Music is an integral part of life’s highly pleasurable activities and has the ability to stimulate intellect as well as emotions. The neural mechanisms that allow for music to be considered as meaningful by humans are, however, poorly understood. Some musicologists have proposed that the creation of anticipatory structures modifying figure/ground relations is at the heart of what allows music to be meaningful and to convey emotion. Here, we review our current knowledge of how music is translated to the subjective meaningful experience of emotion and pleasure in both performers and listeners. We propose that anticipation acts as a fundamental mechanism underlying musical structuring and that this taps into the way that the brain works on different levels with a capacity to evoke pleasure in humans. Exemplified by two distinct, pleasure-evoking responses to music, the so-called ‘chills’, and the sensation of swing, we argue that the hedonic evaluation of both of these responses to music is mediated through the reward system, and is as such related to the underlying principles of musical expectancy.

KEYWORDS Anticipation, Expectancy, Pleasure, Chills, Swing, Making sense

Introduction

Why does music make so much sense to us as humans regardless of cultural background? The question of what musical meaning is and how it is brought about is central to musicology. Recently, this question has been revisited from a biological point of view following a stream of neuroscientific evidence emerging as a consequence of the development of new tools to study the human brain structurally and functionally. As a natural consequence of this biological approach, making sense of music must be seen as a two-way process in which the experience and the emotional qualities associated with a
certain piece of music are shaped by the qualities of the actual musical expression as well as by the interpreting brain. In the present review, we focus on what is probably the most important aspect of the way that music becomes meaningful to the human mind: its ability to convey emotions and to induce pleasure.

When asked about which of the pleasures of life they would miss the most, people consistently rate music as one of the most important, yet the ability to derive pleasure from music listening and performance would appear to be a trait that is unique to humans. There is mounting evidence that the early parent–infant interactions form an important component in shaping our sense of music as demonstrated by the role of motherese (a.k.a. baby talk) or prosody linked to the nurturing and affective nature of these interactions (Marwick and Murray 2008).

While other animals are clearly capable of hearing the sounds that make up music, they appear unable to take pleasure in music (McDermott and Hauser 2007). This could be linked to the lack of extensive caregiving in other animals, given that humans are unique in their prolonged childhood.

However, animal studies clearly demonstrate that there is a difference between the brain regions participating in decoding the sounds that make up music perception (Griffiths 2001; Hauser and McDermott 2003) and subsequent pleasure and emotional processing evoked by music, which are perhaps unique to humans (Blood and Zatorre 2001; Blood et al. 1999; Green et al. 2008; Griffiths et al. 2004).

Studies in other animals including nonhuman primates have consistently failed to show any sort of pleasure or displeasure related to music-like activity or perception (Bates and Horvath 1971; Hauser and McDermott 2003; Steele 2006) — although there is recent evidence that music can act in conjunction with other cues as a significant aversive noisy stressor even in rats (Reynolds and Berridge 2008). While studies in some of our closest cousins have shown that basic abilities underlying music perception, such as octave recognition, may be in place (Hauser and McDermott 2003), the monkeys are unaffected by dissonance and consonance (McDermott and Hauser 2004) and they do not appear to take pleasure in music overall (McDermott and Hauser 2007).

In humans, music can evoke a range of different emotions, which are both similar and different to those found in other activities. These include everyday emotions such as happiness, sadness, surprise, and nostalgia. Here, we argue that there are emotions that are unique to music such as the sensation of ‘swing’. Interestingly, the word emotion is closely linked to movement as implied by its Latin root (‘movere’, to move) as that which moves us in some way. The sensation of swing and music more generally may originate in the interface between emotion, motivation and movement.*

From an evolutionary perspective, it is hard to imagine that music would have survived as a human cognitive ability, if music did not confer an adaptive advantage on our emotional state and our well-being. In this sense, the benefits from a better understanding of human emotional processing are clear to most areas of music research trying to understand what music is and how it works.
It has, however, proven nontrivial to study how music, consisting of organized sequences of sounds, is translated to the wealth of emotions that we can experience and from which we can derive pleasure. Until the recent advent of modern neuroimaging techniques, the lack of any good animal models for the study of music has made it difficult to investigate the neural foundation of musical emotions and pleasure, and even today remarkably little is known about how music evokes emotions and pleasures.

Here, we are reviewing our current knowledge of the neural mechanisms of how sounds and music are translated to the subjective experience of emotion and pleasure in both performers and listeners.

First, we present some recent theoretical frameworks for understanding the relation between music and human emotions. One important model holds that anticipation/prediction is the basic mechanism that drives music perception, which in turn maps onto predictive coding theories of how the brain might work.

This could be said to continue the formalist tradition in the history of music aesthetics, in which musical emotion is generated primarily by anticipation of structural elements. Counterexamples of this view include the supposed role of music in ecstasy and trance as well as the origins of music in ritual. It is clear that musical experience is not necessarily predominantly generated by anticipation of structural elements. However, in this paper, we claim that, in all experiences of music, there is an element of anticipation/prediction which is fundamental not only to music but to our experiences in general.

In this review, prediction/anticipation is not only linked to large scale musical structural events related to the hierarchical system of functional harmony but also to fine grained changes in accentuations, tempo, timbre, intonation, phrasing and swing (Benadon 2006; Clarke 1999; Friberg and Sundström 2002) that are processed online, pre-attentively by the human brain even in the absence of attention — and even consciousness (Bekinschtein et al. 2009). In other words: even if trance and ecstasy may not involve any experience of large scale musical structural events per se, the fundamental perception of the music relies on the auditory, motor and possibly other perceptual and cognitive systems’ modelling of regularity.

Given that our paper is primarily rooted in brain science, we consider anticipation to be a fundamental principle when describing a framework for brain mechanisms of musical emotion. We believe strongly that any framework for understanding music should have a hierarchical structure.

Second, we review the insights into the pleasure of music gained from neuroimaging research. We focus on how musical anticipation allows for the sensation of pleasure evoked by music exemplified by two very common sensations related to musical experience: the so-called chill or shivers down the spine reactions to particular pieces of music and the sensation of swing.

One underlying assumption is that the pleasure induced by music could be related to an increase in dopamine release but this link has never been proven directly. The link between dopamine and the pleasure of music is probably misleading, as suggested by the evidence from other human neuroimaging studies of pleasure (Leyton 2009). Dopamine might be closer linked to prediction/anticipation mechanisms of pleasure-inducing music rather than the hedonic experience per se. If, however, dopamine release is important
to understanding components of why music is pleasurable and motivating, this may also hold the key to understanding the main problem in relation to music in an evolutionary perspective: Does music have survival value and why is it unique to humans?

Translating music into pleasure and emotion

How is it possible for music to induce pleasure and emotions at all? The most common explanations fall into three categories: (1) **Hardwired responses**; or how music evokes survival-related responses connected to the way sound is processed by the auditory system (such as how brainstem responses to loud sounds can trigger fear responses); (2) **Extramusical association**; or how music links to some extramusical space that carries the particular emotion; and (3) **Anticipation**; or how music establishes, fulfils or disappoints anticipatory neural structures and mechanisms which are set up within the music itself.

At first glance, the first two kinds of explanation may seem easiest to fit with recent theories of emotion. However, the third kind of explanation may in fact be more fundamental to the experience of music as such. At the very least, as we shall see later, it offers an explanation to understanding music-specific emotions, for example, the sensation of swing that is not easily explained by the other two kinds of explanation.

A framework has recently been proposed for the different ways in which the human brain might carry out the translational process from music to emotion (Juslin and Västfjäll 2008). The authors point out that the study of emotions evoked by music has suffered from a neglect of the underlying psychological mechanisms evoking these emotions and propose that these mechanisms could be summarized into at least six categories: (a) brainstem reflexes, (b) evaluative conditioning, (c) emotional contagion, (d) visual imagery, (e) episodic memory, and (f) musical expectancy. Some of these mechanisms may be dissociable but could also be shared, since it is clear that the first of their proposed mechanisms falls in the first category of explanations we mentioned, while the next four fall in the second category and the final, musical expectancy, falls into the third category.*

While successful in describing some aspects of this translation from music to emotion, the framework also has several shortcomings. It could be argued that visual imagery is not confined to music but is really about multimodal object perception. Similarly, evaluative conditioning and episodic memory are not necessarily separate categories with the only difference being the awareness of the apparent source of the connection. Also, they claim that brainstem responses to loud noises is just a mechanism which is hard-wired to produce high arousal, but appear to overlook how this in fact demonstrates that the influence of prediction and context are unavoidable. Depending on context, a loud sound can become a soft sound within an environment of even louder sounds.

**Musical anticipation**

The mechanisms proposed by Juslin and Västfjäll account for some aspects of how music may evoke emotion and pleasure in the brain. But perhaps
the most important mechanism relates to musical anticipation, which is the process whereby an emotion is induced in a listener because a specific feature of the music violates, delays, or confirms the listener’s anticipation of the continuation of the music (Vuust and Frith 2008).

As a special case of this, creation of anticipation in music is linked to the motion over time between opposites such as, for example, in harmony, the shift in the authentic cadence from dominant to the expected tonic, and in melody, the motion from approach notes to target notes (Friedman et al. 2001). In the very restricted sense that Juslin and Västfjäll use this terminology, musical anticipation is almost entirely related to the notion of musical syntax (Lerdahl 1971).

This is exemplified in harmony by the anticipation of chords appearing in different places in the tonal cadence. The authentic cadence is composed of tonic (T), dominant (D), and subdominant (S) chords in the following order: T S D T (Bharucha and Krumhansl 1983). The dominant is perceived as tension-creating, demanding resolution to the stable position of the tonic, whereas the subdominant reflects an intermediate position between these two oppositions. Chords incorporating notes outside the prevailing harmonic context usually demand resolution to more stable harmonies of the system (Bharucha and Krumhansl 1983). Chords breaking these harmonic expectations may be perceived as colourful, interesting, or simply erroneous, and give rise to different emotions such as, for example, surprise or sometimes even pleasure (Berent and Perfetti 1993; Meyer 1956).

The neural foundation of violations of harmonic expectancy is one of the more well-understood areas of brain processing of music. In a number of studies, Stefan Koelsch and colleagues have investigated the neural processing of inappropriate chords inserted in the authentic cadence (Koelsch and Friederici 2003; Koelsch et al. 2000). Using electroencephalography (EEG) and magnetoencephalography (MEG), they have found that a brain response termed the early right anterior negativity is elicited when a harmonically incongruous chord is inserted within or at the end of a musical sequence and localized the source of this response to the inferior frontal cortex; more specifically to a component of Broca’s region, or Brodmann area 44, and its right hemispheric homologue; an area often associated with processing of syntax in language. However, the impact of these unexpected chords on the emotional brain still needs to be investigated.

If we consider the vast amount of neuroscientific research in music that has been published in recent years, it is certainly true that the study of music emotions seems to be pointing in different directions. Consider, for instance, the very different activation patterns reported in studies of major and minor mode music supposedly evoking very simple emotions (happy/sad) (Green et al. 2008; Khalfa et al. 2005; Pallesen et al. 2005). Even though these results are probably due to the many different factors contributing to the emotional state of the subjects under different experimental conditions, we agree with Juslin and Västfjäll that there is a need for a coherent theoretical framework.

**Linking music and psychology**

The Juslin and Västfjäll framework gives an overview of the different possible mechanisms to translate between music and brain suggested by the literature. Still, it remains unclear how these different mechanisms relate to each other.
The problem with the framework is that the categories are not ordered hierarchically, and are not mutually exclusive. This limits the scope of the proposed framework somewhat, especially if its purpose is to act as a guideline for researchers trying to understand the modularity of brain structures involved in the processing of emotions in music.

As we shall see shortly, the balance of the data on music in the brain suggests that musical expectancy is a fundamental mechanism, which underlies other translating mechanisms, and it could reorganize the six categories of the Juslin and Västfjäll framework in a hierarchical fashion.

**Musical anticipation and emotion**

It is hard to imagine that musical emotions are evoked without some sort of musical meaning assigned to what is heard, unless we think of emotions such as, for example, fear evoked by the mere advent of a sudden loud, scary sound — in which case, it is questionable whether one could define this as music. Many music theoreticians consider musical anticipation as one of the principal means by which music conveys musical meaning and emotion. According to this point of view, understanding music (Cooper and Meyer 1960; Lerdahl and Jackendoff 1999; Lerdahl 1971; Meyer 1956; Monelle 1992; Narmour 1992) is related to the anticipatory interplay between local auditory events and a deeper structural layer partly inherent in the music as such and partly provided by mental structures in the listeners induced by the music (Palmer and Krumhansl 1990; Vuust et al. 2006a).

In short, the musical experience is dependent on the structures of the actual music as well as on the expectations of the brain that interprets it. These expectations are dependent upon long term learning of musical structures (which could be called *culture-dependent statistical learning*), familiarity with a particular piece of music, short term memory for the immediate musical history while listening to a musical piece as well as on deliberate listening strategies (Huron 2006; Vuust et al. 2006b). Brain structures underlying musical anticipation are thus shaped by culture as well as personal listening history and musical training (Vuust et al. 2005). Moreover, as soon as one hears the first sound of a musical piece, anticipatory structures such as meter, tonality, and memory for particular musical pieces seem to be in place already and unavoidable (see e.g. Brochard et al. 2003). Thus, it is difficult to imagine any of the above proposed mechanisms acting without the involvement of musical anticipation.

According to Juslin and Västfjäll, musical expectancy develops slowly over time during listening experience and is not fully developed until the age of 5–11 years. This is correct if musical expectation is restricted to anticipation of complex musical structures such as the hierarchy of harmony dependent on long term learning (Leino et al. 2007). However, anticipation of more simple repetitive sound patterns, which is a part of all music, such as pitch deviants in successive pitch trains has been detected even before birth, as indicated by the mismatch negativity (MMN) measured by M/EEG (Huotilainen et al. 2005). Moreover, in an elegant study, Winkler et al. (1996) showed that the auditory predictive model is updated for each new acoustic event in the sound environment, indicating that the anticipatory structures of music are in constant flux during the listening experience.
Furthermore, even though the authors claim that the degree of volitional influence on musical anticipation is low, we recently conducted a study in which musicians were asked to maintain either the main meter or a counter meter while listening to Sting’s *The Lazarus Heart* (Vuust et al. 2006b). In this experiment, the subjects volitionally imposed two very different anticipatory frameworks onto the music by tapping different but related rhythms. Another example of volitional control of the anticipatory framework in music would be to deliberately listen to a melody from the perspective of two different tonalities.

Thus, Juslin and Västfjäll use a very narrow definition of musical expectancy encompassing only predictive structures that develop over time. We would like to broaden up the definition of musical anticipation to include any kind of auditory/musical patterning with potential to create predictive musical structures that can be fulfilled or broken. Hence, music should be seen as a constantly evolving wickerwork of expectancies created in different layers of the musical structure (Bharucha and Stoeckig 1986; Meyer 1956; Monelle 1992; Sloboda 1985).

These expectation structures of tension and relief depend critically on the timing structure of music and can develop in music on a timescale that is much smaller than what is required by harmony. The predictive structures that underlie the anticipation of timing in music are provided by the meter, based on a fundamental opposition between strong and weak beats. A 3/4 meter represents a strong beat followed by two weak beats, whereas the accents in a 4/4 meter are ‘strong–weak–intermediate–weak’. The alternating structure of a meter is replicated on the global level of the musical form (Cooper and Meyer 1960; Vuust 2000), but in principle also at smaller levels of subdivisions of the pulse. Meter therefore provides the listener with a temporal, hierarchical expectancy structure, underlying the perception of music, in which each musical time-point encompasses a conjoint prediction of timing and strength (Large and Kolen 1994). This is in accordance with behavioural studies that indicate a human predisposition for temporal regularity (Drake and Bertrand 2001; Drake et al. 2000).

When the expectancy structure of meter is violated, however, this may be followed by a strong perceptual response depending on the degree of violation (Jones and Boltz 1989; Vuust 2000; Huron 2004). Importantly, the hierarchical structure of the meter underlies other expectancy structures in music, for example, rhythm, harmony, melody, intensity, in that it influences perception of any musical event. Hence, anticipatory structures such as the meter (but also, e.g., tonality) provide the listener with a framework for interpreting and remembering music. But how can musical anticipation be translated into emotions other than those related to surprise?

**Expectancy and emotion**

The relationship between musical expectancy and emotion was originally explored by Meyer (1956) and has recently been elaborated in a very convincing way by David Huron in his book *Sweet Anticipation* (Huron 2006). Huron proposes a general model of the anticipatory process leading to an event.*

The complex expectations formed by music can, according to Huron, facilitate the generation of a great variety of emotions. Correct predictions are
rewarded by the brain for survival-related reasons, evoking positive emotions that are attributed to the music itself.

These positive emotions are mediated through the reward system, which plays a central role in relation to the experience of pleasure (Berridge and Kringelbach 2008; Kringelbach 2005; 2009). We will return to the available evidence showing the critical involvement of the reward systems in relation to musical pleasure, but first we will present a brief overview of how the brain might handle predictions.

Predictive coding of music

If music expectancy/anticipation is viewed as the fundamental mechanism for musical experience, this can be made to map nicely onto recent theories of predictive coding in the brain. One such promising model of brain function was proposed by Friston (2005) where predictive coding is the central principle of brain function. It provides an account of how the brain identifies and categorizes the causes of its sensory inputs (Friston 2002; Shepard 2001; Tononi and Edelman 1998). The model posits a hierarchical organization whereby lower level brain regions estimate predictions of their expected input based on contextual information through feedback connections from higher level regions. A comparison between prediction and actual input produces an error term that, if sufficiently large, will try to force an update of the model. This generates a recursive process, which aims at minimizing the difference between input and prediction. As the representational capacity of any neuronal assembly in this model is dynamic and context-sensitive, this, among other issues, addresses the problem of top-down control (Frith and Dolan 1997; Roepstorff and Frith 2004).

Recently, we have argued that, given the anticipatory nature of music, violations of musical anticipation in different aspects of the music may be good substrates for testing the predictive coding hypothesis (Vuust et al. 2009). One such example is our recent MEG experiment with simple rhythm sequences of increasing rhythmic incongruence and measured brain responses (event-related potentials), which were used to test the hypothesis that pre-attentive neural responses to increasing rhythmical incongruity could be identified and would be congruent with an error term and subsequent evaluation. We furthermore compared rhythmically unskilled non-musicians with expert jazz musicians to test if predictive coding schemes in rhythmically skilled musicians means that they have acquired a more detailed expectancy structure (through learning) than non-musicians.

Rhythmic incongruities elicited the magnetic counterpart of the mismatch negativity (MMNm, measured with MEG, hence the ‘m’), an event-related field, peaking around at 110–130 ms from change onset, an index of pre-attentive detection of change in some repetitive aspect of auditory stimulation (Naatanen 1992). The MMNm was accompanied by a later component, the P3am, peaking around 80 ms after the MMNm in expert jazz musicians and some of the rhythmically unskilled subjects, and we observed responses to more subtle rhythmic incongruities in most of the expert musicians compared to non-musicians.

The MMN and the P3a (usually measured with EEG) are thought to reflect two survival-related stages of an attention catching process. The MMN is a
brain response, occurring locally in the auditory cortices, to change in the auditory environment, whereas the P3a is associated with the evaluation of that change for subsequent behavioural action and is believed to indicate activity in a network which contains frontal, temporal, and parietal sources (Friedman et al. 2001).

In our study, the MMNms were localized to the auditory cortices, whereas the P3am showed greater variance in localization between individual subjects. MMNms of expert musicians were stronger in the left hemisphere than in the right hemisphere in contrast to P3ams showing a slight non-significant right lateralization. Thus the observed MMNms and P3ams (measured with MEG) could be interpreted as an error term which is generated locally and used for subsequent evaluation in a broader network including generators in the auditory cortex as well as higher level neuronal sources (see Figure 1).

This is in keeping with expectations based on predictive coding schemes and suggests that there is congruence between perceptual experience of musical anticipation and the way that these are processed by the brain. Furthermore, we found enhanced and earlier processing of rhythmic deviants in expert musicians compared to rhythmically unskilled non-musicians both at the level of the MMNms and the P3am, as well as a left lateralization of the MMNms to both subtle and strong metric violation in experts compared to non-musicians, consistent with earlier suggestions of music being left lateralized in musicians (Altenmüller 2001; Bever and Chiarello 1974; Ohnishi et al. 2001).

Thus, anticipatory structures in music seem to be translated directly by the human brain, which is geared especially to this kind of processing. In the

**FIGURE 1  Predictive coding.** The predictive coding model proposes a specific mode of interaction between lower level brain regions and higher level cortical structures (Vuust and Frith 2008). Functional integration among brain systems that employ driving (bottom-up) and backward (top-down) connections mediates this adaptive and contextual specialization, where higher level systems provide a prediction (P) of the inputs (I) to lower level regions and lower regions respond to failures to predict with an error term, which is propagated to higher areas (right panel). This allows for solving the conflict between input and prediction via changes in the higher level representations, until the mismatch is ‘cancelled’.
above experiment, we only observed brain response to these anticipatory musical structures in cortical brain areas. This was, however, to be expected due to the limitations of the applied method (MEG without magnetometers and using dipole modelling), which is not particularly sensitive toward detecting activity in subcortical brain structures.

In the following, we review some of the very sparse existing evidence of the involvement of the reward system in relation to music processing and try to explain the role of prediction in these experiments.

The pleasure of music, and in particular chills

One of the difficulties in studying emotional responses to music is that these are clearly individual and not stable in a listener during listening or even across several instances of listening to a musical piece. While neuroimaging lends itself to what is perhaps best termed neophrenology, it is not particularly meaningful to measure the average brain activity over seconds and even minutes in participants listening to music evoking pleasant feelings, although such a pilot study has been carried out in non-musicians using positron emission tomography (Brown et al. 2004). Such studies ignore the important temporal dynamics of music, which one functional magnetic resonance imaging (fMRI) study tried to redress by contrasting the effects on brain activity of pleasant and unpleasant music (Koelsch et al. 2006) but other neuroimaging modalities with much better time resolution such as MEG would seem better suited to untangle the hedonic valence associated with music.

One way to address some of these problems is to concentrate on one of the more stable emotional reactions to music, the so-called chills or shivers down the spine, which are particularly salient (Blood and Zatorre 2001; Goldstein 1980; Panksepp 1995; Sloboda 1991). Chills denote the sensation of shivers running up and down the spine, goose pimples, and hair standing up on your arms that can accompany especially delightful musical listening experiences.

Evolutionarily, chills are related to the survival mechanisms of what has been called the four Fs of life (‘fighting’, ‘fleeing’, ‘feeding’, and ‘reproduction’) and in particular to the fulfilment or violation of expectancy such as surprise. In most species, these fundamental responses involve both subcortical and cortical mechanisms and are fast and mostly automatic. As an example, the characteristics of the fight and flight responses are similar changes in general arousal which give rise to the chills response, and may help elicit either aggression or submission. In the case of music, the subsequent appraisal process always determines that the surprising event does not imply any real danger and this might leave the delightful feeling of shivers down the spine.

Surprise always indicates a biological failure to predict future events, and thus the chill effect is directly linked to musical anticipation. According to Huron (2006), the delight from the chills stems from a contrast between a fast track response (the reaction/prediction response) mediated by subcortical structures in the brain, and which is substituted by a ‘slower track’ response (the appraisal response) mediated through cortical structures (LeDoux 1989). The fast response to the surprise is quick and has a negative valence. The slower appraisal responses follow quickly thereafter and, in the
case of music, often have a neutral or positive valence, resulting in an overall positive feeling of pleasure. Also the positive fulfilment of expectancy can give rise to chills and as such are a much desired quality of music.

The chill response can be measured using psychophysical and behavioural measures. Grewe et al. (2005; 2007) used a combination of skin conductance measures, button presses, and subjective reports of goose pimples to determine chill responses. This group, headed by Eckart Altenmüller, developed the EMuJoy software to allow for a participant's continuous self-report of feelings in a two-dimensional emotional space while listening to music in order to combine methods of continuous measurement of physiology and motor responses (Nagel et al. 2007). They measured 38 participants and found that chills as a paradigm for strong emotional responses to music is dependent on familiarity with a musical style and on personality factors, such as reward dependence or sensation seeking.

Chills were also found to be related to changes in loudness; however, no distinct acoustical pattern could be identified that induces chills in a reflex-like way and they suggested that chills are bodily reactions based on subjective feelings. Interestingly, they found that even though a distinct chill-triggering acoustical pattern could not be found, important musical factors seem to be harmonic sequences, the entrance of a voice, and the beginning of a new part, which is a violation of expectancies.

In an elegantly designed study, Anne Blood and Robert Zatorre (2001) investigated the pleasurable chill responses in 10 music students from the Department of Classical Music at McGill University while scanning them with PET, measuring heart rate, skin conductance, and respiration. On the basis of their self-reports, each of the participants chose a classical piece of music that elicited strong emotions and chill experiences. Each of these self-chosen pieces was then used as a control situation for another participant. Participants reported chills that correlated with changes in the psychophysical measures during listening to their own pieces compared to the control pieces. Regression analysis assessing the relationship between increasing intensity ratings related to chills and PET measurements of regional changes in blood flow identified changes in brain structures that are thought to be involved in reward, motivation, emotion, arousal, and pleasure. These included the structures such as the ventral striatum (nucleus accumbens), midbrain, amygdala, and the orbitofrontal cortex.

This result indicates that listening to music can, in certain instances, induce intense pleasure in the reward systems of the brain and suggests that music has an ability to tap directly into these survival-related brain mechanisms. The authors proposed that even though music is not obviously necessary for human survival, it may have psychological benefits.

The Blood and Zatorre experiment was an important step forward in understanding the neural foundation of musical pleasure in linking chills to brain structures involved in reward. Even though the experience of chills is highly subjective, Grewe and colleagues (2005; 2007) have shown that chills are related to surprise accompanying a musical event such as the entrance of a voice or choir or the beginning of something new in the music. The Blood and Zatorre experiment makes a convincing argument of linking their findings to brain structures related to reward, but the poor time resolution of PET is still only indirect evidence that the brain does, in fact, reward music listening.
Pleasurable music on the brain

On balance, these pilot neuroimaging studies of the emotions evoked by music show activity in the reward regions of the brain including the orbitofrontal cortex, anterior cingulate cortex, the nucleus accumbens, the insula, and the amygdala. These brain regions appear to code for the pleasure of many different stimuli.

Similar to many other sensory systems, there are functionally and anatomically separable neural systems mediating music perception and emotion. The perception of music involves superior temporal regions including the auditory cortices as well as the inferior frontal regions, while the emotional processing engages the reward systems. But none of the neuroimaging studies can provide information about the causality of any of these brain regions in the emotional processing of the pleasure of music.

Some light on this question has, however, been shed by a recent case report of a 52-year-old man suffering a stroke, which only affected his music appreciation and not his sound perception (Griffiths et al. 2004). The stroke affected mostly his left insula although the potential additional damage to fibre pathways by his stroke was not assessed. At the very least, this finding would seem to indicate that regions of the left insular cortex are involved in normal musical emotional processing of music.

In addition to these questions regarding necessary and sufficient brain systems for experiencing the pleasure of music, there are many different neurotransmitters linked in nontrivial ways to reward. Dopamine is linked mostly to ‘wanting’ (or expectancy) rather than ‘liking’ (Berridge and Kringelbach 2008; Kringelbach 2005; 2009). Dopamine is increasingly thought to be a key player in relation to reinforcement, learning, and in reward-seeking behaviour, but not to pleasure per se (Kringelbach and Berridge 2009b).

A future step toward a better understanding of the brain mechanisms and neurotransmitters involved in emotional processing of music would be to measure dopamine release in the brain directly, as already demonstrated for other types of stimuli (Leyton 2009). This has recently been attempted by the Zatorre group but has not yet been published.

Another obvious question that remains to be investigated in the context of the Blood and Zatorre experiment is whether the reward system is involved in musical performance rather than listening. Until now, research has mainly been concentrating on emotions involved in musical listening but is performing music different from listening to music?

In other words, why do musicians play? One possible explanation may be the euphoria that many musicians report to experience occasionally when they play and which is an important motivational factor possibly linked both to the music and to social factors (Berliner 1994; Monson 1997). In a questionnaire investigation, 111 out of 129 Danish conservatory students enrolled in programmes designed to make them professional musicians reported to be ‘feeling high’ when playing music (Vuust et al. 2010). It seems to be a plausible hypothesis that the reward system and dopamine is also involved when musicians play. This interesting question, however, remains to be tested experimentally.
Conclusions

In summary, despite the current paucity of available experimental evidence, we have tried to review the actual and putative musical and neural mechanisms that allow music to be translated into emotion and pleasure. We have proposed that anticipation/prediction could act as one of the fundamental mechanisms underlying structuring music as a meaningful percept and that this taps into the way that the brain works on different levels with a capacity to evoke pleasure in humans.

If we consider music from the viewpoint of music theory, it works by way of predictive structures in all possible layers of its structure. These range from simple acoustical patterns to melodic, harmonic, rhythmic hierarchical anticipatory patterns of greater complexity being established, confirmed, delayed, or violated. These anticipatory structures are stored in different kinds of memory systems: schemes (predictions of how music normally develops) are related to semantic memory, veridical anticipation (predictions of music that we have heard before) is stored in long term memory and memory for musical events that have occurred earlier while listening to a particular piece of music is stored in short term memory.

The human brain decoding all this information is rather good at processing such predictive information, and it could be that predictive coding is one of the fundamental ways in which the brain integrates information between different brain regions. In relation to music, the brain appears to be constantly scanning the auditory input for predictive patterns and responds strongly to deviations.

Musical anticipation stimulates the brain in two basic ways underlying our perception of the emotional content. First, anticipatory structures such as tonality and meter are the basis of memorization and learning of musical material in that they provide the background for musical surface structure such as melody, chord changes, and rhythms. For instance, it is impossible to learn and remember a complex rhythm if you do not know the meter. Furthermore, as a direct consequence of the predictive coding theory, the way we make sense of a piece of music is dependent on the cultural and musical background that has shaped the brain that interprets the music.

Second, the predictive patterns act directly on the emotional brain by way of different survival-related responses to anticipation, in particular, the prediction response rewarding correct predictions in order to reinforce correct predictions of the future. Brainstem reflexes, evaluative conditioning, emotional contagion, visual imagery, and episodic memory in relation to music are all dependent on the basic anticipatory structuring of music, described above, allowing for interpretation, memory, and learning of music.

Hence, we would propose that the emotion-evoking mechanisms described by Juslin and Västfjäll act on top of the general principle of musical anticipation and may help to identify how music can influence the reward systems of the brain.

All the different emotions evoked by music — both positive or negative — are potentially pleasurable. Investigations of the neural underpinning of musical pleasure are, however, still in their infancy. While briefly reviewing the neuroimaging correlates of listening to music, we have focused on two distinct responses to music that are widely associated with pleasure and
The pleasure related to music listening and performance is therefore likely ultimately to be mediated through general pleasure and reward systems.

Thus, the hedonic potential of music is linked to the ability of music to help fulfil the evolutionary imperatives of survival and procreation by creating anticipation, fulfilment, or violation. This pleasure is subsequently attributed to the music itself.

This pleasure is very important to most people although some scientists see music as an artefact, a byproduct of the evolution of the human brain that ‘could vanish from our species and the rest of our lifestyle would be virtually unchanged’ (Pinker 1997). A more refined version of this viewpoint is that music is a form of nonadaptive pleasure-seeking, merely exploiting existing brain mechanisms, perhaps to be likened to a drug with no side effects. Others, however, consider music parallel to speech as a language for emotions having great importance for social cohesion and interaction (Huron 2001).

We would argue that, while music may be an accidental byproduct of our species-specific acoustic abilities and as such may be a higher pleasure, which could be unique to humans, it is a vital pleasure that we would be foolish not to enjoy as a perfect counterpart to many of life’s other sensory, sexual, and social pleasures.

Note
* See online supplementary material for further details and discussion at http://maney.co.uk/images/pdf_site/ISR_Vuust_Kringlebach.pdf

Bibliography


**Notes on contributors**

Professor Morten L. Kringelbach, D.Phil., is a prizewinning, highly-cited neuroscientist whose main focus is to understand the functional neuroanatomy of human pleasure. Kringelbach is the Director of *Hedonia: Trygfonden Research Group*, which is a unique transnational research collaboration between Oxford and Aarhus universities. Correspondence to: Morten.Kringelbach@psych.ox.ac.uk

Professor Peter Vuust, PhD, is based at the Danish Royal Academy of Music and Center of Functionally Integrative Neuroscience, Aarhus University Hospital where he is the director of the .Music in the Brain. group. Correspondence to: pv@musik-kons.dk

**INTERDISCIPLINARY SCIENCE REVIEWS**, Vol. 35 No. 2, June, 2010