

Predictions and the brain: how musical sounds become rewarding

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Music has always played a central role in human culture. The question of how musical sounds can have such profound emotional and rewarding effects has been a topic of interest throughout generations. At a fundamental level, listening to music involves tracking a series of sound events over time. Because humans are experts in pattern recognition, temporal predictions are constantly generated, creating a sense of anticipation. We summarize how complex cognitive abilities and cortical processes integrate with fundamental subcortical reward and motivation systems in the brain to give rise to musical pleasure. This work builds on previous theoretical models that emphasize the role of prediction in music appreciation by integrating these ideas with recent neuroscientific evidence.

Why do we love music?

Playing and listening to music are fundamental human behaviors that have existed as far back as the prehistoric era [1]. The abstract and subjective nature of musical experiences has hindered a quantifiable understanding of what sustains our interest in music. However, advances in neuroimaging have fostered a surge of empirical studies on the biological processes that make music rewarding. We summarize recent evidence demonstrating interactions between the sensory, cognitive, and emotional systems with reinforcement circuits that we believe give rise to musical pleasure.

Reward prediction and the brain

A principal goal of the brain is to predict rewarding events. Midbrain dopamine neurons signal potential upcoming rewards, which allows the anticipation of, and motivation to receive, desirable outcomes [2–4]. This neural activity can occur in response to single events or can ramp up as one progressively moves through stages marking approach to rewards [5]. Dopamine cells are thought to encode the degree to which an outcome matches expectations; thus the strongest response occurs to outcomes that are better than expected [4,6], providing a positive prediction error signal that helps to fine-tune future predictions. Although

dopamine is released in response to fundamental rewards that are crucial for survival (e.g., food and sex) [7–9], some rewards (e.g., music) can take more abstract forms, where ‘better-than-expected’ is highly subjective and requires the integration of individualized cortical processes shaped by previous experiences. While the appreciation of music is varied and complex, involving several neural and behavioral mechanisms (see [10,11] for excellent reviews), music pleasure is thought to rely on generation of expectations, anticipation of their development and outcome, and violation or confirmation of predictions [12].

The role of predictions in music

Expectations and anticipation during music listening

Music is essentially a sequence of sounds organized through time. While each of the individual sounds that make up a musical piece may be considered as aesthetically pleasing or not depending on their acoustical properties (notably consonance arising from the harmonicity of their component frequencies (e.g., [13–15]) it is only once these individual sounds are arranged into patterns that unfold over time that they can induce strong pleasure. As such, the temporal dimension is key to understanding how music exerts its powerful affective impact (Box 1). As one listens to music, temporally unfolding patterns of sound are recognized, which leads to continuous generation of expectations and predictions [12,16,17], and a sense of anticipation [18–20].

Two main sources of expectations in music have been proposed: explicit knowledge of how a familiar piece of music will unfold, and implicit understanding of the rules of music in general based on previous music-listening history [19,21]. These two forms of expectations have distinct neural correlates [22]. Implicit expectations arise because temporal and tonal sound patterns vary according to rules and conventions that are specific to particular genres, styles, and cultures. These rules can be derived from statistical learning during past exposures [23–25], social and cultural influences [26–29], and/or musical training [30–33], and impact upon the structure of mental representations and expectations for pattern completion that ultimately determine an individual’s emotional responses [27] and preferences [34] for music.

Converging sources from music cognition research provide empirical evidence for the generation of expectancies

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Box 1. Creation of expectations in music

Composers can strategically manipulate structural and temporal aspects of music as an attempt to achieve a response in the listener. For example, structural variations in frequency, timing, intensity and timbre can manipulate the expressivity of a piece of music by shaping expectations through compositional devices such as suspension, delay, and retardation, deceptive or evaded cadences, or applied dominants. Expectations generally relate to what will happen, and when it will happen. The part of *what* event to expect involves predictions that relate to which notes the listener expects to hear next and the boundary of a phrase [12]. For example, in the Western tonal system, moving away from a tonic chord develops tension but returning to the tonic creates release. Western listeners may develop expectations based on step inertia (a tendency for notes in a melody to move in the same direction), pitch proximity (the tendency for notes to be close to each other), melodic regression (the tendency for notes far from the mean note of a melody to be followed by notes that are closer to the mean note of the melody), and melodic arches (the tendency for a melodic phrase to rise in the beginning and fall towards the end of a phrase). The part of *when* to expect an event involves matching the structure of the music heard with metrical or rhythmic templates that can be extrapolated in the future. Emotions may be manipulated by varying the dynamics of when sounds are heard: an expected note can turn into an unexpected note if it arrives earlier or later than expected, creating a sense of anticipation or delay [12]. Expectations associated with rhythm and beat constitute an important component of temporal predictions in music; for further reading on this and related topics, see [12,91–93].

Expectations may be created on a micro-level, based on local events such as note-to-note and phrase-to-phrase expectations, and also on a macro-level, relating to the larger structure of the music. As expected, different styles of music will utilize different features towards manipulating expectations to maintain the listener's attention and interest. For example, popular music often employs abrupt breaks or changes in orchestration, timbre, or soundscape [94,95]. These manipulations can delay macro-level resolutions (goals) in the music and create new sets of micro-level expectations. These structural manipulations can add new layers of cognitive predictions that may lead to enhanced dopamine activity.

during music listening. Behavioral and priming paradigms demonstrate the role of implicit knowledge on expectancy-driven processing facilitation during the perception of melodic and harmonic sequences, in-key and out-of key targets, and temporal synchronicity [12,17,35–37]. Psychophysiological evidence shows skin conductance changes in response to incongruous chords violating the rules of harmony [38]. Neurophysiological studies demonstrate unique brain potentials (early anterior negativity, EAN) after sound pattern violations, such as irregular tones of melodies, irregular chord functions, rare chord progressions, and harmonic expectations [31,39,40]. Finally, functional magnetic resonance imaging (fMRI) studies find increased hemodynamic activity during violation of musical expectancies in inferior frontal regions [41], caudate [41,42], and amygdala [42], that are implicated in processing structural aspects of music, anticipation, and emotion, respectively. Importantly, evidence from combined psychophysiological, neurophysiological, and subjective self-report measures suggests that violations of expectancies are directly linked with emotion [38,42].

Prediction errors in music

If musical appreciation depends upon expectancy, how is a section of music 'better than expected?' Unlike money or food, a greater quantity of tones or increased volume may

not make music better (only more cacophonous and loud). The answer may lie in the sheer complexity of music, which includes multiple simultaneous dynamic features, reflecting not only the contingencies associated with a single pitch sequence, but multiple sequences, with constantly changing harmonic, spectral and rhythmic features, as well as the unique expressive features of a performer's style [43]. Even gifted musicians and composers can only classify and commit to memory some of this information at a time. On initial exposure, any of several aspects of a piece may cause a positive prediction error due to some acceptable degree of variance relative to music that the person has previously experienced. However, at that point, only some of the features are stored: for instance, the melody, while other aspects of the music may be at best only partially represented in memory. The neural representations of music are likely to be fairly sparse, even after several listenings, with only some features being captured at either implicit or explicit levels. Because our stored representations are incomplete, we can continue to produce positive prediction errors with successful predictions even after multiple listenings or performances of the music.

Dopamine and the reward value of music

A recently proposed hypothesis [20,44] articulated the hypothesis that dopaminergic coding of cues predicting upcoming rewards, and dopaminergic signaling of positive prediction errors, are essential to the high incentive reward value of musical experience. Prior studies had implicated the reward system in musical pleasure [45,46] but two more recent studies provide direct support for the dopamine hypothesis. The first study used a combined [¹¹C]-raclopride positron emission tomography and fMRI to show dopamine release in two regions of the striatum (caudate and nucleus accumbens, NAcc) while participants listened to self-selected highly pleasurable music. This study also found differential hemodynamic responses in these regions during anticipation versus experience of peak pleasure moments in the music [47]. These data show that not only is dopamine released when desirable sound events are heard, but also suggest that musical events leading up to peak pleasure moments may generate a sense of anticipation and lead to dopamine release when individuals listen to familiar music. Explicit familiarity with the music may have contributed to the robust activations in anticipation of peak emotional periods of music, but the importance of familiarity in these responses remained uncertain. A more recent fMRI study [48] used previously unheard music to rule out the possibility of explicit expectations, and demonstrates that implicit expectations alone can activate the same mesolimbic regions involved in forming and assessing predictions [48]. When listening to previously unheard music, prediction errors (positive and negative) are likely to occur as sound events unfold, confirming or violating the listener's predictions, both of which may lead to dopamine release depending on a subjective assessment of whether the events were better than expected. These studies collectively suggest that dopamine may play two distinct but related roles in music appreciation: the desire and anticipation of hearing expected sound

events (with highly familiar music) and positive prediction errors (with less familiar music). This is consistent with the literature showing that dopamine is involved in ‘wanting’ or motivation to receive a stimulus [2,3] as well as in assessing the outcome of a reward prediction [4].

The source of expectations

The finding of the study examining how individuals begin to like previously unheard music [48] are intriguing given data indicating that the positive prediction errors that arise when outcomes are better than expected are associated with increased activity in the NAcc [49–52]. These findings are consistent with the idea that, when we listen to new music, we form implicit predictions about how the sound events will unfold, and prefer music that surpasses our expectations (Box 2). But if so, what is the source of the prediction? Through network analyses, this study suggests that subcortical dopaminergic regions work in concert with higher-order cortical regions to give rise to aesthetic pleasure. As the desirability of the music increased (as indexed by monetary amounts the listener was willing to pay) the NAcc showed increased correlated activity (functional connectivity) with the auditory cortices, inferior frontal gyri (IFG), ventromedial prefrontal cortex (VMPFC), orbitofrontal cortex (OFC), and amygdala. These findings suggest that the reinforcement value of musical experiences

Box 2. How much prediction is too much? Degrees of predictability and music appreciation

Within the predictive coding model of music appreciation there is a core tension between familiarity and uncertainty. Consistent with ‘mere familiarity’ effects [96], unfamiliar music is appreciated more after the first time it is heard [97]. At this early stage, modest familiarity provides an enhanced ability to predict how the music will unfold, but there is enough uncertainty to generate positive prediction errors. However, with enough repetitions, explicit knowledge of the overall structure (melody, chord progressions) and micro-level features (i.e., variations in timing, ornamentation, harmony and timbre from verse to verse) removes the possibility of significant positive prediction errors, resulting in an absence of dopamine release [4] and loss of interest or motivation to hear more. This will be particularly true for recorded music in which variations across listening are limited to minor differences in the playback equipment and where exposures may be massed together (such as with heavy rotation on top-40 radio). By contrast, with enough time between hearings, the precision of macro- or micro-level expectancies may decline, allowing a piece that at one point produced boredom to become rewarding again. Implicit knowledge of the statistical properties of music within a genre will affect the time-course of music appreciation over multiple listenings. Some knowledge of a genre will make pieces of music that have at least some characteristics of that genre more appealing on the first listen, and facilitate the choice to hear the music again in the future. However, if the music is too formulaic, simplistic or repetitive, it may lead to its rapid dismissal as boring or worse. For instance, listening to simple songs made for children may amuse the child over and over again, while becoming increasingly unappealing to a more musically sophisticated parental listener. By contrast, music that is too far from a person’s implicit understanding may provide little desire for subsequent listenings. The key to music’s sustained appeal is a constant interplay between adherence and deviation from typical convention, to allow some level of predictability combined with uncertainty in achieving resolution. More complex music is often able to achieve this because (even among those with musical expertise) it is difficult to have a precise explicit template for all features of a piece.

arises as a result of interactions between regions involved in auditory perception, high-level temporal sequencing, and emotional processing and valuation, as discussed below.

Neural interactions that give rise to musical reward: integration of cortical and mesolimbic networks

Areas involved in auditory perception

The superior temporal cortex (STC), which houses both primary and secondary auditory areas, is involved in a wide range of auditory processing relevant to music, including processing pitch [53–55] and extraction of pitch and tonal relationships [56–59]. It is also thought to store templates of sound events that we have accumulated over the years [60]. Electrical stimulation of the STC elicits musical hallucinations [61], and increased activity in this region is associated with imagery [62] and familiarity of music [60,63], suggesting that it stores previously heard auditory information. Acquired auditory information stored in this region may provide the basis for expectancy generation during music listening. When listening to previously unheard music, similar-sounding auditory templates may be ‘activated’ to generate expectations of how the new sounds will unfold. If the new sounds were better than expected, positive prediction error would result. This is consistent with the finding that liking new music is associated with increased activity in the NAcc (associated with positive prediction error) and coinciding robust connectivity with large clusters of the STC [48]. This connectivity suggests a mechanism through which expectations based on stored templates of previously experienced music become linked to reward confirmation and positive prediction error signaling (Box 3).

Areas involved in high-level temporal sequencing

To appreciate music is to recognize patterns by sequencing structural information, recognizing the underlying structure, and forming predictions. These processes are continuously updated, refined, and revised with incoming information. These operations typically involve the frontal cortices of the brain, particularly the IFG [64,65]. The right IFG has been implicated in processing structural aspects of music [39,66,67]. The IFG and STG are often co-activated [39,66], and may possibly work together to process various aspects of music. Furthermore, there is evidence that white matter connectivity in this pathway is associated with the ability to learn new syntactic structures in the auditory domain [68]. Finally, disruption of STG–IFG pathways has been observed in people with congenital amusia [69,70] who show music perception deficits. It is likely that high-level structural analyses of musical sound patterns in the IFG and previously stored templates of music in the STG may be linked to subcortical regions involved in reinforcement learning, leading to rapid incentivization of an otherwise abstract stimulus.

Areas involved in emotional processing and valuation

The amygdala, VMPFC, and medial OFC are regions of the core and extended limbic system involved in emotional processing, particularly reward detection and valuation [71–73]. In a recent meta-analysis of functional brain

Box 3. Why do different people like different music?

The functional connectivity patterns between the dopaminergic reward regions and cortical areas [48] suggest that predictions are linked to information that is stored in auditory templates, which can then induce emotional arousal and feelings of pleasure in response to music. These findings can help to explain why different individuals appreciate different music. Each individual has his or her own unique set of musical schematic templates, depending on the musical sounds to which he or she has previously been exposed throughout his or her life. This experience will vary within different cultures, age cohorts, social groups, and other demographic factors. Through experiences with particular musical styles, incidental learning takes place as listeners internalize regularities in rhythm, melody, harmony, and other aspects of sound organization. For example, chord changes have very different likelihoods in baroque versus reggae music, which would necessitate a different schema or set of expectations to appreciate each style [19]. These internalized templates of various genres and styles are subsequently used to integrate and organize musical sequences when one is exposed to music, impacting temporal expectations and ultimately influencing appreciation of the music. This can explain generational similarities in music preferences amongst those exposed to the same types of music in their youth, or cultural similarities in music appreciation. Even basic spectral features related to the timbre of instruments or voices (energy contained in first or other partials, level of inharmonicity, etc.) can be stored in terms of templates that evolve over time as expectations themselves change. Thus, what may be experienced by one generation as so far away from expectations to be considered unpleasant may be seen as being well within the bounds of expectation to a later generation.

imaging studies in which subjects made assessments of stimulus value, the VMPFC and ventral striatum were shown to be the only two brain areas that appeared to track value, rather than more non-specific features such as salience or arousal response [74]. The VMPFC and adjacent OFC regions are involved in high-level emotional processing involving the integration of information on internal states with contextual information such as rules and current goals, and also provide the main cortical inputs to the NAcc [75,76]. Similarly, the amygdala provides the main subcortical glutamatergic input to the NAcc [75]. As such, these regions are ideally suited to subsume the integration, evaluation, and decision-making of reward-related stimuli [77,78]. For example, one study found increased VMPFC activity when individuals are exposed to stimuli associated with monetary reward, before making choices [79], suggesting that this region may be maintaining the value of items to be carried forward to inform upcoming decisions. It is therefore likely that the VMPFC, OFC, and amygdala may be assessing the value of incoming sounds and assigning reward-related value to music through their interactions with the NAcc.

Linking dopaminergic hypotheses and pleasure

Dopamine activity can explain why an individual would be motivated to keep listening to a piece of music, or to seek out that music in the future, but it cannot in isolation explain the experience of pleasure when listening to music. Berridge and colleagues describe 'hedonic hotspots' in the NAcc and ventral pallidum that are explicitly linked to the display of pleasure, and are triggered by opioid signaling [80,81]. There are crucial interactions between the dopamine and opioid systems. A rapid increase in dopamine release in humans induces euphoria, with the level of

euphoria correlating with the level of ventral striatal dopamine release [82], which also leads to robust increases of endorphin release in the NAcc [83]. Importantly, opioid antagonists block the subjective 'high' caused by strong dopamine release [84]. Thus, it seems reasonable to hypothesize that a strong induction of dopamine release caused by music can trigger opioid stimulation of so-called hedonic hotspots. In the other direction, the opioid system robustly modulates VTA dopamine cell firing and dopamine release in to the NAcc [85]. This likely provides a mechanism through which music that is experienced as pleasing can enhance dopamine-mediated positive prediction error signaling and reinforcement learning. Thus, the association of dopamine release and NAcc activation during peak musical pleasure may be a direct manifestation of this opioid-dopamine interaction.

Concluding remarks

Perceiving sound events as pleasurable involves an intricate interplay between the dopaminergic system and cortical regions that contain previously acquired sound templates, track temporal and hierarchical structure, integrate emotions with reward value, detect internal states, assign reward value to stimuli, and make value-based decisions about reward-related stimuli. It should be noted that the STC, VMPFC, and amygdala are also involved in a wide range of other processes, suggesting that we must be careful about reverse inference and estimating power [86] when interpreting the findings as they relate directly to music. Future priorities include examining how these systems interact with other areas involved in music perception, including the hippocampus [87–89], hypothalamus, insula, and anterior cingulate cortex [48,89,90], as well as how other neurotransmitter systems contribute to musical pleasure. Furthermore, computational models of expectation may be useful towards quantifying the link between predictability, neural activation, and the listener's experience. This information can be integrated with theories of musical emotion [10] and aesthetic experiences [11] to gain a comprehensive understanding of how music exerts its powerful impact on humanity.

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