

# Ever-Changing Cycles of Musical Pleasure: The Role of Dopamine and Anticipation

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Music listening is highly pleasurable and important part of most people's lives. Because music has no obvious importance for survival, the ubiquity of music remains puzzling and the brain processes underlying this attraction to music are not well understood. Like other rewards (such as food, sex, and money), pleasurable music activates structures in the dopaminergic reward system, but *how* music manages to tap into the brain's reward system is less clear. Here we propose a novel framework for understanding musical pleasure, suggesting that music conforms to the recent concept of pleasure cycles with phases of "wanting/expectation," "liking," and "learning." We argue that expectation is fundamental to musical pleasure, and that music can be experienced as pleasurable both when it fulfills and violates expectations. Dopaminergic neurons in the midbrain represent expectations and violations of expectations (prediction errors) in response to "rewards" and "alert/incentive salience signals." We argue that the human brain treats music as an alert/incentive salience signal, and suggest that the activity of dopamine neurons represents aspects of the phases of musical expectation and musical learning, but not directly the phase of music liking. Finally, we propose a computational model for understanding musical anticipation and pleasure operationalized through the recent theory of predictive coding.

*Keywords:* music, pleasure, reward, dopamine, anticipation

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Some people prefer Mozart whereas others prefer Nirvana or Bob Dylan, but common to most of us is that we find great pleasure in listening to music. Indeed, music is consistently rated to be among the top 10 things people find pleasurable in life (Dubé & Lebel, 2003). Consequently, researchers have suggested that music listening is rewarding in itself (Huron, 2001, 2003; Vuust & Kringelbach, 2009; Wallin, Merker, & Brown, 2000; Zald & Zatorre, 2011). This might explain why music is so widely used across situations in our everyday life and why music has sustained

such prominence in human cultural development (Fitch, 2005; Rentfrow & Gosling, 2003).

Similar to the processing of other rewards, the brain structures that mediate musical perception and pleasure are thought to be anatomically and functionally separated (Peretz, 2010). This separation of perception and pleasure has permeated existing music research (Peretz, 2010), and consequently most studies concentrate entirely on one or the other system. This may partly be owing to the advantages and disadvantages associated with different brain imaging methods. Functional MRI (fMRI) and positron emission tomography (PET) have high spatial resolution, allowing the study of emotion processing by midbrain structures. However, the high spatial resolution comes at the cost of the temporal resolution, which is essential for studying online musical anticipation. A high temporal resolution measuring changes on the basis of milliseconds is an integrated part of electroencephalography (EEG) and magneto-encephalography (MEG). Consequently many EEG and MEG studies describe anticipatory processes in the auditory cortices (Brattico et al., 2009; Brattico, Tervaniemi, Naatanen, & Peretz, 2006; Fujioka, Trainor, Ross, Kakigi, & Pantev, 2004; Garza Villarreal, Brattico, Leino, Ostergaard, & Vuust, 2011; Janata, 1995; Koelsch, 2009; Koelsch, Jentschke, Sammler, & Mietchen, 2007; Leino, Brattico, Tervaniemi, & Vuust, 2007; Loui, Grent-“t-Jong, Torpey, & Woldorff, 2005; Maess, Koelsch, Gunter, & Friederici, 2001; Patel, Gibson, Ratner, Besson, & Holcomb, 1998; Schiavetto, Cortese, & Alain, 1999; Toiviainen &

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Krumhansl, 2003; Trainor, McDonald, & Alain, 2002), but few relate this knowledge to the pleasure of music.

In this article, we propose a novel framework for understanding musical pleasure. Our argument runs as follows: (1) We briefly summarize the vast literature on the reward system and in particular the recent concept of pleasure cycles, with phases of “wanting/expectation,” “liking,” and “learning” (Georgiadis & Kringelbach, 2012; Kringelbach, Stein, & van Hartevelt, 2012). We review neuroimaging studies of musical pleasure, suggesting that music activates the brain’s dopaminergic reward system in similar ways as other rewards, and that musical pleasure conforms to the concept of pleasure cycles. (2) Musical pleasure cycles are driven by the dynamic interplay between the listener’s expectations and the statistical regularities in musical structure. (3) Music is pleasurable when expectations are fulfilled, but probably even more so when they are slightly violated. (4) The degree of violation leading to optimal pleasure can be described by an inverse U-curve (also referred to as the Wundt curve). The optimal level of violation will be highly individual depending on cultural background, personality, musical training, and listening history. (5) No solid framework for describing musical expectations exists to date, thus we propose a hierarchical computational framework based on Bayesian predictive coding for describing the continuous creation of musical expectations in the listener on a psychological and neurobiological level. (6) Dopaminergic neurons in the brain’s reward system are involved in the representation of expectations and violations of expectations (prediction errors). (7) The firing patterns of dopaminergic neurons conform to the assumptions made based on the predictive coding theory. (8) Dopaminergic neurons represent expectations and prediction errors for reward stimuli and sensory alert/incentive salience signals. We argue that music constitutes an alert/incentive salience signal and that musical expectations activate dopaminergic neurons similarly to rewards like food, money, and sex. (9) Dopaminergic neurons represent aspects of the phases of musical wanting/expectation and musical learning, but not directly the phase of music liking. (10) We conclude with suggestions for future development of the theory and put forward experimental hypotheses to test the theory.

### Musical Pleasure Cycles and the Brain’s Reward System

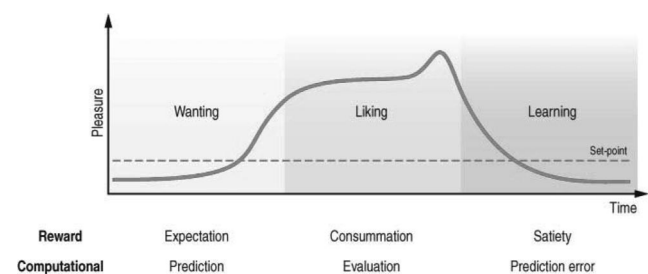
Pleasure may seem difficult to define and study with scientific methods. However, significant progress has been made recently, and one strategy has been to define pleasure as a driving force allowing species and organisms to ensure survival and procreation in both individuals and species (Kringelbach, 2005; Kringelbach & Berridge, 2010a). As such, pleasure could be seen as a crucial adaptive mechanism. Hence, neural mechanisms for pleasure have been selected for and conserved only if they ultimately served a central role in fulfilling Darwinian imperatives of gene proliferation via improved survival and procreation, suggesting that the capacity for pleasure must have been fundamentally important in evolutionary fitness (Berridge & Schulkin, 1989; Cabanac, 2010; Darwin, 1872; Huron, 2003; Nesse, 2002; Panksepp, 1998; Rolls, 2005; Schulkin, 2004; Tindell, Smith, Pecina, Berridge, & Aldridge, 2006).

The main challenge for the brain is to successfully balance resource allocation for survival and procreation (Lou, Joensson, &

Kringelbach, 2011). To achieve this balance, different rewards compete for resources and therefore typically follow a cyclical time course (see Figure 1).

Accordingly, anticipation helps to initiate, sustain, and terminate the phases of *wanting*, *liking*, and *learning* and as such plays a crucial role in guiding the survival-related decision-making involved in optimizing resource allocation of brain resources.

As suggested by a large body of work (e.g., see Berridge & Kringelbach, 2008), *liking* is the actual pleasure component or hedonic impact of a reward, which comprises two levels: (1) core “liking” reactions that need not necessarily be conscious, (2) conscious experiences of pleasure, in the ordinary sense of the word, which may be elaborated out of core “liking” reactions by cognitive brain mechanisms of awareness. *Wanting* is the motivation for reward, which includes both (1) “wanting” processes that are not necessarily conscious and (2) conscious desires for incentives or cognitive goals. *Learning* constitutes the associations, representations, and predictions about future rewards based on past experiences. Learned predictions include both (1) explicit, cognitive predictions, and (2) implicit knowledge acquired through associative conditioning, such as basic Pavlovian and instrumental associations. Extensive research has demonstrated that these different psychological components are mediated by partly dissociable brain substrates (e.g., Kringelbach & Berridge, 2010b). Pleasure is never merely a sensation, even for sensory pleasures such as eating food or listening to music (Kringelbach, 2010; Kringelbach & Berridge, 2010b; Ryle, 1954). Instead pleasure always requires the recruitment of specialized brain systems to add the hedonic and motivational drive to a sensation. Active recruitment of the brain’s reward systems is what makes a pleasant experience “liked.” Recent progress in *hedonia* research (from the ancient Greek word *hedone*, from the sweet taste of honey, *hedus*) has demonstrated that pleasure consists of multiple brain networks



*Figure 1.* Pleasure cycles. Fundamental pleasures (i.e., rewards associated with behavior necessary for species survival) and higher order pleasures (such as music) are associated with a cyclical time course. Rewarding moments go through a phase of expectation or wanting for a reward, which sometimes leads to a phase of consummation or liking of the reward, which can have a peak level of pleasure (e.g., musical chill, encountering a loved one, a tasty meal, sexual orgasm, drug rush, winning a gambling bet). This can be followed by a satiety or learning phase, where one learns and updates predictions for the reward. These various phases have been identified at many levels of investigation of which the recent research on the computational mechanisms underlying prediction, evaluation, and prediction error are particularly interesting (Friston & Kiebel, 2009b; Pearce et al., 2010; Zhang, Berridge, Tindell, Smith, & Aldridge, 2009). A color version of this figure is available as supplemental material at: <http://dx.doi.org/10.1037/a0031126.supp>.

and processes relating to wanting/expectation, liking, and learning (Berridge & Kringelbach, 2008; Finlayson, King, & Blundell, 2007; Robinson & Berridge, 1993, 2003). Key nodes in these networks include subcortical structures (nucleus accumbens, ventral pallidum, periaqueductal gray, ventral tegmental area, and amygdala) and cortical structures (orbitofrontal, cingulate, and insular cortices; see Figure 2).

Similarly, when it comes to music processing in the human brain, perceptual features of music will elicit activity in primary auditory cortex and associated areas, whereas the pleasure of music is associated with the above-mentioned reward network (for a review see [Koelsch, 2010] and [Zald & Zatorre, 2011]). In particular, the musical pleasure cycle has been shown to involve the reward system and in particular parts of the orbitofrontal cortex, the ventral tegmental area, and the nucleus accumbens (Blood & Zatorre, 2001; Brown, Martinez, & Parsons, 2004; Koelsch, Fritz, D.Y., Muller, & Friederici, 2006; Menon & Levitin, 2005; Mitterschiffthaler, Fu, Dalton, Andrew, & Williams, 2007; Osuch et al., 2009; Suzuki et al., 2009). This is remarkably similar to the brain networks involved in the pleasure cycles of food (Kringelbach et al., 2012) and sex (Georgiadis & Kringelbach, 2012).

Dopamine is a key neurotransmitter within these structures, and the dopaminergic system has consistently been associated with the motivational salience or *wanting* of a range of physiological and psychological rewards, from the pleasure of sex and gambling, to the taste of chocolate or the pleasure of a good laugh (Berridge & Robinson, 1998; Kalivas & Volkow, 2005; Knutson & Cooper, 2005; Mobbs, Greicius, Abdel-Azim, Menon, & Reiss, 2003; Morgan et al., 2002; Pfaus, 2009; Robbins & Everitt, 1996). These associations between the dopaminergic reward system and various

pleasures have led many researchers to suggest a similar link between the brain's reward system and music listening (for a review see [Vuust & Kringelbach, 2009] and [Zald & Zatorre, 2011]).

Blood and Zatorre (2001) pioneered the study of the neural correlates of pleasurable musical chills, which correspond to the peak pleasure of the liking phase of the pleasure cycle, similarly to the peak moments of pleasure for other rewards such as food and sex. In a PET study in healthy participants, they found that chill intensity ratings correlated with activity in the brain's reward circuitry, and more specifically with activity in the ventral striatum. Results from the same lab had previously shown an inverse coupling with increased activity in the ventromedial prefrontal cortex and decreased activity in the parahippocampal gyrus to mildly pleasant music, and vice versa for unpleasant music (Blood, Zatorre, Bermudez, & Evans, 1999). Another PET study of pleasurable feelings elicited by music was later carried out by Brown, Martinez, and Parsons (2004), who also found activity in the reward system of the human brain. Although this study studied a larger part of the musical pleasure cycle, the findings also included activity in the ventral striatum in response to pleasant music.

Suzuki et al. (2009) found that listening to consonant chords (regardless of key), which the subjects identified as beautiful, compared with listening to ugly dissonant chords, elicited activity in the dorsomedial midbrain, including the ventral striatum and substantia nigra. Menon and Levitin (2005) used fMRI and found increased activity in the nucleus accumbens, ventral tegmental area, and the hypothalamus in response to pleasurable classical music. In addition, their connectivity analysis showed interactions between the nucleus accumbens, ventral tegmental area, and hypothalamus, suggesting that these structures interact to modulate responses to musical rewards and emotions. They concluded that this modulation of the nucleus accumbens from the ventral tegmental area strongly indicates involvement of the dopaminergic reward system in pleasurable music listening. Similar results have subsequently been found by Koelsch et al. (2006) and Mitterschiffthaler et al. (2007). The study by Koelsch et al. further found that neural responses to pleasant or unpleasant music changed over time, indicating that the pleasure response to music corresponds to the pleasure cycle by having an extended time course.

In an fMRI study, Osuch et al. (2009) investigated neural responses to pleasant music in healthy people compared with people with depression. A key symptom of depression is *anhedonia*, the lack of interest and enjoyment in previously pleasurable activities. When the participants' favorite music was contrasted with neutral music, the study found greater activity in medial orbitofrontal cortex and ventral striatum in healthy subjects compared with people with depression. Furthermore, they found that activity in the medial prefrontal cortex and ventral striatum correlated with the self-reported capacity to experience pleasure in a range of different situations.

All these studies measured changes in either cerebral blood flow or blood oxygenation level-dependent (BOLD) signal in dopamine-innervated brain areas in response to pleasurable music, but none of them measured dopamine release directly. Nevertheless, these studies all imply that the dopaminergic reward system is involved in pleasurable responses to music listening.

To date, only one study has directly demonstrated the involvement of dopamine. This remarkable study combined fMRI with

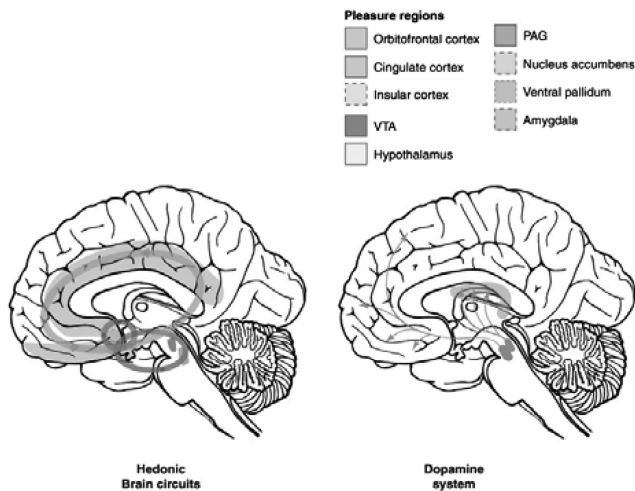


Figure 2. Pleasure networks in the mammalian brain. The figure shows pleasure regions in the human brain. The pleasure networks include the orbitofrontal cortex (gray), the cingulate cortex (light blue), ventral tegmental area in the brainstem (light red), hypothalamus (yellow), periventricular gray/periaqueductal gray (PVG/PAG, green), nucleus accumbens (light green), ventral pallidum (light purple), amygdala (light red), and the insular cortices (not shown). The right-most panel shows the dopaminergic system in the human brain. A color version of this figure is available as supplemental material at: <http://dx.doi.org/10.1037/a0031126.supp>.

PET scanning using the dopamine-specific tracer [ $^{11}\text{C}$ ] Raclopride and showed a functional dissociation between striatal dopamine release during two different phases of the musical pleasure cycle: “wanting/expectation” and “liking” (Salimpoor, Benovoy, Larcher, Dagher, & Zatorre, 2011). Where dopamine release during “peak pleasure,” that is, music-induced chills, seems to occur mostly in the nucleus accumbens, “anticipation of pleasure” is associated with dopamine release in the caudate. The presence of dopamine was established by the binding potential of [ $^{11}\text{C}$ ] Raclopride, whereas the functional and temporal distinctions of “anticipation of pleasure” and “peak pleasure” were established by fMRI.

This intriguing study used state-of-the-art methods to show dopamine release in response to musical anticipation and pleasure. Nevertheless, given the lack of temporal resolution in the PET study, the possibility still remains that the relatively spatially and temporally diffuse dopamine release measured with PET do not adhere to the functional distinction found using fMRI. Dopamine may solely (or partly) be released in response to anticipation of pleasure, whereas other neurotransmitters in the nucleus accumbens, such as opioids and endo-cannabinoids (Stefano, Zhu, Cadet, Salamon, & Mantione, 2004), could account for the “peak pleasure” activity found with fMRI. This is especially likely given the evidence from other animals where opiate-mediated hedonic hotspots have been identified in the nucleus accumbens shell (Kringelbach & Berridge, 2009; Pecina & Berridge, 2005).

The above reviewed studies have revealed much about the functional localization of musical pleasure in the brain, which is remarkably similar to that found for other basic pleasures such as food and sex. In addition to this, the empirical finding of temporal variation of neural activity during pleasurable music listening, shown by Koelsch et al. (2006), is in accordance with the concept of a temporally extended musical pleasure cycle. For music, the wanting or expectation phase can be defined as the anticipation of a specific (pleasurable) musical structure. The liking phase includes moments of peak pleasure corresponding to time intervals where the pleasure of the music is experienced most intensely; this can for instance be a certain chord progression, strong emotional responses, or the time window around music-induced chills. The liking phase also includes pleasurable experiences with less defined peaks. A distinction between the wanting/expectation phase and the peak pleasure part of the liking phase is further corroborated by the finding of different neural responses to the two during music listening (Salimpoor et al., 2011). The learning phase is also a crucial part of musical pleasure, since it changes musical expectations (Loui, Wessel, & Hudson Kam, 2010), and thus ultimately changes both the wanting/expectation phase and the liking phase for future listening experiences. Repeated exposure (and thus learning) of a musical piece increases liking, but only up to a certain point of satiety or overexposure, where the music is perceived as less pleasant (Green, Baerentsen, Stodkilde-Jorgensen, Roepstorff, & Vuust, 2012; Loui et al., 2010; Peretz, Gaudreau, & Bonnel, 1998; Tan, Sackman, & Peaslee, 2006; Zajonc, Shaver, Tavis, & van Kreveld, 1972). A similar satiety phase is found for other rewards (Gottfried, O’Doherty, & Dolan, 2003; Kringelbach et al., 2003), whereas few rewards, such as money and drugs that directly affect the dopamine systems, might lack a satiety phase completely (Kringelbach & Berridge, 2010).

Yet, the reviewed neuroimaging studies reveal little about *how* musical pleasure is created. The study by Salimpoor et al. suggests that anticipation is a key agent in activating the reward system and eliciting musical pleasure, but the study does not provide any putative mechanisms underlying musical pleasure. In the following, we will argue that musical anticipation is fundamental to understanding both the psychological and neurobiological mechanisms underlying musical pleasure.

### Musical Anticipations

The structure of music is highly repetitive and governed by statistical regularities (Loui et al., 2010; Pearce, Ruiz, Kapasi, Wiggins, & Bhattacharya, 2010; Pearce & Wiggins, 2006; Saffran, Aslin, & Newport, 1996; Saffran, Johnson, Aslin, & Newport, 1999). The creation of musical expectations in the listener (of for instance, meter and tonality) seems to happen within the first few seconds of listening to a musical piece, and without a conscious cognitive effort (Eerola, 2003; Koelsch, Gunter, Friederici, & Schroger, 2000; Krumhansl, Bharucha, & Castellano, 1982; Tillmann, 2005). These musical expectations have been proposed to rely on general learning mechanisms sensitive to the statistic contingencies in the musical structure (Loui et al., 2010; Pearce & Wiggins, 2006). Very basic auditory expectations (of pitch, timbre, loudness, direction, and temporal sequencing), as demonstrated by the neural mismatch negativity (MMN), have been found in newborns and even at the prenatal state (Naatanen, Paavilainen, Rinne, & Alho, 2007; Winkler, Haden, Ladinig, Sziller, & Honing, 2009). Meanwhile, more musically enriched paradigms have also shown variations in the MMN signal between musicians and nonmusicians (Vuust, Brattico, Seppanen, Naatanen, & Tervaniemi, 2012), suggesting that, though the MMN is a very fundamental brain response, and is seemingly present very early in life, it is sensitive to exposure and learning. Violation of harmonic expectations have also been widely studied and have been found to elicit a neural early (right/bilateral) anterior negativity (ERAN) (Garza Villarreal et al., 2011; Koelsch et al., 2000; Koelsch & Jentschke, 2008; Koelsch et al., 2007; Koelsch & Mulder, 2002; Leino et al., 2007) followed by a later negative component (N5), presumably representing a higher order integration of the novel information (Koelsch et al., 2000; Loui et al., 2005; Steinbeis, Koelsch, & Sloboda, 2006). Like the MMN, the ERAN also seems to be sensitive to musical training (Jentschke & Koelsch, 2009; Tervaniemi, Tupala, & Brattico, 2012). Similarly, developmental differences in pitch perception (Schellenberg et al., 2002; Stalinski & Schellenberg, 2010; Stalinski, Schellenberg, & Trehub, 2008), sensitivity to tonal hierarchies (Krumhansl & Keil, 1982), and key and harmony perception (Corrigall & Trainor, 2009) have been documented, supporting the notion that musical expectancy depends strongly on learning.

In their theoretical framework, Pearce and Wiggins (2006) describe how unsupervised statistical learning provides a superior account of empirical findings of melodic expectation compared with previous theories, such as the implication-realization theory proposed by Narmour (1991), and later revisions of this (Krumhansl, 1995; Schellenberg, 1997). Pearce and colleagues (2010) further demonstrated how different conditional probabilities (high and low) between notes in ecological music stimuli, elicited distinct patterns of neural activity. Low probability se-



quences elicited a larger negative event-related potential, followed by long-range phase synchronization across multiple brain areas. Behaviorally, high-probability sequences were also recognized as expected where low-probability sequences were rated as unexpected. Thus, both neural processing and behavioral responses seem to correspond with the predictions from their statistical learning model. The statistical learning approach of musical expectations is further supported by an elegantly conducted study by Loui and colleagues (2010), showing that people spontaneously pick up an artificial musical grammar just through passive listening.

Thus, although some musical expectations may be more or less universal, such as the MMN to deviant sounds (Näätänen, Teder, Alho, & Lavikainen, 1992; Vuust et al., 2011; Vuust et al., 2012), others are shaped by the musical culture we are born into (Demorest & Osterhout, 2012; Drake & Ben El Heni, 2003; Krumhansl et al., 2000) and the musical training we receive (Jentschke & Koelsch, 2009; Krumhansl, 1991; Tervaniemi et al., 2012; Vuust et al., 2012). The more complex the predictions, the more likely it is that such predictions must be learned. In this way our auditory system achieves maximal adaptability to different contexts while keeping “preprogrammed” survival-related mechanisms unchangeable.

Although there is a sizable literature on the significance of musical anticipation, the link between anticipation and aesthetic pleasure is not well understood and has rarely been examined in empirical research. Musical anticipation is assumed to create pleasure by establishing, fulfilling, or disappointing the anticipatory structures formed in the listener (Huron, 2006; Meyer, 1956; Narmour, 1991; Vuust & Frith, 2008). Mismatch between the musical structure and the listener’s expectations have further been associated with strong emotions, laughter, awe, and music-induced chills (Huron, 2006; Sloboda, 1991). It is however unlikely that there is only one mechanism capable of creating the pleasurable experiences we get from listening to music; many extramusical factors may also contribute. In their extensive review from 2008, Juslin & Västfjäll proposed six mechanisms through which music listening may induce emotions, and potentially create pleasure in the listener. The mechanisms are episodic memory, visual imagery, emotional contagion, associative conditioning, brain stem reflexes, and anticipation. Though all the proposed mechanisms are clearly capable of influencing pleasurable responses to music, it has been argued that anticipation must be seen as the most fundamental mechanism underlying musical pleasure (Vuust & Frith, 2008). Musical anticipation links musical and psychological mechanisms directly, whereas other of the proposed mechanisms (such as episodic memory, visual imagery, emotional contagion, and associative conditioning) emphasizes extramusical associations as the main propagators of musical emotions and pleasure. The six mechanisms proposed by Juslin & Västfjäll are not mutually exclusive or hierarchically organized. For instance, visual imagery may be important in determining the pleasure experienced in relation to one specific melody, but completely unrelated to the pleasurable response to another. Meanwhile, it is difficult to imagine music listening devoid of musical anticipation, so though other mechanisms are influential they can be suggested to act “on top” of musical anticipations (Vuust & Frith, 2008). Accordingly, we shall in the

following argue that the anticipatory interplay between the listener’s expectations and the anticipations created by the music may be a fundamental mechanism guiding the musical pleasure cycle.

### When Failed Anticipations Become a Pleasurable Surprise

Correct predictions are of crucial importance for our survival. Consequently, it makes sense that the brain rewards correct expectations, and thus that music which fulfills our expectations is experienced as rewarding and pleasurable. Music which, on the other hand, violates expectations will initially be perceived as a potential threat, as our failed prediction makes us less prepared to respond appropriately to the situation. It can therefore seem counterintuitive that failed expectations have been found to create tension and pleasure in music (Huron, 2006; Meyer, 1956). Grewe, Nagel, Kopiez, & Altenmüller (2005) found that pleasurable chills are related to the musical structure, specifically to violations of expectations. This is also in accordance with the finding by Krumhansl (2002), suggesting that tension is indeed a multivalent quality associated with both positive and negative emotions.

Thus, unfulfilled expectations create surprise and orientation, but they can also result in pleasure and positive emotions. This is nicely captured by Huron’s (2006) theoretical framework, where he describes how musical surprise can be transferred into positive emotions via fear-related brain mechanisms. Unanticipated events are responded to with surprise, that is, increased physiological arousal and optimized attention, but can be modulated by our secondary cognitive appraisal of the event. So, the delights we get from unanticipated events in music are due to the contrast between our predictions and the musical structure, and then the following resolution in the music. Musicians might use this contrast by creating expectations in sound, which are not, or only partially, resolved and thereby create a fear reaction or tension, which can then be resolved. Since music listening in itself is harmless, the fear is soon evaluated as being a false alarm, which gives rise to positive emotions. This is supported by the finding that tension or violation of expectations seem to be correlated with physiological arousal (Krumhansl, 2002). Increased physiological arousal might be a consequence of the fight/flight response initiated by the unanticipated musical sequence. Salimpoor, Benovoy, Longo, Cooperstock, & Zatorre (2009) also found a positive correlation between physiological arousal and the pleasure participants experienced while listening to music, supporting the notion of an optimal level of music-induced arousal proposed by Berlyne (1971; North & Hargreaves, 1997b). Berlyne proposed that an inverted U-shaped curve (otherwise known as the negative quadratic curve, or the Wundt curve) reflects the relationship between aesthetic appreciation and structural complexity in art. According to this relationship, degree of complexity correlates positively with liking, arousal, and pleasure until an optimal point, after which a continuous increase in complexity correlates negatively with these measures. The theory was first empirically demonstrated for music by Heyduk (1975) in the context of objective measures of complexity in classical piano compositions, and was subsequently shown for ratings of subjective complexity of popular music pieces (North & Hargreaves, 1995, 1997a, 1998). However, what constitutes the optimal level of complexity depends on musical context

(North & Hargreaves, 1997a) and personality (McNamara & Ballard, 1999). Accordingly, pleasure seems to follow an inverted U-shape, and whether a mismatch between the listener's expectation and the musical structure is experienced as pleasurable or gives rise to negative feelings, is dependent on the degree to which the musical structure violates the anticipation. The degree of violation one tolerates is probably dependent on a range of personality factors, one's musical background, and competence, which all might contribute to personal musical preferences (Bharucha & Krumhansl, 1983; Grewe et al., 2005; Vuust et al., 2010; Orr & Ohlsson, 2005).

Although many music researchers recognize the association between musical anticipation, especially failed anticipations, and the pleasure that is experienced from listening to music (Huron, 2006; Juslin & Vastfjall, 2008; Meyer, 1956; Narmour, 1991; Pearce et al., 2010; Pearce & Wiggins, 2006; Peretz, 2010; Vuust & Kringelbach, 2009), little is known about how anticipations elicit pleasure and affect the brain's reward system. However, Steinbeis et al. (2006) investigated the emotional effect of harmonic expectancy violations in musicians and nonmusicians. Harmonic expectancy violations elicit an early right anterior negativity (ERAN) in the brain. The ERAN is known as a more cognitive component of music processing, relating to hierarchical predictions of harmony, and had not previously been linked to pleasure processing. The results suggested that heightened harmonic unexpectedness is associated with increased emotionality as measured by subjective reports and electrodermal activity. The ERAN proved to be sensitive to the degree of violation, as was the perceived emotionality, suggesting an association between the two. Although pleasure was not directly investigated by Steinbeis et al., their results suggest that unfulfilled expectations have the potential to create strong emotions and pleasure in the listener. However, Koelsch et al. (2006) found that irregular chords (which also elicit an ERAN) were perceived as more unpleasant than regular/expected chords. The unpleasantness of irregular chords was associated with increased amygdala activity measured with fMRI. This suggests that a high degree of unexpectedness may also be experienced as unpleasant, but it remains difficult to establish where exactly the border between unpleasurable and pleasurable surprises lies. How this relates to the Wundt curve described by Berlyne and others (Berlyne, 1971; North & Hargreaves, 1995, 1997b; Orr & Ohlsson, 2005) should be further investigated.

More research is needed for nuancing this area and clarifying the relations between fulfilled/unfulfilled anticipation in music perception and pleasure. Future studies would especially benefit from a more precise definition and operationalization of musical anticipation, since the term is currently used loosely to cover everything from basic, preattentive auditory expectations to complex, high level expectations based on years of familiarity with a certain genre or even a specific musical piece. Some music theoretical accounts distinguish between prediction, expectation, prospection (Bubic, von Cramon, & Schubotz, 2010), expectancy, and anticipation (Rohrmeier & Koelsch, 2012). According to this view, "prediction" refers to future-directed information processing, "expectation" to the subject's representation of the predicted, "prospection" for expectations with a greater temporal extension, "expectancy" is the mere expectation that something will happen, and finally "anticipation" is the occurrence of an event earlier than expected (Rohrmeier & Koelsch, 2012). This terminological dis-

inction is clearly helpful in some models of anticipation and prediction. In the present article, we do, however, not adhere to this strict division, since our model of musical anticipation incorporates expectation, prediction, and prospection into one hierarchical model. Our use of the term anticipation does not refer to the occurrence of events prior to what is expected. It rather describes the online, context-sensitive formation and evaluation of the listener's expectations.

In the following, we suggest that musical anticipation can be operationalized according to Bayes's theorem and predictive coding theory. Furthermore, musical anticipations will be suggested to be hierarchically organized, composed of both low-level expectations, to which we have no conscious access, and more elaborate high-level expectations, which integrate the low-level information into a functional whole. Accordingly, many different aspects of the musical structure (e.g., rhythm, harmony, melody, timbre, musical form) may give rise to different musical expectations that may act together or be in direct opposition. Consequently, musical anticipations can be fulfilled or violated at very different hierarchical levels, be more or less conscious, and thus instigate different phases of the musical pleasure cycle. The integration between sensory inputs across hierarchically organized anticipatory structures in the brain describes the interaction between sensory perception of music and musical pleasure.

### Predictive Coding Theory & Bayes' Theorem

Musical anticipation can be formulated according to Bayes's theorem, which is the corner stone of Bayesian statistics and fundamental to the predictive coding theory (Friston, 2009, 2010). Central to this perspective is that the brain is seen as a "hypothesis tester," which constantly tries to minimize prediction errors (i.e., incorrect predictions). The predictive coding theory was first applied to sensory perception, describing how the brain infers the causes of sensory input based on Bayesian inference. That is, the brain predicts the causes of sensations based on the actual sensory input and previous "knowledge" (Friston, 2005). This is not trivial, as a variety of environmental causes can result in similar sensory input. The predictive coding theory overcomes this perceptual challenge by using internal generative predictive models. These models continuously predict what the sensory input will be if it is caused by a certain (predicted) environmental event. Accordingly, the models are continually updated to maximize the correspondence with the sensory input and minimize prediction errors. In this way the causes of our sensory input are not backtracked from the sensory input, but inferred and anticipated based on contextual cues and previous sensory inputs. These suggestions align closely with the statistical learning approach proposed by Pearce and Wiggins (2006) to account for melodic perception. The predictive coding theory was initially proposed to account for perception only, but, in the past few years, many studies in other areas of cognitive neuroscience have also found the Bayesian framework to be fruitful (Brown & Friston, 2012; Edwards, Adams, Brown, Parees, & Friston, 2012; Friston et al., 2012; Hohwy, 2012; Hohwy, Roepstorff, & Friston, 2008; Kilner, Friston, & Frith, 2007; Nazimek, Hunter, & Woodruff, 2012; Schiffer, Ahlheim, Wurm, & Schubotz, 2012; Seth & Critchley, 2011; Vuust, Ostergaard, Pallesen, Bailey, & Roepstorff, 2009; Wacongne et al., 2011). This has led to the suggestion that the predictive coding theory might be

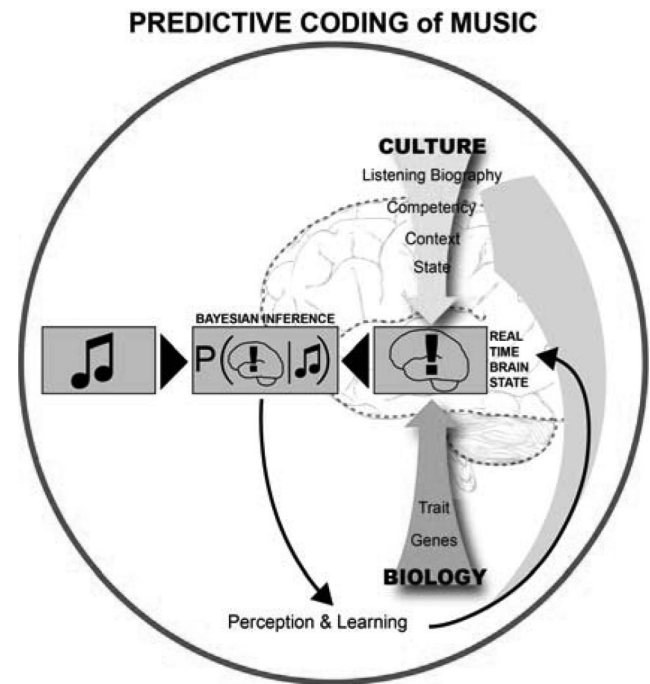
a prominent candidate for a unified theory of brain function (Friston, 2010; Huang, 2008).

The predictive coding theory explains neuronal signals passing between different levels of cortical hierarchies, and this view of hierarchical functional organization is in accordance with brain anatomy (Friston, 2002a). The key principles of the predictive coding theory are as follows: (1) functional segregation, meaning that cells with common functional properties are grouped in the same area, and (2) functional integration, meaning that information from a range of different specialized neuronal populations is integrated at higher cortical levels (Friston, 2002b, 2005).

Obviously, the brain cannot make up models or predictions *de novo*, but needs to rely on prior experience to model expectations for the future. This prior experience gives a prior probability, describing how probable an internal hypothesis is to be true. Prior probabilities are context-sensitive and hierarchical, hence we have a range of possibilities available to us where some are more likely to be correct than others and they change according to the context. Thus, the hypotheses the brain generates in a specific situation are constrained by hypotheses at the same or higher levels and guide the processing of lower levels (Friston, 2002a). Therefore, when we have access to accurate information about the context, more specific hypotheses will be generated, due to the many contextual constraints, and hence the predictions of the sensory input will improve. Consequently, these predictions are a product of the interplay between the subject's prior experience and the available sensory information, which forms the internal hypothesis or model. In this way, our predictions are built on prior experience and learning, but are still dynamic and context-sensitive.

Each hierarchical level provides a predictive model (or models, as competing horizontal models are present as soon as the situation becomes vaguely ambiguous or uncertain) of what the input to the specific layer is expected to be. The hierarchical layers "communicate" through forward and backward connections (Friston, 2005). The internal predictive models are communicated from high-level structures to specialized low-level structures through backward connections. These backward connections have a strong modulatory effect on the functionally specialized brain areas, and can thus exert contextual constraints on the models of lower layers. Sensory information is processed through forward connections from lower to higher cortical levels, and works as driving signals. At each level the sensory information is matched to the internal predictive model. If there is a mismatch between the model and the sensory input at any level of the hierarchy, it creates a prediction error and a neuronal error-message is fed forward to higher, more integrative levels. Here the prediction error is evaluated and depending on the degree to which it violates the internal prediction, the brain can either change its internal model or it can change the way it samples information from the environment. Consequently, prediction errors are fundamental for adaptive learning. When predictions change, the connectivity between neurons is believed to change accordingly. In this way, neuron A predicts neuron B's response to a stimuli in the given context (Friston, 2005). The brain is constantly trying to optimize its internal model to correspond to the world, and thereby minimize prediction errors (Friston, 2010; Friston & Kiebel, 2009a). Thus, the minimization of prediction errors is imperative for brain function, because neuronal prediction error signals are fundamental to learning and improvement of the internal model.

Predictive coding and Bayesian principles have previously been suggested to provide a useful framework for understanding music perception (Temperley, 2007; Vuust et al., 2009; Wacongne et al., 2011). Vuust et al. describes predictive coding of rhythmic expectations in musicians and nonmusicians, whereas Wacongne et al. refines this account with a paradigm showing how predictions at different hierarchical levels work in parallel. The findings from Pearce et al. (2010) are also in accord with the predictive coding approach; the initial neuronal error message followed by synchronized activity in various brain areas in response to low-probability sequences corresponds to a local prediction error at a low hierarchical level, whereas the following synchronization across various brain areas could represent the integration of new information into the models at higher hierarchical layers. Because predictions are fundamental to both music perception and pleasure, we here argue that these are interrelated, but few, if any, have extended the predictive coding approach to pleasure processing. However, in the following section, we aim to show how dopamine neurons in the midbrain seem to adhere to the rules described in predictive coding theory, and thus how musical pleasure is tightly linked to the anticipatory interplay between the musical input and the listener's expectations (see Figure 3).



*Figure 3.* Bayesian predictive coding framework for investigating music in the brain. Music listening takes place in a dynamic interplay between anticipatory structures in music and the predictive brain on the other. The real time brain model is dependent on cultural background, personal listening history, musical competence, context, brain state (including attentional state and mood), and innate biological factors. Our hypothesis suggests that the brain is constantly trying to minimize the discrepancy between its interpretation model and the musical input by iteratively updating the real time brain model (or prior) by weighting this model with the likelihood (musical input) through Bayes' theorem. A color version of this figure is available as supplemental material at: <http://dx.doi.org/10.1037/a0031126.supp>.

### The Role of Dopamine Neurons in Anticipation

The fact that pleasurable music listening elicits activity in the dopaminergic reward system has led researchers to assume a direct link between the pleasurable feeling and the release of dopamine. Wise, Spindler, deWit, & Gerberg (1978) were among the first to suggest that dopamine was involved in pleasure and euphoria. This suggestion was based on the observation that rats, when given neuroleptic drugs, which block dopamine, became oblivious to previously rewarding stimuli, and as a consequence ended up starving because they apparently did not find any pleasure in eating (Wise, 1982; Wise et al., 1978). However, the assumption that dopamine is the prime agent in hedonic sensations has been questioned by subsequent research showing that dopamine depletion of the striatum and the nucleus accumbens does not affect hedonic pleasure (Berridge, Venier, & Robinson, 1989). Similarly, people with Parkinson's disease, which is caused by degeneration of dopamine neurons in the midbrain, show no signs of decreased pleasure from sweet tastes compared to healthy controls (Sienkiewicz-Jarosz et al., 2005). This has generated renewed assumptions about the role of dopamine in reward, namely that dopamine is associated with the anticipation of reward (the wanting phase) and coding of prediction errors (the learning phase), rather than with the reward or liking in itself. Thus, dopamine is more related to wanting and learning, than the feeling of pleasure per se (Berridge & Kringelbach, 2008).

Different dopaminergic neuron populations are now believed to be involved in reward anticipation and registration of prediction errors (Schultz, 2010), suggesting that dopaminergic neurons play a key role in the different phases of the pleasure cycle. Dopaminergic neurons show two types of firing, slow changing tonic activations and fast trains of synchronous phasic burst firing (Joshua et al., 2009). These types of firing and their effect on different dopaminergic receptors are supporting the formation of reward anticipations and the registration of prediction errors following failed anticipations.

### Reward Anticipation

Using a conditioned stimulus paradigm with macaque monkeys, Schultz et al. (Schultz, Apicella, Scarnati, & Ljungberg, 1992) showed that dopaminergic neurons in the midbrain fire even before the reward is delivered. Consequently, when reward associations are reinforced, dopaminergic neurons respond to events predicting reward but not to the actual rewarding stimuli (Schultz, 1998). Dopaminergic neurons have been found to fire in anticipation of reward regardless of the nature of the reward (Schultz, 2000, 2002). The anticipatory firing of dopaminergic neurons do not only represent the expectation of "a reward," but they also represent how good the reward is likely to be (expected reward value, [Tobler, Fiorillo, & Schultz, 2005]), how likely the reward is to occur (reward probability; [Fiorillo, Tobler, & Schultz, 2003]), and when the reward is expected to occur (Hollerman & Schultz, 1998). Likewise, the ambiguity or reward variance is also registered by dopaminergic neurons (Burke & Tobler, 2011). So, specific neuron populations in the striatum and the orbitofrontal cortex seem to selectively code for specific aspects of anticipation, either magnitude, time of delivery, probability, or uncertainty (see Figure 4). Dopaminergic pathways from the striatum to the orbitofrontal cortex and the posterior cingulate cortex show sustained

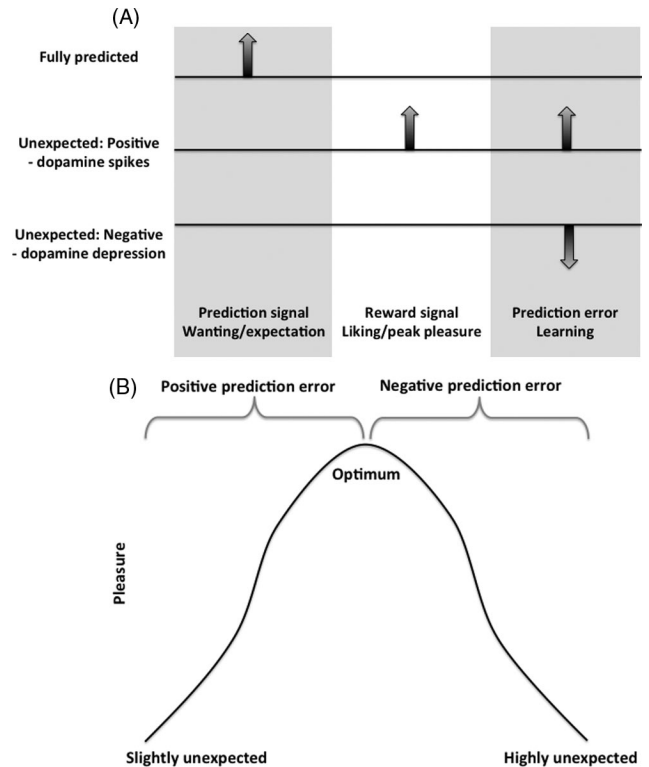


Figure 4. Dopamine signals and optimal unpredictability. (A) A stylized representation of the hypothesized dopamine signal during the musical pleasure cycle. Arrows indicate the direction of the dopamine signal increase or decrease. (B) Positive and negative prediction errors follow the inverted U-curve, so that highly unexpected musical structures result in a negative prediction error manifest as a dopamine depression, while optimally predictable/unpredictable musical structures result both in a reward signal and a positive prediction error leading to increased dopamine release. A color version of this figure is available as supplemental material at: <http://dx.doi.org/10.1037/a0031126.suppl>.

dopamine firing in response to increased uncertainty, leading to improved learning. Reward anticipation and monitoring is not a fixed process, but it continually adapts to the incoming information (Nomoto, Schultz, Watanabe, & Sakagami, 2010).

### Prediction Errors

When anticipations are incorrect, this results in a prediction error. Prediction errors reflected in the activity of dopamine neurons are bidirectional (Schultz, 2002, 2010), in the sense that positive events result in increased firing and negative events result in decreased firing. The registration of prediction errors and adjustment of predictions seem to be modulated by the mesocortical dopaminergic pathway (see Figure 2). Dopamine might further contribute to the update of expectations through its involvement in learning-dependent synaptic plasticity (Lisman & Grace, 2005). The orbitofrontal cortex is found to code outcome expectations and update these during learning (Schoenbaum, Roesch, Stalnaker, & Takahashi, 2009; Walton, Behrens, Buckley, Rudebeck, & Rushworth, 2010). Results from rats and monkeys indicate that the amygdala (especially the basolateral part) is involved in coding



predictive relations between stimuli and rewards, or more precisely updating reward estimations in the face of changing conditions (Murray & Izquierdo, 2007). The amygdala also projects to the orbitofrontal cortex, where the new adjusted reward estimation seems to be stored. The dopamine signal is probably the most well-characterized of neuronal activations in brain structures associated with goal-directed behaviors (Schultz, 2010).

### The Potential Role of Dopamine in Musical Anticipation and Learning

We propose that similar dopaminergic mechanisms as those associated with anticipation and registration of prediction errors for other rewards (reviewed above), account for the association between musical anticipation and pleasure. Ideas like these have previously been alluded to in Gebauer and Vuust (2010) and Zald and Zatorre (2011).

Music is, however, not a concrete reward like money or food rewards, where value or magnitude can be calculated exactly. So, how is music transferred into these reward-coding dopaminergic neurons? It was recently found that the majority (60%–90%) of dopaminergic neurons also show burst responses to different types of sensory events that are not directly associated with rewarding stimuli (Bromberg-Martin, Matsumoto, & Hikosaka, 2010; Horvitz, 2000). These responses are suggested to depend on a number of neural and psychological factors, including direct sensory input, surprise, novelty, arousal, attention, salience, generalization, and pseudoconditioning (Berridge, 2007; Horvitz, 2000; Redgrave & Gurney, 2006; Redgrave, Prescott, & Gurney, 1999; Schultz, 1998, 2010). An underlying *alerting signal* or *incentive salience* has been proposed to be the cause of these burst responses by dopaminergic neurons to sensory events (Berridge, 2007; Bromberg-Martin et al., 2010; Schultz, 1998). Sensory information is believed to be projected through the superior/inferior colliculus to the dopaminergic neurons in the midbrain (substantianigra comparta and VTA), where the alerting signals are found (Redgrave & Gurney, 2006). Alerting/salience signals are manifest in reward-coding dopaminergic neurons, and are suggested to regulate brain processing and behavior in the same way as reward signals (Berridge, 2007; Bromberg-Martin et al., 2010). Incentive salience was first described by Berridge (2003, 2007) as a wanting or motivation to engage in specific activities (e.g., music listening). This is in accordance with Bromberg-Martin et al.'s (2010) description of alerting signals as caused by a sensory cue that captures attention based on rapid assessment of its potential importance, using simple features such as its localization, size, intensity, and sensory modality. Alerting signals occur in response to sensory input that have to be examined to determine their meaning or that have the potential to provide information about rewarding or salient events.

This can also be applied to the perceptual features of music. Within music, there is constant change of minor elements, which may or may not catch our attention and engage our brain in a search for meaning (Vuust & Kringelbach, 2010). Alerting signals to sounds are indeed generated by dopaminergic neurons (Strecker, Steinfels, Abercrombie, & Jacobs, 1985). As with the reward signal, the alerting signal is reduced (but not absent) if the sensory input is fully predicted (see Figure 4 [Schultz, 1998; Steinfels, Heym, Strecker, & Jacobs, 1983; Strecker et al., 1985; Takikawa, Kawagoe, & Hikosaka, 2004]). Thus, the predictive coding model

of musical anticipations and the hypotheses about how music elicits dopamine release by establishing, fulfilling, and disappointing these expectations appears to correspond well with the firing patterns seen in dopaminergic neurons.

Like reward signals, alert signals seem to be projected to the ventromedial and orbitofrontal cortex (Porrino & Goldman-Rakic, 1982; Williams & Goldman-Rakic, 1998). Accordingly, Bromberg-Martin et al. argue that alerting events can be assigned positive value and be sought after in a manner similar to rewards. Consequently, with regard to music, the listener's expectations of the musical structure may be represented by small dopaminergic neuron populations in the midbrain, such that dopaminergic neurons fire more extensively when we anticipate a particular sequence of notes in a melody, or at a higher level maybe a harmonic structure or the instrumentation. In addition to this, because dopaminergic neurons are known to code the timing of predicted rewards quite accurately (Hollerman & Schultz, 1998), dopaminergic neurons may also represent the expected temporal sequencing of the musical structure, that is, the meter and rhythm.

Correspondingly, the change in the musical pleasure cycle from anticipation to liking is likely to be mediated by dopaminergic neurons representing information about the probability of the listener's musical predictions. When the actual musical structure is revealed to the listener, the expectations represented by the dopaminergic neurons can either be fulfilled or violated. This is analogous to the idea that music can be pleasurable when it fulfills expectations as well as when it violates them (Huron, 2006). Violated expectations give rise to prediction errors, and on the neurobiological level, these prediction errors are registered by dopaminergic neurons. In response to a prediction error, dopaminergic neurons will increase their firing in response to a stimulus, which is better than expected, show unchanged firing if the stimulus corresponds to the anticipations and show a depression of the neuronal activity if the stimulus is worse than predicted (see Figure 4A [Schultz, 2010]). The concepts of "better" or "worse" may seem somewhat artificial in relation to music. We would argue that better corresponds to "close to optimal" complexity in the terms of the Wundt curve, whereas "worse" corresponds to a level of complexity that deviates in either direction from this optimal point (see Figure 4B). Thus, musical violations can be either positive or negative, and give rise to pleasure or aversion. If expectations on all hierarchical levels are violated, this will probably be experienced as very unpleasant, whereas subtle violations of one stream of expectations, that is, melody, phrase structure, harmony, key, meter, or rhythm, might just create the kind of tension that gives rise to pleasure. This is an example of why musical surprises might create pleasure in the listener.

Accordingly, when anticipations are violated dopaminergic neurons show both an anticipatory response and a response in relation to the prediction error. Correct prediction, on the contrary, is only accompanied by an anticipatory response. Because the dopamine spike, in response to fully predicted rewards occurs before the actual reward delivery, it seems unlikely that dopamine directly is causing the pleasurable experience. Equally, correct prediction of the musical structure is probably only associated with an anticipatory dopamine release, and thus the pleasure experienced from the music may not be directly related to the dopamine release. It could still be argued that the dopamine spike in response to prediction errors gives rise to the pleasure we experience from

music and hence only musical structures which fail to meet expectations are experienced as pleasurable. However, we know that familiarity usually increases liking for music, thus there seems to be an optimal balance between predictability and unpredictability when it comes to pleasurable responses to music. Correspondingly, music that is highly ambiguous, such as for instance jazz or other improvisational music, should give rise to a sustained dopamine firing. This can be suggested to lead to a quantitatively bigger dopamine release and heightened attention. Thus, many people will experience music that manages to play with this ambiguity as more interesting and more pleasurable.

To sum up, most aspects of the proposed model still need to be tested experimentally. The hypotheses that could be derived from this model are:

(1) The three phases of the musical pleasure cycle (wanting/expectation, liking, and learning) can be identified in behavior and neural activity, as well as in music theoretic and computational models of music perception.

(2) Music has features that result in the activation of alert/incentive salience signaling dopaminergic neurons in the midbrain. Relatively little is known about which events or features are registered as important or alerting, but we suggest that music may indeed be an example of a collection of sound features to which the brain subscribes perceptual salience and thus responds to with alert signals. However, this should be confirmed experimentally to verify which sound features are essential for evoking such alert signals. Indeed, music might be a valuable tool for further investigation of alert signals in the human dopamine system.

(3) Dopaminergic neurons represent aspects of the phases of musical wanting/anticipation and musical learning, but not directly of the phase of music liking, which is probably more associated with opioids and endo-cannabinoids (which we note are contrary to Salimpoor et al.'s [2011] interpretation of their data). The neural foundation of the three phases of the pleasure cycle needs to be investigated more thoroughly with respect to the differential effects of wanting/anticipation, liking, and learning, and the influence of neurotransmitters besides dopamine.

(4) Musical anticipations are hierarchically organized; they are based on prior experiences but are still highly context-sensitive. Dopaminergic neurons represent musical anticipations according to statistical regularities learned through musical exposure. At the moment there are several methodological constraints on testing whether musical anticipations are coded by midbrain dopaminergic neurons in the same way as anticipations about other rewards or alerting signals. The *in vivo* firing of dopaminergic neurons is usually measured using single-cell electrophysiological recording. This is an invasive method and experimental recordings have mostly been obtained in animals. Because animals seemingly do not experience pleasure comparable with the human music experience (Haznedar et al., 2005; McDermott & Hauser, 2007), it seems implausible that an animal model will be able to resolve this question. A potential avenue for measuring firing of dopaminergic neurons directly is in patients with deep-brain stimulation in the midbrain. In the first few days postoperatively, parts of the implanted electrodes are still externalized through the skull, and direct measurement from neuronal populations in the midbrain can be acquired. We acknowledge, however, that it may be difficult to generalize findings about music and reward processing in patients to neurologically normal controls. The rapid development of MEG

equipment and analysis methods allowing the recording of neuronal activity in midbrain structures with millisecond precision may also provide a fruitful method for investigating this issue.

(5) There is an association between the dopamine signal and physiological arousal, which conforms to the Wundt curve as described by Berlyne (1971). This could, in theory, be tested experimentally using psychopharmacology (dopamine agonists and antagonists) in healthy volunteers to alter the dopamine level in the midbrain and measure physiological and behavioral responses to musical structures that vary in their predictability. An artificial musical grammar such as that developed by Loui et al. (2010) would be instrumental to eliminate the effect of individual music listening history.

(6) Failed anticipations are linked to dopaminergic anticipatory firing followed by a prediction error. There is likely to be an individual optimum for when an unanticipated musical sequence is experienced as a pleasurable surprise, resulting in increased dopamine firing and thus a higher dopamine release than a fully predicted musical sequence, and when it is too novel and results in a prediction error manifested as a depression of dopaminergic firing.

(7) Music with a high uncertainty might result in sustained dopamine firing and increased higher order neural integration as a result of learning.

(8) Following dopaminergic prediction errors (both positive and negative), the internal predictive model is updated (learning), which may be integrated across multiple areas of the brain. Musical anticipation is thus present in functionally segregated brain areas as well as higher-level integrative areas. These assumptions could be investigated in a paradigm inspired by that of Pearce and colleagues (2010).

The proposed framework for understanding musical pleasure as mediated by the anticipatory interplay between the listener's expectations and the musical structure does not, of course, apply to all instances of pleasurable music listening. This model accounts for the pleasure that has music as its direct object, but there are certainly other ways to get aesthetic enjoyment from music such as through cognitive evaluation, semantic analysis of songs or others of the mechanisms proposed by Juslin & Västfjäll (2008).

Meanwhile, it should be noted that musical anticipations are unlikely to be represented solely by the dopamine system. Musical anticipation is rather supported by brain structures in various areas of the brain, which all code for prediction errors in different domains and levels of the musical structure. Recent studies have found that coding of reward predictions is not functionally located in the dopaminergic neurons in the striatum, but are distributed across the brain (Burke & Tobler, 2011)—most significantly in the striatum, orbitofrontal cortex, amygdala, hippocampus, lateral intraparietal and anterior cingulate cortices. Interestingly these are, with the exception of the intraparietal cortex (which has been implicated in attention), the very regions that are consistently found to be active in studies of musical emotions (Koelsch, 2010).

This suggests that musical pleasure is not an isolated phenomenon, but a direct product of our expectation-guided music perception. Pleasurable responses might be seen as evaluations of how well our brain predicts the future, but not in a black or white manner where correct predictions result in pleasure and failed predictions in aversion. Rather that the pleasure cycle serves as a motivational guide, directing our attention and behavior toward

potentially rewarding stimuli. Thus, music is attributed high attentional significance by our brain because it continues to stimulate our prediction schemes, by being on the one hand highly predictable and on the other hand continually changing, resulting in minute prediction errors. These prediction errors can be at different levels at the hierarchical structure. Sometimes music creates low-level error messages such as the MMN, which are afterward overwritten by higher order predictions acquired through lifelong learning. Our higher order expectations will modulate the lower levels, probably by the backward modulation from ventromedial and orbitofrontal cortex on the dopamine system.

The anticipatory interplay between the listener's expectations and the structure provided by the music is not a one-way process with a beginning and an end but continues throughout the musical pleasure cycle. The anticipatory interplay is a continuous dynamic transaction, where new information in the musical structure continually influences the expectations of the listener and the expectations influence the perception of the subsequent music. Subsequently, the musical brain is shaped by cultural influence and training over the span of a lifetime, such that the anticipatory mechanisms guiding musical experience gradually change. This has dramatic effects on the way we experience music as evidenced by large differences between musicians and nonmusicians in brain processing of auditory stimuli (Vuust et al., 2005) and in brain structure (Chakravarty & Vuust, 2009; Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Gaser & Schlaug, 2003).

### Conclusion

The evidence from the literature shows that music is remarkably similar to other primary rewards such as food and sex with distinct phases of wanting/expectation, liking/peak pleasure, and learning (see Figure 1). Musical anticipation contributes to initiate, sustain, or terminate the different phases of the musical pleasure cycle and thus helps to optimize resource allocation of brain resources. Here we are proposing that musical anticipation, operationalized in a Bayesian predictive coding framework, is a good candidate for a key mechanism for mediating the changes of the pleasure cycle, and as such is important for an integrated model of musical perception, learning and pleasure. The predictive coding framework for musical anticipation applies both as a psychological and neurobiological theory; furthermore, the framework is not limited to music perception and pleasure but might account for perception and brain function in general. It should be acknowledged, however, that this still lacks solid experimental data to back it up, and that there are other recent music modeling efforts that target some of these questions successfully (for a review see Rohrmeier & Koelsch, 2012).

Dopamine is a key neurotransmitter for helping to guide the anticipatory interplay between the listener's expectations and the actual music as it unfolds, and as a consequence dopamine-related structures in the midbrain are active during pleasurable music listening. Music is suggested to be capable of activating the brain's reward system through alert signals. Consequently, music may be pleasurable both when the brain correctly predicts the musical structure, but probably to an even greater extent, when the musical structure is slightly unpredicted or ambiguous since this gives rise to a greater dopamine release. Music listening is pleasurable because it exploits the brain's

fundamental tendency to make predictions, and to respond to slight deviations with prediction errors, both in primary sensory areas and dopamine neurons in the midbrain. These slightly unexpected events are perceived as pleasurable because they provide a learning opportunity, and the brain rewards our engagement in these kinds of stimuli because they improve our adaptation and thus our survival. The motivational force of dopamine, directing behavior toward rewarding stimuli (Berridge & Kringelbach, 2008) and representing reward and sensory expectations (Bromberg-Martin et al., 2010), makes it a good candidate for explaining why people are so motivated to spend time listening to and performing music, and why we find it so rewarding. This may not only provide an explanation for why music is such an important factor in human life, it may also help us understand why and how music has sustained such prominence throughout our history.

### References

- Berlyne, D. E. (1971). *Aesthetics and psychobiology*. New York: Appleton-Century-Crofts.
- Berridge, K. C. (2003). Pleasures of the brain [Review]. *Brain and Cognition*, *52*, 106–128.
- Berridge, K. C. (2007). The debate over dopamine's role in reward: The case for incentive salience [Research Support, N.I.H., Extramural Research Support, Non-U.S. Gov't Review]. *Psychopharmacology (Berl)*, *191*, 391–431. doi:10.1007/s00213-006-0578-x
- Berridge, K. C., & Kringelbach, M. L. (2008). Affective neuroscience of pleasure: Reward in humans and animals. *Psychopharmacology (Berl)*, *199*, 457–480. doi:10.1007/s00213-008-1099-6
- Berridge, K. C., & Robinson, T. E. (1998). What is the role of dopamine in reward: Hedonic impact, reward learning, or incentive salience? *Brain Research. Brain Research Reviews*, *28*, 309–369. doi:10.1016/S0165-0173(98)00019-8
- Berridge, K. C., & Schulkin, J. (1989). Palatability shift of a salt-associated incentive during sodium depletion. *Quarterly Journal of Experimental Psychology B: Comparative and Physiological Psychology*, *41*, 121–138.
- Berridge, K. C., Venier, I. L., & Robinson, T. E. (1989). Taste reactivity analysis of 6-hydroxydopamine-induced aphagia: Implications for arousal and anhedonia hypotheses of dopamine function. *Behavioral Neuroscience*, *103*, 36–45. doi:10.1037/0735-7044.103.1.36
- Bharucha, J., & Krumhansl, C. L. (1983). The representation of harmonic structure in music: Hierarchies of stability as a function of context. *Cognition*, *13*, 63–102. doi:10.1016/0010-0277(83)90003-3
- Blood, A. J., & Zatorre, R. J. (2001). Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 11818–11823. doi:10.1073/pnas.191355898
- Blood, A. J., Zatorre, R. J., Bermudez, P., & Evans, A. C. (1999). Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions. *Nature Neuroscience*, *2*, 382–387. doi:10.1038/7299
- Brattico, E., Pallesen, K. J., Varyagina, O., Bailey, C., Anourova, I., Jarvenpaa, M., . . . Tervaniemi, M. (2009). Neural discrimination of nonprototypical chords in music experts and laymen: An MEG study. *Journal of Cognitive Neuroscience*, *21*, 2230–2244. doi:10.1162/jocn.2008.21144
- Brattico, E., Tervaniemi, M., Naatanen, R., & Peretz, I. (2006). Musical scale properties are automatically processed in the human auditory cortex. *Brain Research*, *1117*, 162–174. doi:10.1016/j.brainres.2006.08.023



- Bromberg-Martin, E. S., Matsumoto, M., & Hikosaka, O. (2010). Dopamine in motivational control: Rewarding, aversive, and alerting. *Neuron*, 68, 815–834. doi:10.1016/j.neuron.2010.11.022
- Brown, H., & Friston, K. J. (2012). Free-energy and illusions: The corn-sweet effect. *Front Psychol*, 3, 43. doi:10.3389/fpsyg.2012.00043
- Brown, S., Martinez, M. J., & Parsons, L. M. (2004). Passive music listening spontaneously engages limbic and paralimbic systems. *Neuroreport*, 15, 2033–2037. doi:10.1097/00001756-200409150-00008
- Bubic, A., von Cramon, D. Y., & Schubotz, R. I. (2010). Prediction, cognition and the brain. *Frontiers in Human Neuroscience*, 4, 25. doi:10.3389/fnhum.2010.00025
- Burke, C. J., & Tobler, P. N. (2011). Coding of reward probability and risk by single neurons in animals. *Front Neuroscience*, 5, 121. doi:10.3389/fnins.2011.00121
- Cabanac, M. (2010). The dialectics of pleasure. In K. C. B. M. L. Kringsbach (Ed.), *Pleasures of the brain*. Oxford, UK: Oxford University Press.
- Chakravarty, M. M., & Vuust, P. (2009). Musical morphology. *Annals of the New York Academy of Sciences*, 1169, 79–83. doi:10.1111/j.1749-6632.2009.04780.x
- Corrigall, K. A., & Trainor, L. (2009). Effects of musical training on key and harmony perception. *Annals of the New York Academy of Sciences*, 1169, 164–168.
- Darwin, C. (1872). *The expression of the emotions in man and animals*. London: J. Murray. doi:10.1037/10001-000
- Demorest, S. M., & Osterhout, L. (2012). ERP responses to cross-cultural melodic expectancy violations. *Annals of the New York Academy of Sciences*, 1252, 152–157. doi:10.1111/j.1749-6632.2012.06464.x
- Drake, C., & Ben El Heni, J. (2003). Synchronizing with music: Intercultural differences. *Annals of the New York Academy of Sciences*, 999, 429–437. doi:10.1196/annals.1284.053
- Dubé, L., & Lebel, J. (2003). The categorical structure of pleasure. *Cognition and Emotion*, 17, 263–297.
- Edwards, M. J., Adams, R. A., Brown, H., Parees, I., & Friston, K. J. (In press). A bayesian account of ‘hysteria’. *Brain*. doi:10.1093/brain/aw129
- Eerola, T. (2003). *The dynamics of musical expectancy: Cross-cultural and statistic approaches to melodic expectation* (PhD thesis). University of Jyväskylä, Finland.
- Elbert, T., Pantev, C., Wienbruch, C., Rockstroh, B., & Taub, E. (1995). Increased cortical representation of the fingers of the left hand in string players. *Science*, 270, 305–307. doi:10.1126/science.270.5234.305
- Finlayson, G., King, N., & Blundell, J. E. (2007). Liking vs. wanting food: Importance for human appetite control and weight regulation. *Neuroscience and Biobehavioral Reviews*, 31, 987–1002. doi:10.1016/j.neubiorev.2007.03.004
- Fiorillo, C. D., Tobler, P. N., & Schultz, W. (2003). Discrete coding of reward probability and uncertainty by dopamine neurons. *Science*, 299, 1898–1902. doi:10.1126/science.1077349
- Fitch, W. T. (2005). The evolution of music in comparative perspective. *Annals of the New York Academy of Sciences*, 1060, 29–49. doi:10.1196/annals.1360.004
- Frijda, N. H. (2010). Impulsive action and motivation. *Biological Psychology*, 84, 570–579. doi:10.1016/j.biopsycho.2010.01.005
- Friston, K. (2002a). Beyond phrenology: What can neuroimaging tell us about distributed circuitry? *Annual Review of Neuroscience*, 25, 221–250. doi:10.1146/annurev.neuro.25.112701.142846
- Friston, K. (2002b). Functional integration and inference in the brain. *Progress in Neurobiology*, 68, 113–143. doi:10.1016/S0301-0082(02)00076-X
- Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, 360, 815–836. doi:10.1098/rstb.2005.1622
- Friston, K. (2009). The free-energy principle: A rough guide to the brain? *Trends in Cognitive Science*, 13, 293–301. doi:10.1016/j.tics.2009.04.005
- Friston, K. (2010). The free-energy principle: A unified brain theory? *Nature Reviews Neuroscience*, 11, 127–138. doi:10.1038/nrn2787
- Friston, K., & Kiebel, S. (2009a). Predictive coding under the free-energy principle. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 364, 1211–1221. doi:10.1098/rstb.2008.0300
- Friston, K., & Kiebel, S. (2009b). Predictive coding under the free-energy principle. *Philosophical transactions of the Royal Society of London Series B, Biological sciences*, 364, 1211–1221. doi:10.1098/rstb.2008.0300
- Friston, K. J., Shiner, T., FitzGerald, T., Galea, J. M., Adams, R., Brown, H., . . . Bestmann, S. (2012). Dopamine, affordance and active inference. *PLoS Computational Biology*, 8, e1002327. doi:10.1371/journal.pcbi.1002327
- Fujioka, T., Trainor, L. J., Ross, B., Kakigi, R., & Pantev, C. (2004). Musical training enhances automatic encoding of melodic contour and interval structure. *Journal of Cognitive Neuroscience*, 16, 1010–1021. doi:10.1162/0898929041502706
- Garza Villarreal, E. A., Brattico, E., Leino, S., Ostergaard, L., & Vuust, P. (2011). Distinct neural responses to chord violations: A multiple source analysis study. *Brain Research*, 1389, 103–114. doi:10.1016/j.brainres.2011.02.089
- Gaser, C., & Schlaug, G. (2003). Gray matter differences between musicians and nonmusicians. *Annals of the New York Academy of Sciences*, 999, 514–517. doi:10.1196/annals.1284.062
- Gebauer, L., & Vuust, P. (2010). The rewards of music listening: The role of midbrain dopamine in musical anticipation. *ICMPC11 Conference Proceedings*, Seattle, August 2010.
- Georgiadis, J. R., & Kringsbach, M. L. (2012). The human sexual response cycle: Brain imaging evidence linking sex to other pleasures. *Progress in Neurobiology*, 98, 49–81. doi:10.1016/j.pneurobio.2012.05.004
- Gottfried, J. A., O’Doherty, J., & Dolan, R. J. (2003). Encoding predictive reward value in human amygdala and orbitofrontal cortex. *Science*, 301, 1104–1107. doi:10.1126/science.1087919
- Green, A. C., Baerentsen, K. B., Stodkilde-Jorgensen, H., Roepstorff, A., & Vuust, P. (2012). Listen, learn, like! Dorsolateral prefrontal cortex involved in the mere exposure effect in music. *Neurology Research International*, 2012, 846270. doi:10.1155/2012/846270
- Grewe, O., Nagel, F., Kopiez, R., & Altenmuller, E. (2005). How does music arouse “chills”? Investigating strong emotions, combining psychological, physiological, and psychoacoustical methods. *Annals of the New York Academy of Sciences*, 1060, 446–449. doi:10.1196/annals.1360.041
- Haznedar, M. M., Roversi, F., Pallanti, S., Baldini-Rossi, N., Schnur, D. B., Licalzi, E. M., . . . Buchsbaum, M. S. (2005). Fronto-thalamostriatal gray and white matter volumes and anisotropy of their connections in bipolar spectrum illnesses. *Biological Psychiatry*, 57, 733–742. doi:10.1016/j.biopsycho.2005.01.002
- Heyduk, R. (1975). Rated preference for musical compositions as it relates to complexity and exposure frequency. *Perception & Psychophysics*, 17, 84–90. doi:10.3758/BF03204003
- Hohwy, J. (2012). Attention and conscious perception in the hypothesis testing brain. *Front Psychol*, 3, 96. doi:10.3389/fpsyg.2012.00096
- Hohwy, J., Roepstorff, A., & Friston, K. (2008). Predictive coding explains binocular rivalry: An epistemological review. *Cognition*, 108, 687–701. doi:10.1016/j.cognition.2008.05.010



- Hollerman, J. R., & Schultz, W. (1998). Dopamine neurons report an error in the temporal prediction of reward during learning. *Nature Neuroscience*, *1*, 304–309. doi:10.1038/1124
- Horvitz, J. C. (2000). Mesolimbocortical and nigrostriatal dopamine responses to salient non-reward events [review]. *Neuroscience*, *96*, 651–656. doi:10.1016/S0306-4522(00)00019-1
- Huang, G. (2008). Is this a unified theory of the brain? *New Scientist*, *2658*, 30–33.
- Huron, D. (2001). Is music an evolutionary adaptation? *Annals of the New York Academy of Sciences*, *930*, 43–61. doi:10.1111/j.1749-6632.2001.tb05724.x
- Huron, D. (2003). Is music an evolutionary adaptation. In I. P. R. J. Zatorre (Ed.), *The cognitive neuroscience of music* (pp. 57–75). Oxford: Oxford University Press. doi:10.1093/acprof:oso/9780198525202.003.0005
- Huron, D. (2006). *Sweet anticipation: Music and the psychology of expectation*. Cambridge, Massachusetts: MIT Press.
- Janata, J. (1995). ERP Measures assay the degree of expectancy violation of harmonic contexts in music. *Journal of Cognitive Neuroscience*, *7*, 153–164. doi:10.1162/jocn.1995.7.2.153
- Jentschke, S., & Koelsch, S. (2009). Musical training modulates the development of syntax processing in children. *NeuroImage*, *47*, 735–744. doi:10.1016/j.neuroimage.2009.04.090
- Joshua, M., Adler, A., Prut, Y., Vaadia, E., Wickens, J. R., & Bergman, H. (2009). Synchronization of midbrain dopaminergic neurons is enhanced by rewarding events. *Neuron*, *62*, 695–704. doi:10.1016/j.neuron.2009.04.026
- Juslin, P. N., & Västfjäll, D. (2008). Emotional responses to music: The need to consider underlying mechanisms. *Behavioral and Brain Sciences*, *31*, 559–575; discussion 575–621. doi:10.1017/S0140525X08005293
- Kalivas, P. W., & Volkow, N. D. (2005). The neural basis of addiction: A pathology of motivation and choice. *American Journal of Psychiatry*, *162*, 1403–1413. doi:10.1176/appi.ajp.162.8.1403
- Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). The mirror-neuron system: A Bayesian perspective. *Neuroreport*, *18*, 619–623. doi:10.1097/WNR.0b013e3281139ed0
- Knutson, B., & Cooper, J. C. (2005). Functional magnetic resonance imaging of reward prediction. *Current Opinion in Neurology*, *18*, 411–417. doi:10.1097/01.wco.0000173463.24758.f6
- Koelsch, S. (2009). Music-syntactic processing and auditory memory: Similarities and differences between ERAN and MMN. *Psychophysiology*, *46*, 179–190. doi:10.1111/j.1469-8986.2008.00752.x
- Koelsch, S. (2010). Towards a neural basis of music-evoked emotions. *Trends in Cognitive Science*, *14*, 131–137. doi:10.1016/j.tics.2010.01.002
- Koelsch, S., Fritz, T., DY, V. C., Muller, K., & Friederici, A. D. (2006). Investigating emotion with music: An fMRI study. *Human Brain Mapping*, *27*, 239–250. doi:10.1002/hbm.20180
- Koelsch, S., Fritz, T., & Schlaug, G. (2008). Amygdala activity can be modulated by unexpected chord functions during music listening. *Neuroreport*, *19*, 1815–1819. doi:10.1097/WNR.0b013e32831a8722
- Koelsch, S., Gunter, T., Friederici, A. D., & Schroger, E. (2000). Brain indices of music processing: “nonmusicians” are musical. *Journal of Cognitive Neuroscience*, *12*, 520–541. doi:10.1162/089892900562183
- Koelsch, S., & Jentschke, S. (2008). Short-term effects of processing musical syntax: An ERP study. *Brain Research*, *1212*, 55–62. doi:10.1016/j.brainres.2007.10.078
- Koelsch, S., Jentschke, S., Sammler, D., & Mietschen, D. (2007). Untangling syntactic and sensory processing: An ERP study of music perception. *Psychophysiology*, *44*, 476–490. doi:10.1111/j.1469-8986.2007.00517.x
- Koelsch, S., & Mulder, J. (2002). Electric brain responses to inappropriate harmonies during listening to expressive music. *Clinical Neurophysiology*, *113*, 862–869. doi:10.1016/S1388-2457(02)00050-0
- Kringelbach, M. L. (2005). The human orbitofrontal cortex: Linking reward to hedonic experience. *Nature Reviews Neuroscience*, *6*, 691–702. doi:10.1038/nrn1747
- Kringelbach, M. L. (2010). *The hedonic brain: A functional neuroanatomy of human pleasure*. Oxford, UK: Oxford University Press.
- Kringelbach, M. L., & Berridge, K. C. (2009). Towards a functional neuroanatomy of pleasure and happiness. *Trends in Cognitive Science*, *13*, 479–487. doi:10.1016/j.tics.2009.08.006
- Kringelbach, M. L., & Berridge, K. C. (2010a). The functional neuroanatomy of pleasure and happiness. *Discovery Medicine*, *9*, 579–587.
- Kringelbach, M. L., & Berridge, K. C. (2010b). The neuroscience of happiness and pleasure. *Social Research*, *77*, 659–678.
- Kringelbach, M. L., O’Doherty, J., Rolls, E. T., & Andrews, T. (2003). Activation of the human orbitofrontal cortex to a liquid food stimulus is correlated with its subjective pleasantness. *Cerebral Cortex*, *13*, 1064–1071. doi:10.1093/cercor/13.10.1064
- Kringelbach, M. L., Stein, A., & van Hartevelt, T. J. (2012). The functional human neuroanatomy of food pleasure cycles. *Physiology and Behavior*, *106*, 307–316. doi:10.1016/j.physbeh.2012.03.023
- Krumhansl, C. L. (1991). Music psychology: tonal structures in perception and memory. *Annual Review of Psychology*, *42*, 277–303. doi:10.1146/annurev.ps.42.020191.001425
- Krumhansl, C. (1995). Music psychology and music theory: Problems and prospects. *Music Theory Spectrum*, *17*, 53–80. doi:10.2307/745764
- Krumhansl, C. (2002). Music: A link between cognition and emotion. *Current Directions in Psychological Science*, *11*, 45–50.
- Krumhansl, C. L., Bharucha, J., & Castellano, M. A. (1982). Key distance effects on perceived harmonic structure in music. *Perception and Psychophysics*, *32*, 96–108. doi:10.3758/BF03204269
- Krumhansl, C. L., & Keil, F. C. (1982). Acquisition of the hierarchy of tonal functions in music. *Memory and Cognition*, *10*, 243–251. doi:10.3758/BF03197636
- Krumhansl, C. L., Toivanen, P., Eerola, T., Toivainen, P., Jarvinen, T., & Louhivuori, J. (2000). Cross-cultural music cognition: Cognitive methodology applied to North Sami yoiks. *Cognition*, *76*, 13–58. doi:10.1016/S0010-0277(00)00068-8
- Leino, S., Brattico, E., Tervaniemi, M., & Vuust, P. (2007). Representation of harmony rules in the human brain: Further evidence from event-related potentials. *Brain Research*, *1142*, 169–177. doi:10.1016/j.brainres.2007.01.049
- Lisman, J. E., & Grace, A. A. (2005). The hippocampal-VTA loop: Controlling the entry of information into long-term memory. *Neuron*, *46*, 703–713. doi:10.1016/j.neuron.2005.05.002
- Lou, H. C., Joansson, M., & Kringelbach, M. L. (2011). Yoga lessons for consciousness research: A paralimbic network balancing brain resource allocation. *Front Psychol*, *2*, 366. doi:10.3389/fpsyg.2011.00366
- Loui, P., Grent-t-Jong, T., Torpey, D., & Woldorff, M. (2005). Effects of attention on the neural processing of harmonic syntax in Western music. *Brain Research. Cognitive Brain Research*, *25*, 678–687. doi:10.1016/j.cogbrainres.2005.08.019
- Loui, P., Wessel, D. L., & Hudson Kam, C. L. (2010). Humans rapidly learn grammatical structure in a new musical scale. *Music Percept*, *27*, 377–388. doi:10.1525/mp.2010.27.5.377
- Maess, B., Koelsch, S., Gunter, T. C., & Friederici, A. D. (2001). Musical syntax is processed in Broca’s area: An MEG study. *Neurosci*, *4*, 540–545. doi:10.1038/87502
- McDermott, J., & Hauser, M. D. (2007). Nonhuman primates prefer slow tempos but dislike music overall. *Cognition*, *104*, 654–668. doi:10.1016/j.cognition.2006.07.011

- McNamara, L., & Ballard, M. E. (1999). Resting arousal, sensation seeking, and music preference. *Genetic, Social, and General Psychology Monographs*, *125*, 229–250.
- Menon, V., & Levitin, D. J. (2005). The rewards of music listening: Response and physiological connectivity of the mesolimbic system. *NeuroImage*, *28*, 175–184. doi:10.1016/j.neuroimage.2005.05.053
- Meyer, L. B. (1956). *Emotion and meaning in music*. Chicago, IL: University of Chicago Press.
- Mitterschiffthaler, M. T., Fu, C. H., Dalton, J. A., Andrew, C. M., & Williams, S. C. (2007). A functional MRI study of happy and sad affective states induced by classical music. *Human Brain Mapping*, *28*, 1150–1162. doi:10.1002/hbm.20337
- Mobbs, D., Greicius, M. D., Abdel-Azim, E., Menon, V., & Reiss, A. L. (2003). Humor modulates the mesolimbic reward centers. *Neuron*, *40*, 1041–1048. doi:10.1016/S0896-6273(03)00751-7
- Morgan, D., Grant, K. A., Gage, H. D., Mach, R. H., Kaplan, J. R., Prioleau, O., . . . Nader, M. A. (2002). Social dominance in monkeys: Dopamine D2 receptors and cocaine self-administration. *Nature Neuroscience*, *5*, 169–174. doi:10.1038/nn798
- Murray, E. A., & Izquierdo, A. (2007). Orbitofrontal cortex and amygdala contributions to affect and action in primates. *Annals of the New York Academy of Sciences*, *1121*, 273–296. doi:10.1196/annals.1401.021
- Nätänen, R., Paavilainen, P., Rinne, T., & Alho, K. (2007). The mismatch negativity (MMN) in basic research of central auditory processing: A review. *Clinical Neurophysiology*, *118*, 2544–2590. doi:10.1016/j.clinph.2007.04.026
- Naatanen, R., Teder, W., Alho, K., & Lavikainen, J. (1992). Auditory attention and selective input modulation: A topographical ERP study. *Neuroreport*, *3*, 493–496. doi:10.1097/00001756-199206000-00009
- Narmour, E. (1991). The top-down and bottom-up systems of musical implication: Building on Meyer's theory of emotional syntax. *Music Perception*, *9*, 1–26. doi:10.2307/40286156
- Nazimek, J. M., Hunter, M. D., & Woodruff, P. W. (2012). Auditory hallucinations: Expectation-perception model. *Medical Hypotheses*, *78*, 802–810. doi:10.1016/j.mehy.2012.03.014
- Nesse, R. M. (2002). Evolutionary biology: A basic science for psychiatry. *World Psychiatry*, *1*, 7–9.
- Nomoto, K., Schultz, W., Watanabe, T., & Sakagami, M. (2010). Temporally extended dopamine responses to perceptually demanding reward-predictive stimuli. *The Journal of Neuroscience*, *30*, 10692–10702. doi:10.1523/JNEUROSCI.4828-09.2010
- North, A. C., & Hargreaves, D. J. (1995). Subjective complexity, familiarity and liking of popular music. *Psychomusicology: Music, Mind & Brain*, *14*:77–93.
- North, A. C., & Hargreaves, D. J. (1997a). Experimental aesthetics and everyday music listening. In D. J. Hargreaves & A. C. North (Eds.), *The social psychology of music*. Oxford: Oxford University Press.
- North, A. C., & Hargreaves, D. J. (1997b). Liking, arousal potential, and the emotions expressed by music. *Scandinavian Journal of Psychology*, *38*, 45–53. doi:10.1111/1467-9450.00008
- North, A. C., & Hargreaves, D. J. (1998). Complexity, prototypicality, familiarity, and the perception of musical quality. *Psychomusicology*, *17*, 77–80. doi:10.1037/h0094058
- Orr, M. G., & Ohlsson, S. (2005). Relationship between complexity and liking as a function of expertise. *Music Perception*, *22*, 583–611. doi:10.1525/mp.2005.22.4.583
- Osuch, E. A., Bluhm, R. L., Williamson, P. C., Theberge, J., Densmore, M., & Neufeld, R. W. (2009). Brain activation to favorite music in healthy controls and depressed patients. *Neuroreport*, *20*, 1204–1208. doi:10.1097/WNR.0b013e32832f4da3
- Panksepp, J. (1998). *Affective neuroscience: The foundations of human and animal emotions*. Oxford, UK: Oxford University Press.
- Patel, A. D., Gibson, E., Ratner, J., Besson, M., & Holcomb, P. J. (1998). Processing syntactic relations in language and music: An event-related potential study. *Journal of Cognitive Neuroscience*, *10*, 717–733. doi:10.1162/089892998563121
- Pearce, M. T., Ruiz, M. H., Kapasi, S., Wiggins, G. A., & Bhattacharya, J. (2010). Unsupervised statistical learning underpins computational, behavioural, and neural manifestations of musical expectation. *NeuroImage*, *50*, 302–313. doi:10.1016/j.neuroimage.2009.12.019
- Pearce, M. T., & Wiggins, G. A. (2006). Expectation in melody: The influence of context and learning. *Music Perception*, *23*, 377–405. doi:10.1525/mp.2006.23.5.377
- Pecina, S., & Berridge, K. C. (2005). Hedonic hot spot in nucleus accumbens shell: Where do mu-opioids cause increased hedonic impact of sweetness? *Journal of Neuroscience*, *25*, 11777–11786. doi:10.1523/JNEUROSCI.2329-05.2005
- Peretz, I. (2010). Towards a neurobiology of musical emotions. In P. J. J. Sloboda (Ed.), *Handbook of music and emotion: Theory, research, applications*. Oxford: Oxford University Press.
- Peretz, I., Gaudreau, D., & Bonnel, A. M. (1998). Exposure effects on music preference and recognition. *Memory and Cognition*, *26*, 884–902. doi:10.3758/BF03201171
- Pfaus, J. G. (2009). Pathways of sexual desire. *Journal of Sexual Medicine*, *6*, 1506–1533. doi:10.1111/j.1743-6109.2009.01309.x
- Porrino, L. J., & Goldman-Rakic, P. S. (1982). Brainstem innervation of prefrontal and anterior cingulate cortex in the rhesus monkey revealed by retrograde transport of HRP. *Journal of Comparative Neurology*, *205*, 63–76. doi:10.1002/cne.902050107
- Redgrave, P., & Gurney, K. (2006). The short-latency dopamine signal: A role in discovering novel actions? *Nature Reviews Neuroscience*, *7*, 967–975. doi:10.1038/nrn2022
- Redgrave, P., Prescott, T. J., & Gurney, K. (1999). Is the short-latency dopamine response too short to signal reward error? *Trends in Neurosciences*, *22*, 146–151. doi:10.1016/S0166-2236(98)01373-3
- Rentfrow, P. J., & Gosling, S. D. (2003). The do re mi's of everyday life: The structure and personality correlates of music preferences. *Journal of Personality and Social Psychology*, *84*, 1236–1256. doi:10.1037/0022-3514.84.6.1236
- Robbins, T. W., & Everitt, B. J. (1996). Neurobehavioural mechanisms of reward and motivation. *Current Opinion in Neurobiology*, *6*, 228–236. doi:10.1016/S0959-4388(96)80077-8
- Robinson, T. E., & Berridge, K. C. (1993). The neural basis of drug craving: An incentive-sensitization theory of addiction. *Brain Research. Brain Research Reviews*, *18*, 247–291. doi:10.1016/0165-0173(93)90013-P
- Robinson, T. E., & Berridge, K. C. (2003). Addiction. *Annual Review of Psychology*, *54*, 25–53. doi:10.1146/annurev.psych.54.101601.145237
- Rohrmeier, M. A., & Koelsch, S. (2012). Predictive information processing in music cognition. A critical review. *International Journal of Psychophysiology*, *83*, 164–175. doi:10.1016/j.ijpsycho.2011.12.010
- Rolls, E. T. (2005). *Emotions explained*. Oxford: Oxford University Press. doi:10.1093/acprof:oso/9780198570035.001.0001
- Ryle, G. (1954). Pleasure. *Proceedings of the Aristotelian Society*, *28*, 135–146.
- Saffran, J. R., Aslin, R. N., & Newport, E. L. (1996). Statistical learning by 8-month-old infants. *Science*, *274*, 1926–1928. doi:10.1126/science.274.5294.1926
- Saffran, J. R., Johnson, E. K., Aslin, R. N., & Newport, E. L. (1999). Statistical learning of tone sequences by human infants and adults. *Cognition*, *70*, 27–52. doi:10.1016/S0010-0277(98)00075-4
- Salimpoor, V. N., Benovoy, M., Larcher, K., Dagher, A., & Zatorre, R. J. (2011). Anatomically distinct dopamine release during anticipation and experience of peak emotion to music. *Nature Neuroscience*, *14*, 257–262. doi:10.1038/nn.2726

- Salimpoor, V. N., Benovoy, M., Longo, G., Cooperstock, J. R., & Zatorre, R. J. (2009). The rewarding aspects of music listening are related to degree of emotional arousal. *PLoS One*, *4*, e7487. doi:10.1371/journal.pone.0007487
- Schellenberg, E. G. (1997). Simplifying the implication- realisation model of melodic expectancy. *Music Perception*, *14*, 295–318. doi:10.2307/40285723
- Schellenberg, E. G. Adachi, M., Purdy, K. T., McKinnon, M. C. (2002). Expectancy in melody: Tests of children and adults. *Journal of Experimental Psychology: General*. 2002 Dec, *131*, 511–537. doi:10.1037/0096-3445.131.4.511
- Schiavetto, A., Cortese, F., & Alain, C. (1999). Global and local processing of musical sequences: An event-related brain potential study. *Neuroreport*, *10*, 2467–2472. doi:10.1097/00001756-199908200-00006
- Schiffer, A. M., Ahlheim, C., Wurm, M. F., & Schubotz, R. I. (2012). Surprised at all the entropy: Hippocampal, caudate and midbrain contributions to learning from prediction errors. *PLoS One*, *7*, e36445. doi:10.1371/journal.pone.0036445
- Schoenbaum, G., Roesch, M. R., Stalnaker, T. A., & Takahashi, Y. K. (2009). A new perspective on the role of the orbitofrontal cortex in adaptive behaviour. *Nature Reviews Neuroscience*, *10*, 885–892. doi:10.1038/nrn2753
- Schulkin, J. (2004). *Allotaxis, homeostasis, and the costs of physiological adaptation*. New York: Cambridge University Press.
- Schultz, W. (1998). Predictive reward signal of dopamine neurons. *Journal of Neurophysiology*, *80*, 1–27.
- Schultz, W. (2000). Multiple reward signals in the brain. *Nat Rev Neurosci*, *1*, 199–207. doi:10.1038/35044563
- Schultz, W. (2002). Getting formal with dopamine and reward. *Neuron*, *36*, 241–263. doi:10.1016/S0896-6273(02)00967-4
- Schultz, W. (2010). Dopamine signals for reward value and risk: Basic and recent data. *Behavioral and Brain Function*, *6*, 24. doi:10.1186/1744-9081-6-24
- Schultz, W., Apicella, P., Scarnati, E., & Ljungberg, T. (1992). Neuronal activity in monkey ventral striatum related to the expectation of reward. *Journal of Neuroscience*, *12*, 4595–4610.
- Seth, A. K., S. K., Critchley, H. D. (2011). An interoceptive predictive coding model of conscious presence. *Frontiers in Psychology*, *2*, 395.
- Sienkiewicz-Jarosz, H., Scinska, A., Kuran, W., Ryglewicz, D., Rogowski, A., Wrobel, E., . . . Bienkowski, P. (2005). Taste responses in patients with Parkinson's disease. *Journal of Neurology Neurosurg Psychiatry*, *76*, 40–46. doi:10.1136/jnnp.2003.033373
- Sloboda. (1991). Music structure and emotional response: Some empirical findings. *Psychology of Music*, *19*, 112–120.
- Stalinski, S. M., & Schellenberg, E. G. (2010). Shifting perceptions: Developmental changes in judgments of melodic similarity. *Developmental Psychology*. 2010, *46*, 1799–1803. doi:10.1037/a0020658
- Stalinski, S. M., Schellenberg, E. G., & Trehub, S. E. (2008). Developmental changes in the perception of pitch contour: Distinguishing up from down. *Journal of the Acoustical Society of America*, *124*, 1759–63. doi:10.1121/1.2956470
- Stefano, G. B., Zhu, W., Cadet, P., Salamon, E., & Mantione, K. J. (2004). Music alters constitutively expressed opiate and cytokine processes in listeners. *Medical Science Monitor*, *10*, MS18–27.
- Steinbeis, N., Koelsch, S., & Sloboda, J. A. (2006). The role of harmonic expectancy violations in musical emotions: Evidence from subjective, physiological, and neural responses. *Journal of Cognitive Neuroscience*, *18*, 1380–1393. doi:10.1162/jocn.2006.18.8.1380
- Steinfels, G. F., Heym, J., Strecker, R. E., & Jacobs, B. L. (1983). Response of dopaminergic neurons in cat to auditory stimuli presented across the sleep-waking cycle. *Brain Research*, *277*, 150–154. doi:10.1016/0006-8993(83)90917-4
- Strecker, R. E., Steinfels, G. F., Abercrombie, E. D., & Jacobs, B. L. (1985). Caudate unit activity in freely moving cats: Effects of phasic auditory and visual stimuli. *Brain Research*, *329*:350–353. doi:10.1016/0006-8993(85)90548-7
- Suzuki, M., Okamura, N., Kawachi, Y., Tashiro, M., Arao, H., Hoshishiba, T., Gyoba, J., & Yanai, K. (2009). Discrete cortical regions associated with the musical beauty of major and minor chords. *Cognitive Affective and Behavioral Neuroscience*, *8*, 126–131. doi:10.3758/CABN.8.2.126
- Takikawa, Y., Kawagoe, R., & Hikosaka, O. (2004). A possible role of midbrain dopamine neurons in short- and long-term adaptation of saccades to position-reward mapping. *Journal of Neurophysiology*, *92*, 2520–2529. doi:10.1152/jn.00238.2004
- Tan, S. L., Sackman, M. P., Peaslee, C. L. (2006). The effects of repeated exposure on liking and judgment of intact and patchwork compositions. *Music Perception*, *23*, 407–421. doi:10.1525/mp.2006.23.5.407
- Temperley, D. (2007). *Music and probability*. Cambridge, Massachusetts: MIT Press.
- Tervaniemi, M., Tupala, T., & Brattico, E. (2012). Expertise in folk music alters the brain processing of Western harmony. *Annals of the New York Academy of Sciences*, *1252*, 147–151. doi:10.1111/j.1749-6632.2011.06428.x
- Tillmann, B. (2005). Implicit investigations of tonal knowledge in non-musical listeners. *Annals of the New York Academy of Sciences*, *1060*, 100–110. doi:10.1196/annals.1360.007
- Tindell, A. J., Smith, K. S., Pecina, S., Berridge, K. C., & Aldridge, J. W. (2006). Ventral pallidum firing codes hedonic reward: When a bad taste turns good. *Journal of Neurophysiology*, *96*, 2399–2409. doi:10.1152/jn.00576.2006
- Tobler, P. N., Fiorillo, C. D., & Schultz, W. (2005). Adaptive coding of reward value by dopamine neurons. *Science*, *307*, 1642–1645. doi:10.1126/science.1105370
- Toivianen, P., & Krumhansl, C. L. (2003). Measuring and modeling real-time responses to music: The dynamics of tonality induction. *Perception*, *32*, 741–766. doi:10.1068/p3312
- Trainor, L. J., McDonald, K. L., & Alain, C. (2002). Automatic and controlled processing of melodic contour and interval information measured by electrical brain activity. *Journal of Cognitive Neuroscience*, *14*, 430–442. doi:10.1162/089892902317361949
- Vuust, P., Brattico, E., Glerean, E., Seppänen, M., Pakarinen, S., Tervaniemi, M., & Naatanen, R. (2011). New fast mismatch negativity paradigm for determining the neural prerequisites for musical ability. *Cortex*, *47*, 1091–1098. doi:10.1016/j.cortex.2011.04.026
- Vuust, P., Brattico, E., Seppänen, M., Naatanen, R., & Tervaniemi, M. (2012). The sound of music: Differentiating musicians using a fast, musical multi-feature mismatch negativity paradigm. *Neuropsychologia*, *50*, 1432–1443. doi:10.1016/j.neuropsychologia.2012.02.028
- Vuust, P., & Frith, C. (2008). Anticipation is the key to understanding music and the effects of music on emotion. *Behavioral and Brain Sciences*, *31*, 599–600.
- Vuust, P., Gebauer, L., Hansen, N. C., Jørgensen, S. R., Moeller, A., & Linnet, J. (2010). Personality influences career choice: Sensation seeking in professional musicians. *Music Education Research*, *12*, 219–230. doi:10.1080/14613801003746584
- Vuust, P., Kringselbach, L. M. (2010). The pleasure of making sense of music. *Interdisciplinary science reviews*, *35*, 166–182. doi:10.1179/030801810X12723585301192
- Vuust, P., & Kringselbach, M. L. (2010). The pleasure of music. In M. L. Kringselbach & K. C. Berridge (Eds.), (2010). *Pleasures of the brain* (p. 255–269). Oxford: Oxford University Press.
- Vuust, P., Ostergaard, L., Pallesen, K. J., Bailey, C., & Roepstorff, A. (2009). Predictive coding of music–brain responses to rhythmic incongruity. *Cortex*, *45*, 80–92. doi:10.1016/j.cortex.2008.05.014



- Vuust, P., Pallesen, K. J., Bailey, C., van Zuijen, T. L., Gjedde, A., Roepstorff, A., & Ostergaard, L. (2005). To musicians, the message is in the meter: pre-attentive neuronal responses to incongruent rhythm are left-lateralized in musicians. *NeuroImage*, *24*, 560–564. doi:10.1016/j.neuroimage.2004.08.039
- Wacongne, C. L. E., van Wassenhove, V., Bekinschtein, T., Naccache, L., Dehaene, S. (2011). Evidence for a hierarchy of predictions and prediction errors in human cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 20754–20759. doi:10.1073/pnas.1117807108
- Wallin, N. L., Merker, B., & Brown, S. (Eds.). (2000). *The origins of music*. Cambridge, MA: MIT Press.
- Walton, M. E., Behrens, T. E., Buckley, M. J., Rudebeck, P. H., & Rushworth, M. F. (2010). Separable learning systems in the macaque brain and the role of orbitofrontal cortex in contingent learning. *Neuron*, *65*, 927–939. doi:10.1016/j.neuron.2010.02.027
- Williams, S. M., & Goldman-Rakic, P. S. (1998). Widespread origin of the primate mesofrontal dopamine system. *Cerebral Cortex*, *8*, 321–345. doi:10.1093/cercor/8.4.321
- Winkler, I., Haden, G. P., Ladinig, O., Sziller, I., & Honing, H. (2009). Newborn infants detect the beat in music. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 2468–2471. doi:10.1073/pnas.0809035106
- Wise, R. A. (1982). Neuroleptics and operant behavior: The anhedonia hypothesis. *Behavioral and Brain Sciences*, *5*, 39–87. doi:10.1017/S0140525X00010372
- Wise, R. A., Spindler, J., deWit, H., & Gerberg, G. J. (1978). Neuroleptic-induced “anhedonia” in rats: Pimozide blocks reward quality of food. *Science*, *201*, 262–264. doi:10.1126/science.566469
- Zajonc, R. B., Shaver, P., Tavis, C., & van Kreveld, D. (1972). Exposure, satiation, and stimulus discriminability. *Journal of Personality and Social Psychology*, *21*, 270–280. doi:10.1037/h0032357
- Zald, D. H., & Zatorre, R. J. (2011). Music. In J. A. Gottfried (Ed.), *Neurobiology of sensation and reward*. FL, Boca Raton. doi:10.1201/b10776-24
- Zhang, J., Berridge, K. C., Tindell, A. J., Smith, K. S., & Aldridge, J. W. (2009). A neural computational model of incentive salience. *PLoS Computational Biology*, *5*, e1000437. doi:10.1371/journal.pcbi.1000437

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### ***The Neurosciences of Music IV: Learning and Memory***

Closely related to the present special issue of *Psychomusicology: Music, Mind, & Brain* on music and neuroscience is the recent book *The Neurosciences of Music IV: Learning and Memory*. Edited by Katie Overy, Isabelle Peretz, Robert J. Zatorre, Luisa Lopez, and Maria Majno, and published by the Mariani Foundation in the *Annals of the New York Academy of Sciences*, Volume 1252, 2012 (ISBN 978-1-57331-841-9). The 367-page text begins with a multi-authored introduction followed by 46 chapters presented under the following headings:

- Experimental methods
- Social/real world methods
- Mechanisms of rhythm and meter learning over the life span
- Impact of musical experience on cerebral language processing
- The cultural neuroscience of music
- Memory and learning in music performance
- Mind and brain in musical imagery
- Music as a means to induce brain plasticity and malplasticity in health and disease
- The role of music in stroke rehabilitation: neural mechanisms and therapeutic techniques
- Music: a unique window into the world of autism
- Learning and memory in musical disorders

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