also be regarded as an improvement in Bayesian inference (including more precise prediction errors, and more efficient encoding of probabilistic distribution of environmental events and updating of priors.

In addition, Bugos (2019) examined the effects of bimanual coordination in MBIs on cognitive performance in healthy older adults and found that piano training significantly enhanced bimanual motor synchronization skills (including both fine and gross motor control) and working memory abilities as compared to percussion instruction (i.e., control condition that does not require motor control). Improvements in working memory have implications for Bayesian inference processes. To form a probabilistic distribution for a specific sensory event, a large amount of sensory stimulation similar to this event is required (see *Section 3* , Bastos et al., 2012). In this view, working memory is the temporal accumulation of sensory signals that serves as evidence to validate prior prediction. Thus, improvements in the precision of sensory encoding will constitute a clearer working memory.

Studies have also reported significant improvements in executive functions in older adults across differing types of MBIs. These range from recorder group lesson (one hour lessons conducted over 12 weeks; MacAulay et al., 2019), group singing program (also conducted over 12 weeks; Fu et al., 2018) to a randomized-controlled trial (RCT) designed to investigate the effects of a choral singing intervention ($n = 47$) compared to a health education program (n=46) (intervention method: weekly one-hour choral singing/health education for two years) (Feng et al., 2020). Executive function includes inhibition control and set switching on top of working memory (Miyake et al., 2000). Inhibition control and set switching have important functional roles in attentional gain and bias competition. Attention mediates the resource allocation among bottom-up processes that are propagating competitive sensory evidence, and is closely related to the concept of precision in Bayesian inference. Resource allocation mediated by attention should be biased towards the most precise information, i.e., activity of neurons signaling precise information should be turned up, while activity of neurons signaling less precise information should be turned down. Effective executive control relies on the computation of precision and probabilistic distributions within Bayesian inference. As mentioned in *Section 3.4.1* ., the cerebellum in particular has been implicated in executive control, and has the potential to encode precise probabilistic distributions by varying the postsynaptic potentials of its neurons (Aitchison et al., 2021; Blackwood et al., 2004; Friston and Herreros, 2016; Popa and Ebner, 2019). Therefore, enhanced executive function in older adults after MBIs may potentially be explained by its positive effects on the plasticity and structure of the cerebellum (see *Section 4.3.3* .).

Despite these promising behavioral outcomes associated with MBIs in older adults (e.g., Bugos and Kochar, 2017; Coubard et al., 2011; MacAulay et al., 2019), relatively fewer neuroimaging studies clarified the neural correlates (including structural and functional connectivity, changes in neuromodulation) underlying these improvements in the aging brain. To gain a more holistic understanding of the benefits of music on aging, future studies could consider employing neuroimaging techniques (such as structural, functional, diffusion magnetic resonance imaging (MRI), MR spectroscopy and PET), which allows the examination of the structure, function, and neurotransmitter concentration in the brain. For instance, it would be insightful to examine the changes in functional and structural connectivity between anterior and posterior regions of the brain after a period of music- or dance-training in older adults using fMRI and diffusion spectrum imaging (DSI). It has long been established that there is a change between the functional dynamics of the posterior and anterior regions of the brain that is associated with aging cognition (PASA, see *Section 4.1.1* .). Thus it will be interesting to investigate whether music can potentially mitigate some of these changes in older adults. Similar lines of research could also be extended to inquire neurochemical changes (e.g., dopamine, acetylcholine, and norepinephrine, concentration or receptor occupancy) with the use of MRs or PET.

Furthermore, probabilistic tasks, such as the probabilistic Serial Reaction Time Task (pSRTT), can be used to probe the behavioral and neural correlates of Bayesian inference (e.g., adaptive learning rates, uncertainty estimation and possible changes in precision-weighting during multisensory integration) in older adults before and after MBIs. Such tasks usually require the individual to predict the upcoming stimulus, and the frequency is underlied by a probabilistic distribution of a latent (and sometimes hierarchical) order. Thus, to make fast and accurate responses, individuals must implicitly learn the hidden rules guiding stimulus transitions. The behavior (e.g., reaction time) of individuals in such experiments can be modeled with Bayesian mathematical models to produce Bayesian inference parameters, such as prediction error, and precision of prediction error for each individual (e.

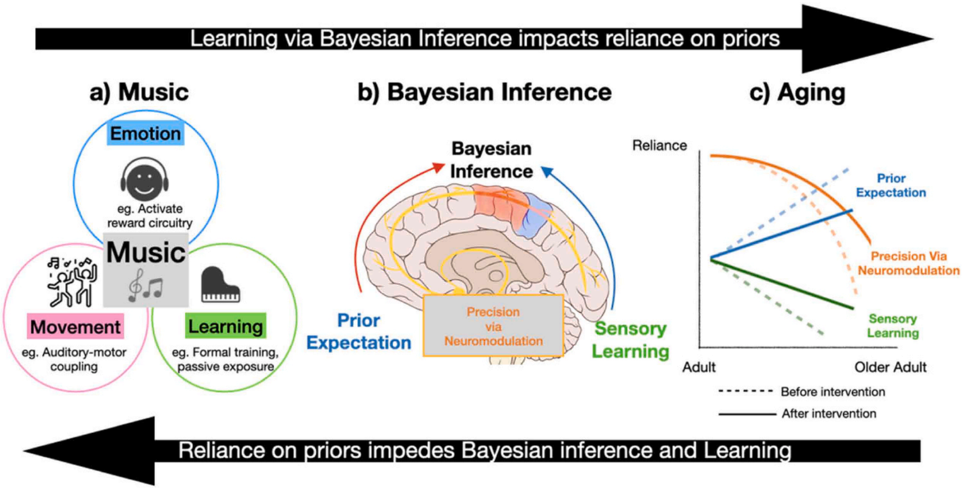

Fig. 4. *Bidirectional Influences of Music and Bayesian Inference on the Aging Brain. Note.* a) Music evokes emotion, results in movement and learning via Bayesian inference processes such as activating the motivational circuitry and auditory-motor coupling mechanism. b) The Bayesian Inference framework involves the updating of sensory learning in posterior brain regions and prior expectations in the anterior frontal region, resulting in prediction errors. The precision of prediction errors are modulated via neurotransmitters such as dopamine, norepinephrine and acetylcholine. c) In aging, sensory learning declines as reliance on prior expectations increases, resulting in an attenuation of precision via neuromodulation (represented by solid lines). Here, we postulate that music-based interventions, through its ability to promote re-engagement of Bayesian inference processes in the aging brain, could help to ameliorate the declines in older adults and therefore explain beneficial effects of music in older adults (represented by the dotted lines).

g., see Hierarchical Gussian Filter; Mathys et al., 2014). This allows the quantification of Bayesian inference in older adults before and after MBIs.

5.2.2. Emotions, cognition and social factors: need for integration of studies from neurocognitive and psychological domains

While the current review outlined the close inter-relationships between movement and learning effects of music as well as Bayesian inference and aging, the relationship between the emotional effects of music, Bayesian inference and aging appear to be less well-understood. Existing literature has provided a wealth of evidence and theoretical explanations underlying the emotional powers of music through a Bayesian inference perspective (i.e., musical expectancy, probabilistic predictions and statistical learning). However, the scope of emotions and aging via a Bayesian inference perspective seems to be more focused on the phenomenon that older adults tend to prefer positive experiences over negative ones (see Lima and Castro, 2011; Trapp et al., 2022). This is also known as the positivity effect, which is beyond the scope of inquiry for this review. Thus, there is first a need to further examine each research field in greater depth, and draw similarities and points of departure in each research domain, so as to bridge this research gap in the explanation of using music for emotional experiences in older adults.

Moreover, improvements in emotional outcomes as a result of MBIs have been consistently associated with improved quality of life, social function and psychological well-being. It is widely recognized that a significant contribution to the success of MBIs is that learning in a group provides opportunity for social engagement and social bonding in older adults (Sutcliffe et al., 2020). For instance, group music training not only resulted in subjective improvements in cognition, but also enhanced self-efficacy and emotional well-being (MacAulay et al., 2019). Studies have also suggested that enhanced emotional well-being is often linked to simply being in a group in and of itself, which provides valuable socialization and camaraderie (MacAulay et al., 2019). Thus, it is no surprise that many older adults prefer to participate in group-based lessons, as it provides them with an opportunity to form new social connections, interact with others, and be part of collective music performances (Perkins et al., 2020; Perkins and Williamon, 2014). Access to these opportunities often help to combat loneliness, which is prevalent among older adults (Schäfer et al., 2020; Shankar et al., 2011). These psychological benefits are also associated with reduced levels of anxiety and depression, improved mental health-related quality of life, and improved morale (Coulton et al., 2015).

Despite the illustrated importance of social engagement and social bonding in MBIs, investigation into the possible underlying predictive processes of musical communication and social factors is only in infancy (e.g., Chabin et al., 2022; Khalil et al., 2022; Müller and Lindenberger, 2023). This is thus certainly an important avenue for future research. Besides the aforementioned recommendations, future studies can also employ these biomarkers identified in naturalistic environments, using techniques that enable investigations of group dynamics (such as

Box 2
Music, Bayesian inference, Aging: Highlights.

Neural principles of Bayesian inference

- Inference in the brain constitutes (1) ***minimization of prediction error*** - the difference between expected sensory outcomes of an action, and sensory information received by the sensory faculties (i.e., perceptual inference), and (2) ***action planning and selection*** that will evince the current prior understanding of the environment (i.e., active inference).
- Precision of prediction errors determines the impact of the signal to subsequent processing. This is represented by synaptic gain in the brain, which is mediated by attentional mechanisms (e.g., selective attention) and neuromodulators (i.e., dopamine, acetylcholine, norepinephrine) that control the postsynaptic excitability of neuronal populations encoding sensory information.

Bayesian Inference in Music

- The statistical regularities within a piece of music sets up predictions and expectations about the continuation of the music in accordance to prior musical exposure.
- This Bayesian account of music perception could offer a holistic understanding of the neurological underpinnings of emotions, movements and learning.

Bayesian Inference in Aging

- Sensory learning attenuates while reliance on internal prior beliefs increases
- While this is resource efficient and therefore adaptive, it limits cognitive and behavioral flexibility.

Beneficial Effects of Music in Aging

- Improvements in emotion, movements and learning in older adults as a result of music-based interventions could potentially be explained by mechanisms related to Bayesian inference.
- Through the activation of the dopaminergic system, the experience of musical pleasure and reward in older age could potentially delay the decline in prediction error signaling.
- Music, as an external cue for motor rehabilitation, taps on the mechanisms of rhythmic entrainment and auditory-motor coupling, which activate neural substrates crucial to action affordance and active inference (i.e., basal ganglia, cerebellum, and the dopaminergic system)
- Active musical engagement necessitates multisensory integration, thereby necessitating the older brain to repeatedly engage in sensory learning which may otherwise have declined with age

Recommendations for Future Research

- Imaging studies to examine the effect of music-based interventions on the functional, structural and neurochemical changes in the aging brain
- Consider using probabilistic tasks as behavioral markers of Bayesian inference as outcome measures to assess the effects of music-based interventions on older adults
- Bridge research gap between music, emotions, and aging (incorporating the phenomenon of positivity effect)
- More investigations of the neural correlates of social factors in group music-based interventions

wearable EEG technology, motion capture or hyper-scanning), to probe the underlying predictive processing mechanisms.

Furthermore, the current review has also illustrated the crucial role of neuromodulation underlying Bayesian inference, particularly in explaining musical reward and pleasure. While there are studies documenting the neurochemistry of music (Fancourt et al., 2014; Ferreri et al., 2019; Menon and Levitin, 2005), it is relatively lacking in terms of examining possible changes in neurotransmitters in older adults. Nonetheless, we can tap on recent technological advances in neuroimaging to examine modulatory effects of neurochemicals crucial in the Bayesian inference process (e.g., dopamine, norepinephrine, acetylcholine).

5.3. General considerations

Music-based interventions entail a number of multimodal effects. Improvements in general cognition are often not isolated, but occur in conjunction with improvements in other domains such as behavioral or emotional outcomes. This viewpoint, that improvements in one domain is not in isolation, has also been echoed in several other papers in engineering research (see Mane et al., 2020; Robinson et al., 2021). Increasingly, studies have started to note the limitations of a unitary approach in rehabilitation (i.e., only targeting one outcome aspect, such as motor rehabilitation), but instead push for a holistic approach. It is interesting to note that even though these studies are not anchored in social sciences, they also recognize the importance of a holistic approach in preventive or rehabilitative interventions. This provides a strong impetus for implementing MBIs and treatments in rehabilitation, given its multifaceted ability to influence a variety of domains (cognitive, behavior, neural), which in this review, we sought to demonstrate that Bayesian inference could be considered as the foundational unifying principle.

All things considered, a common point of consideration is the optimal dosage of music-based intervention required for cognitive maintenance and/or rehabilitation. While this is beyond the scope of the current review, it is hoped that the current review offered some ideas to identify potential biomarkers related to predictive processing, which can be tested empirically and eventually applied in clinical settings to serve as better prognostic identifiers of interventions (see Box 2). With these biomarkers identified, we can next inquire about optimal dosage and duration of music-based interventions.

6. Conclusions

This review is one of the first endeavors to illustrate the potential of Bayesian inference as the fundamental principle in explaining music, aging, and the effects of music-based interventions on aging. Through the synthesis of behavioral, neuroimaging and neurochemical studies, we suggest that music can be an important tool to reinvigorate the process of Bayeian inference in older adults as it (1) provides an avenue to ameliorate age-related declines in neuroplasticity and behavioral flexibility, (2) enriches the sensory exposure of older adults and increases the complexity of their predictive models, and (3) is able to optimally challenge the musical experiences of older adults to introduce new sets of sensory events that may not be a part of their prior predictive model. The aforementioned mechanisms encourage older adults to engage in model-updating via sensory learning, which may mitigate some of the neurological changes due to aging. By adopting the framework of Bayesian inference to understand neurocognitive changes in aging and in music perception, we hope that new research directions and queries can be generated to further our understanding of predictive processing in aging and music, and consequently develop new strategies in using music for preventive or rehabilitative purposes.

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