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 [^{11}C]-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