Neural Mechanisms of Musical Pleasure Experience

Authors: Zhou Can, Zhou Linshu, Jiang Cunmei, Zhou Linshu

Date: 2020-10-22T00:00:00+00:00

Abstract

Pleasant emotional experience constitutes the most prevalent psychological phenomenon in musical activities. Through systematic review of relevant neuroscience research, musical pleasure experience is associated with activity in the brain' s reward system, involving interactions between the nucleus accumbens and other brain regions such as the auditory cortex. In this process, dopamine transmission demonstrates a causal link with musical pleasure experience. From an expectation-based perspective, reward prediction error and music information theory models can explain the generation mechanisms of musical pleasure experience. Future research should further examine the functions of the nucleus accumbens and various cortical regions in musical pleasure experience, and integrate different expectation theories.

Full Text

Neural Mechanisms of Musical Pleasure

ZHOU Can; ZHOU Linshu; JIANG Cunmei
Music College, Shanghai Normal University, Shanghai 200234, China

Abstract

Pleasant emotional experience is the most common psychological phenomenon in musical activities. Through a systematic review of relevant neuroscience research, we propose that musical pleasure is related to activity in the brain reward system and involves interactions between the nucleus accumbens and other brain regions such as the auditory cortex. In this process, dopamine transmission has a causal relationship with musical pleasure. From an expectation perspective, reward prediction errors and information-theoretic models can explain the generation mechanism of musical pleasure. Future research should further examine

the functions of the nucleus accumbens and various cortical regions in musical pleasure and integrate different expectation theories.

Keywords: musical pleasure; emotional experience; reward; expectation; musical anhedonia
Classification Number: B842

Humans have been listening to and performing music since prehistoric times (Conard et al., 2009). Across history and cultures, every known society possesses music. This antiquity and universality suggest that music holds significant meaning for humanity (Huron, 2001). Why is music so important to us? This may stem from music' s capacity to induce pleasant emotions, an experience considered among the most pleasurable available to humans (Dubé & Le Bel, 2003; Juslin & Sloboda, 2013). As recorded in the *Analects*, "When Confucius heard the Shao music in Qi, for three months he did not know the taste of meat." Unlike food, music is not essential for human survival, yet musical activities may provide reward in an abstract form. Understanding the source of this abstract reward and its underlying mechanisms could help explain how music acquired its value during human evolution.

To explore the connection between music and reward, this paper focuses on musical pleasure experience during music appreciation. This term specifically refers to the subjective pleasant emotional feelings and responses evoked or aroused in listeners during music listening, also known as musical pleasure. It is important to note that because perception and experience of musical emotion are somewhat dissociated, listening to pleasant music does not necessarily produce pleasant experiences. Therefore, musical pleasure experience is not equivalent to the emotional experience produced by listening to pleasant music (Juslin & Sloboda, 2013; Schubert, 2013). This article systematically reviews literature on musical pleasure, examining its neural basis and mechanisms. Specifically, we first review the neural correlates between musical pleasure and the brain reward system from a neuropsychological perspective, elaborating on the role of dopamine transmission in musical pleasure and summarizing the neural foundations of musical pleasure. Building on this foundation, we discuss from an expectation theory perspective how music generates pleasant experiences, analyzing reward prediction error theory and the information-theoretic model of music and their supporting evidence. Finally, we outline future research directions from perspectives of brain region function, cognitive mechanisms, conceptual definitions, and research paradigms.

Neural Basis of Musical Pleasure

Certain stimuli can produce intense pleasure responses, such as primary rewards (e.g., food and sex) and secondary rewards (e.g., money). Neuroscience research has found that despite their differences, reward processing relies on a shared brain system: the brain reward system. This system encompasses reward-sensitive brain regions including the striatum (comprising the nucleus accumbens and caudate nucleus), amygdala, insula, orbitofrontal cortex, ventral tegmental area, and ventral prefrontal cortex (Berridge & Kringelbach, 2015; Sescousse et al., 2013). It regulates reward-related cognition and behavior and is responsible for associative learning, approach behavior, and the generation of pleasant emotional experiences (Schultz, 2015), with its activity largely mediated by dopaminergic activity in the mesolimbic system (Egerton et al., 2009). Early neuroimaging studies showed that musical pleasure can activate reward brain regions such as the ventral striatum (Blood & Zatorre, 2001; Koelsch et al., 2006; Menon & Levitin, 2005; Mitterschiffthaler et al., 2007), suggesting that the brain reward system may be involved in musical pleasure. To investigate its neural mechanisms in depth, many researchers have focused on brain regions associated with abnormal musical pleasure experience, revealing the neural basis of musical pleasure from a neuropsychological perspective. Additionally, researchers have examined the role of dopamine transmission in musical pleasure. We discuss these two aspects below.

Brain Reward System Involvement in Musical Pleasure

Sensitivity to musical pleasure shows considerable individual differences. A small minority of individuals exhibit extremely low sensitivity to musical pleasure and cannot derive pleasure from music, while another minority show exceptionally high sensitivity, experiencing pleasure from music that ordinary people cannot attain (Belfi et al., 2017; Mas-Herrero et al., 2013). Both ends of this sensitivity spectrum represent abnormalities in musical pleasure experience. Researchers have found that certain brain injuries can cause musicophilia or acquired musical anhedonia. Interestingly, the former refers to individuals showing extreme pleasure responses or abnormal cravings for music, while the latter refers to individuals who selectively lack pleasant emotional experiences and responses to music (Belfi & Loui, 2020).

Brain regions damaged in individuals with abnormal musical pleasure experience overlap with reward system regions. For instance, musicophilia is associated with damage to the frontotemporal and parietal cortices (Fletcher et al., 2013; Jacome, 1984; Rohrer et al., 2006; Sacks, 2007). Similarly, acquired musical anhedonia involves reward system regions including the frontal lobe, amygdala, insula, and striatum (Belfi et al., 2017; Clark et al., 2018; Griffiths et al., 2004; Satoh et al., 2016), though some cases involve non-reward regions such as the inferior parietal lobule and temporal lobe (Mazzoni et al., 1993; Satoh et al., 2011). These findings suggest that damage to the reward system may cause abnormal musical pleasure experience.

To overcome the heterogeneity problem of brain injury research, recent studies have focused more on individuals with congenital musical anhedonia. Congenital musical anhedonics are healthy individuals without depression or generalized anhedonia who show normal responses to other reward stimuli (e.g., money) and other aesthetic experiences (visual art and emotional sounds), and who do not have deficits in music perception ability, yet find it difficult to obtain pleasant experiences from music (Mas-Herrero et al., 2014; Mas-Herrero, Karhulahti, et al., 2018). The internationally accepted measurement tool is the Barcelona Musical Reward Questionnaire (BMRQ) developed by Mas-Herrero and colleagues (2013).

To investigate the neural basis of this congenital musical anhedonia, Martínez-Molina et al. (2016) selected three groups of participants with high, medium, and low sensitivity to musical pleasure based on the BMRQ, and had them complete music listening and monetary gambling tasks during fMRI scanning. Results showed no group differences in nucleus accumbens activation during the gambling task, but the musical anhedonia group (low sensitivity) showed significantly lower nucleus accumbens activation during the music task. Additionally, compared to the other two groups, the musical anhedonia group showed weaker functional connectivity between the right superior temporal gyrus and nucleus accumbens. This indicates that musical anhedonia is associated with reduced nucleus accumbens activation and weakened functional connectivity between the nucleus accumbens and auditory cortex.

In a follow-up study, Martínez-Molina et al. (2019) again selected three groups with different sensitivities to musical pleasure and investigated the relationship between musical pleasure experience and white matter microstructure using music and gambling tasks. Results showed that individual differences in musical pleasure sensitivity were related to white matter microstructure in connections between the superior temporal gyrus and orbitofrontal cortex, as well as between the nucleus accumbens and orbitofrontal cortex. These findings reveal the importance of information exchange between perceptual, integrative, and reward systems in musical pleasure, providing evidence for interactions between subcortical reward systems and higher-order cortical regions in musical pleasure experience.

These studies demonstrate that damage to reward brain regions may lead to abnormal musical pleasure experience. Research on congenital musical anhedonia also shows that insensitivity to musical pleasure is associated with abnormalities in the nucleus accumbens and its connections with temporo-frontal cortices. Although these studies cannot directly establish causality, their findings suggest an association between musical pleasure experience and brain reward mechanisms.

Role of Dopamine Transmission in Musical Pleasure

Dopamine is the most studied neurotransmitter in the reward system, playing an important role in learning and prediction of reward events (Berridge & Kringelbach, 2008). To examine dopamine system involvement in music listening, some studies have used PET to compare specific dopamine release in the striatum when listening to pleasant versus neutral music. Researchers found that when participants experienced intense pleasure from music, endogenous dopamine transmission increased in both dorsal and ventral striatum. To investigate the temporal dynamics of dopamine release, researchers also conducted fMRI scans on the same participants using identical stimuli, revealing a functional dissociation: the caudate nucleus was more involved during reward anticipation, while the nucleus accumbens was more involved during peak emotional experience of music (Salimpoor et al., 2011). This study confirmed that highly pleasurable subjective responses to music are associated with dopamine release in dorsal and ventral striatum of the reward system, thereby linking music with other biological reward stimuli and advancing understanding of musical pleasure.

To further explore causality, Mas-Herrero, Dagher, et al. (2018) used transcranial magnetic stimulation (TMS) to alter dopaminergic activity in the fronto-striatal circuit and examined whether this could modulate participants' pleasurable emotional experience from music. Results showed that compared to sham stimulation, excitatory stimulation of the fronto-striatal pathway significantly increased participants' pleasurable emotional experience during music listening, skin conductance, and willingness to pay for music, while inhibitory stimulation produced opposite effects. These findings not only demonstrate that stimulating or inhibiting the fronto-striatal circuit can bidirectionally modulate music-evoked emotional responses and motivation to purchase music, but also provide causal evidence that musical pleasure is directly related to reward system activity.

To directly manipulate dopamine and modulate pleasurable emotional experience during music listening, Mallik et al. (2017) used naltrexone (NTX), a mu-opioid antagonist, to reduce dopaminergic activity and investigate whether musical pleasure is governed by the same reward system as other experiences (e.g., food, drugs, and sex). In this experiment, participants first took NTX or placebo, then listened to music while providing real-time ratings of their pleasure. Results showed that compared to placebo, after taking NTX, participants reported significantly reduced pleasure when listening to self-selected highly pleasant music, but no change in pleasure when listening to neutral music. Additionally, NTX administration significantly reduced activity in both zygomaticus and corrugator muscles when listening to pleasant and neutral music. Researchers interpreted this as indicating that NTX reduces emotional responses to music and decreases subjective pleasant experience, confirming that NTX reduces both positive and negative emotional responses to music and causes deficits in musical pleasure.

More recently, Ferreri et al. (2019) validated the role of dopamine transmission in music-evoked pleasant emotional experience through a double-blind within-subjects experiment. The study comprised three phases, in each of which participants received either a dopamine precursor (L-dopa), dopamine antagonist (risperidone), or placebo (lactose). After drug or placebo administration, participants listened to both experimenter-selected and self-selected music while continuously rating their experienced pleasure level. Additionally, an auction task was introduced where participants decided how much money to spend purchasing the experimenter-selected music. Results showed that compared to placebo, participants reported stronger pleasant experiences when listening to music after taking L-dopa and were willing to spend more money to purchase music, while risperidone produced opposite effects on both musical pleasure and motivation. This study demonstrates a causal relationship between dopamine and musical pleasure, revealing the role of the human dopamine system in this abstract reward.

In summary, neuropsychological research has revealed associations between musical pleasure and the brain reward system. Musical pleasure is not only related to core reward regions such as the nucleus accumbens but also to functional connectivity between reward regions and other cortical regions like the auditory cortex. This suggests that musical pleasure results from interactions between perceptual system activity and reward system activity. Dopamine transmission not only participates in this process but can directly modulate the intensity of musical pleasure, indicating a causal link between musical pleasure and dopamine reward mechanisms.

How is Musical Pleasure Generated?

How does musical pleasure arise during music listening? In recent years, researchers have attempted to explain the generation mechanism of musical pleasure from a predictive processing perspective. Indeed, during music listening, listeners not only process acoustic features but also anticipate upcoming musical events, a process long considered a source of emotion and pleasure (Meyer, 1956; Koelsch, 2012). Against this background, both reward prediction error theory and the information-theoretic model of music have attempted to explain the occurrence mechanism of musical pleasure from an expectation perspective, with supporting research evidence.

Reward Prediction Error Theory

According to reward prediction error theory, people anticipate upcoming rewards, forming two stages: reward anticipation and reward receipt. The theory centers on expectation and reward, where reward prediction error is essentially the difference between expected and actual rewards. A positive reward prediction error occurs when the outcome is better than expected (Heydari & Holroyd, 2016; Schultz, 2016, 2017; Watabe-Uchida et al., 2017). Indeed, studies using familiar music found a functional dissociation in the temporal dynamics of dopamine release during music listening, with the caudate nucleus more involved during reward anticipation and the nucleus accumbens more involved during peak emotional experience of music (Salimpoor et al., 2011).

Salimpoor et al. (2013) further selected unfamiliar music to verify the link between expectation and reward. This study innovatively introduced a neuroeconomic research paradigm, requiring participants to state how much money they would be willing to pay for music after listening, with bid amount indirectly representing pleasure level. Results showed that higher bids were associated with stronger activation in the right nucleus accumbens and enhanced functional connectivity between the nucleus accumbens and bilateral superior temporal gyrus, ventromedial prefrontal cortex, orbitofrontal cortex, and right inferior frontal gyrus. On one hand, involvement of expectation-related brain regions (inferior frontal gyrus) suggests people can form expectations about unfamiliar music based on implicit knowledge. On the other hand, this study verified connections between perceptual systems responsible for sound computation and prediction and reward systems responsible for evaluating prediction outcomes. A recent study on cannabis-music interaction also supported these results (Freeman et al., 2018), although another study found reduced functional connectivity between nucleus accumbens and auditory cortex during music listening (Brodal et al., 2017). Based on this, researchers propose that musical pleasure may arise from positive reward prediction errors: during the reward anticipation stage, the perceptual system generates expectations based on relationships between sound elements and explicit or implicit knowledge, with this analysis and prediction process handled by cortical systems; during the reward receipt stage, the reward system evaluates the anticipated outcome, and generating emotional experience of the expected result requires interaction between cortical systems and striatal dopamine systems. When the outcome is better than expected, a positive reward prediction error emerges, giving rise to musical pleasure (Salimpoor et al., 2015; Zatorre, 2015).

To investigate the association between positive reward prediction errors and musical pleasure, Gold, Mas-Herrero, et al. (2019) conducted an fMRI experiment examining whether the nucleus accumbens responds to reward prediction errors in music. They required participants to complete a probabilistic decision-making task while listening to music, making choices about cues where each choice was associated with specific listening outcomes, with music ending on either consonant or dissonant chords. Importantly, outcomes were probabilistic and could produce prediction errors. Results showed that participants learned to make choices producing pleasant consonant endings, and nucleus accumbens activation was significantly correlated with reward prediction errors. This suggests that through reward prediction errors implemented by the nucleus accumbens, musical events can become rewards, and such prediction errors can guide decision-making and drive learning.

Nevertheless, some conclusions remain debatable. First, although Gold, Mas-Herrero, et al.' s (2019) paradigm had probabilistic properties, its design did not fully conform to reward prediction errors in natural music listening. For instance, the prediction processing in this study involved participants' outcome expectations for visual cue choices, making it difficult to generalize conclusions to actual music listening contexts (de Fleurian et al., 2019). Second, although the study focused on "reward prediction" (predicting rewards of future events), it did not distinguish this from "sensory prediction" (predicting future events), leading to confusion between reward prediction errors and sensory prediction errors (see de Fleurian et al., 2019; Hansen et al., 2017).

Information-Theoretic Model of Music

As music unfolds over time, musical events occur sequentially. The brain actively and continuously predicts auditory stimuli and updates mental representations based on new input, so listeners continuously form expectations about upcoming musical structures or acoustic events (Koelsch, 2014; Koelsch et al., 2019). According to the information-theoretic model, higher information entropy in music means lower predictability, making prediction more difficult for listeners, while information content can reflect the surprise listeners actually experience when hearing music (Hansen & Pearce, 2014; Pearce, 2018). Accordingly, researchers propose that musical expectations can be divided into two different temporal states: prospective and retrospective states (Hansen & Pearce, 2014; Koelsch et al., 2019). Taking harmonic expectation as an example, the prospective state can be represented by uncertainty during anticipation, reflecting the probability of chord occurrence given a tonal harmonic context, while the retrospective state can be represented by surprise when the actual chord deviates from expectation, reflecting listeners' prediction accuracy. This perspective suggests that emotional experiences or rewards evoked by musical expectation are modulated by different states.

Unlike reward prediction error theory, the information-theoretic model focuses on the degree of deviation from expectation without emphasizing whether the outcome is better or worse than expected. Recent research by Cheung et al. (2019) provided evidence for this view. Using machine learning models, this study transformed predictive uncertainty and surprise of chords in popular songs into continuous variables to investigate how different states of expectation affect musical pleasure. Behavioral results showed that musical pleasure depends on the interaction between chord uncertainty and surprise. High pleasure can be produced in two situations: (1) low uncertainty with high surprise, and (2) high uncertainty with low surprise. Indeed, another study showed that although listeners generally prefer music with moderate predictive complexity, under conditions of high uncertainty, individuals prefer expected musical outcomes more (Gold, Pearce, et al., 2019). Cheung et al. further found that the interaction between uncertainty and surprise significantly modulated activation in bilateral amygdala, hippocampus, and auditory cortex, while activation in right nucleus accumbens and left caudate nucleus could only explain chord uncertainty. Researchers interpret these findings as suggesting that pleasant experience of chords is built on close connections between perceptual analysis and emotional evaluation, with amygdala, hippocampus, and auditory cortex playing important roles in musical pleasure, while the nucleus accumbens only modulates attention allocation to these regions based on uncertainty. Based on this, the study suggests that musical pleasure depends on the interaction between prospective and retrospective states of expectation, and that amygdala, hippocampus, and auditory cortex participate in this interaction. Although this study used different musical materials, tasks, and paradigms from previous research, its conclusions nevertheless challenge previous cortico-striatal neural models centered on the nucleus accumbens.

It should be noted that Cheung et al.' s (2019) study differs substantially from previous musical pleasure research. In earlier studies, participants almost always listened to entire musical pieces or songs, or directly extracted music segments. In Cheung et al.' s study, although chord sequences were extracted from popular songs and thus had higher ecological validity than artificially composed harmonic progressions, the study focused only on the harmonic dimension of music. It remains unclear whether pleasant experiences of other musical dimensions and of music as a whole also depend on the interaction between uncertainty and surprise, and whether they are all reflected in activation of amygdala, hippocampus, and auditory cortex.

Summary and Outlook

In summary, although damage to frontal, temporal, and parietal cortices may directly cause acquired musical anhedonia or musicophilia, research on congenital musical anhedonia shows that obtaining musical pleasure depends on functional connectivity between the reward system and auditory cortex. This suggests that experiencing musical pleasure may generally rely on complex interactions between the reward system and various cortical regions (Belfi & Loui, 2020; Mas-Herrero et al., 2014; Salimpoor et al., 2015; Zatorre & Salimpoor, 2013). Further investigation of its neural mechanisms reveals that musical pleasure can directly activate reward-related brain circuits, promoting dopamine neurotransmitter release in certain subcortical pathways. Dopamine transmission has been shown to have a causal link with musical pleasure. Building on this foundation, reward prediction error theory and the information-theoretic model of music explain the occurrence mechanism of musical pleasure from an expectation perspective, but due to different theoretical foundations, their supporting evidence and conclusions show clear divergence. Future research can advance musical pleasure studies in three directions.

First, future comprehensive and thorough investigations of the roles and functions of the reward system and various cortices in musical pleasure will be essential. Currently, the core neural circuits remain controversial. Although many studies support the role of cortico-striatal neural pathways centered on the nucleus accumbens in musical pleasure, other research suggests that hippocampus, amygdala, and auditory cortex are the core of musical pleasure (Cheung et al., 2019). Additionally, previous research indicates that musical expectation processing mainly involves the inferior frontal gyrus, inferior parietal lobule, orbitofrontal cortex, and amygdala (Koelsch et al., 2005; Lehne et al., 2013; Royal et al., 2016). Therefore, whether the nucleus accumbens and its represented reward prediction errors are key to musical pleasure requires further verification.

Second, future research should compare and validate reward prediction error theory and the information-theoretic model, and further integrate different expectation theories. Musical pleasure is not only generated at peaks of musical emotional experience but may also arise from more sustained, relatively low-intensity pleasant experiences. If musical pleasure is a continuous phenomenon, expectations of pleasant emotion may involve multiple different cognitive processing stages. Comparing and validating different components involved in the two expectation theories will help reveal the psychological processes and neural mechanisms underlying musical pleasure. Although reward prediction error theory and the information-theoretic model have fundamentally different theoretical foundations—the former based on reward prediction and the latter on prediction of musical events—future research could attempt to integrate these two theories from a predictive coding perspective (Hansen et al., 2017).

Finally, future research should further integrate findings from musical pleasure and musical emotion research, and clarify the connotations of different concepts and their corresponding processing mechanisms. Although musical pleasure is an important component of musical emotion experience, the connotations of related core concepts and their corresponding processing mechanisms remain unclear. For instance, previous research suggested that musical pleasure is more related to emotional arousal (Salimpoor et al., 2009), but recent pharmacological studies show that dopamine drugs can modulate participants' musical pleasure and willingness to purchase music without modulating their experience of music valence and arousal (Ferreri et al., 2019). This prompts us to consider: How does musical pleasure connect with different dimensions of musical emotion experience? How does it relate to behaviors such as music purchasing? These questions fundamentally affect our definition of "musical pleasure" and the design of related experimental paradigms.

In conclusion, although musical pleasure is the most common psychological phenomenon in daily musical activities, how the dopamine reward system functions during this experience and which neural structures are decisive remain open questions. It is precisely based on music' s complexity and diversity that tracing the origins of musical pleasure allows us to better understand the complexity of the human brain and cognition, and more clearly recognize why music is so important to us.

Note: Figure translations are in progress. See original paper for figures.