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Chapter 19 Music

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19.1. INTRODUCTION

Why do humans take pleasure from sequences of tones? This question has perplexed many scientists and philosophers over the years. The great science fiction writer Arthur C. Clarke (1953) went so far as to suggest that an alien race would be puzzled and astonished by the amount of time we spend listening to sounds that have no apparent purpose or utility. Yet, humans consistently rank music among the top ten things that bring pleasure, usually above such things as money, food, or art (<u>Dubé and LeBel 2003</u>). So why do temporally organized pitch sequences as found in music bring such pleasure? In the present chapter, we outline some of the critical mechanisms that make music both rewarding and motivating, and attempt to link these factors to recent neuroscientific insights into the networks that mediate reward.

19.2. ORIGINS

Because of the seemingly superfluous nature of music to human survival, many theorists have speculated as to why humans evolved musical abilities at all. Indeed, Darwin (1871) declared, "As neither the enjoyment nor the capacity of producing musical notes are faculties of the least use to man in reference to his daily habits of life, they must be ranked amongst the most mysterious with which he is endowed." Proposed explanations have ranged from advantages in mate selection to the idea that music represented a prelinguistic form of communication (see Fitch 2006 for a discussion of the evidence for and against these hypotheses). At the other end of the spectrum lies the idea that music is a consequence of another set of adaptations, such as those required for language and other higher cognitive functions, rather than a process that was itself adaptive (Gould and Lewontin 1979). Perhaps more extreme, Pinker (1997) suggests that music serves little adaptive function, but provides an ability to "push our pleasure buttons." A more nuanced approach to this question has recently been provided by Patel (2007), who point out that it is not necessary to assume some specific advantage in natural selection in order to explain music's appearance, as it may well be the consequence of other adaptations, but that this would by no means indicate that music hence serves no purpose or is not itself valuable.

From an evolutionary perspective, it is notable that our closest primate relatives show little in the way of developed organized pitch and rhythmic sequencing. Some bird species have been reported to entrain to external sounds, such as musical rhythms, with body movements (Patel et al. 2009; Schachner et al. 2009), although there is as yet no evidence that they respond in terms of humanlike metrical representations, that they do so to any self-produced sounds, or that this a natural behavior in the wild. Among primates, several ape species will beat their chest or other surfaces (Fitch 2006), but they do not entrain to rhythmic sounds. Probably the closest example of pitch sequencing occurs in gibbons, who make "duetting" calls together (Geissmann 2000). However, there is no evidence that gibbons or other nonhuman primates routinely learn melodies. Indeed, to the extent that it has been tested, nonhuman primates show little enjoyment or preference for music. When presented with a choice between musical stimuli and silence, tamarins and marmosets prefer silence (McDermott and Hauser 2007), suggesting the uniqueness of human's development of musical interests. So in spite of that harmonious adage, music may *not* tame the savage beast.

19.3. NEURAL CIRCUITRY INVOLVED IN MUSICAL PLEASURE

Before discussing theoretical proposals for the pleasure-inducing effects of music, we will review the empirical evidence that informs current hypotheses. At present, there is a small, but growing, literature that directly addresses the neural substrates for music-induced pleasure. Although this field is still in its early stages, the interpretation of these studies rests on a reasonably solid foundation of research in other domains. In particular, the large body of animal literature on pathways associated with auditory processing, reward, and motivation (as explored in Chapter 9) provides a critical basis for interpreting these studies. But since musical enjoyment appears to be a uniquely human trait, it is only in paradigms adapted to studying human responses that we can really address this issue. Data on this topic come from three primary sources: lesion studies, functional neuroimaging, and psychophysiology.

19.3.1. LESION STUDIES

We begin with an evaluation of the human lesion literature in relation to musical emotion. Whereas a relatively extensive experimental literature exists on the effects of brain lesions for music perception (for review, see Stewart et al. 2006), few of these studies have systematically explored musical emotions in general, or the emotions associated with pleasure in particular. There are reasonably clear reports that perceptual disorders can lead to a complete loss of pleasure derived from music; in cases where musical perception is so disordered that it sounds completely distorted, such a lack of pleasure is of course to be expected (e.g., Griffiths et al. 1997). In some instances, this phenomenon may also be part of a broader auditory agnosia where not only music, but all sounds, become incomprehensible to the patient (e.g., Habib et al. 1995; also see Chapter 10 in this volume). The lesion sites associated with such disorders are typically in the posterior temporal region, often bilaterally or sometimes on the right alone (Stewart et al. 2006). A clear example of this inability to derive emotional content because of perceptual loss was demonstrated by Peretz et al. (2001), who found that a patient unable to distinguish consonance from dissonance was also unable to indicate the degree of pleasantness or unpleasantness associated with dissonance. Interestingly, the lesions in this individual, which were primarily within auditory cortices bilaterally, did not overlap at all with the cortical and paralimbic regions associated with the evaluation of affective dissonance identified by Blood et al. (1999) in a neuroimaging study of healthy individuals (see below). This finding strongly suggests that the patient's inability to evaluate the affective value of dissonant music was a consequence of her perceptual deficit, since the neural regions associated with affect processing per se were intact, and since she had no generalized deficit in processing emotions in other domains.

In distinction to such cases, there are also reports of primary musical affect disorders subsequent to brain lesions. For example, Griffiths et al. (2004) report a case of a man who lost his affective response to music (in particular the experience of chills to some of his favorite pieces), following an infarct involving the left amygdala and insular regions. Unlike the patients described above, this individual had no disorder of musical perception that could account for the loss of pleasure he experienced. Another example is provided by a well-controlled experimental study of patients with amygdala damage (Gosselin et al. 2005) who rated music that usually elicits fear as expressing less fear than a control group. There was no accompanying perceptual disorder in this population either, leading to the conclusion that music perception and affective responses can be dissociated. In a parallel study, Gosselin et al. (2006) found that patients with damage to the parahippocampal region were relatively insensitive to the unpleasantness of dissonant music. The investigators reported that the degree of damage to this structure, but not to other structures (amygdala or hippocampus), correlated with affective judgments, indicating a likely dissociation between the roles of these structures. A similar finding regarding unpleasantness judgments was

more recently reported by Khalfa et al. (2008), who additionally found that patients with left medial temporal damage were less likely to perceive the positive affect in music pieces that are usually rated as happy. It should be noted that these impairments may not be specific to music, but may instead reflect more general deficits in affective processing. For example, amygdala damage such as studied by Gosselin et al. (2006) also usually leads to abnormally low affective arousal in response to fearful faces, suggesting the presence of a general multimodal deficit in response to fear, rather than a deficit specific to music.

The picture that emerges from these studies is that musical perception and emotion can be dissociated in one direction but not the other. That is, perceptual deficits, if sufficiently severe, lead to a loss of musical emotional response, whereas an isolated loss of emotional response can occur in the absence of any perceptual disorder. What this likely means is that the affective evaluation depends on a distinct neural system from that required for perceptual analysis, but that this affective system depends upon input from the perceptual system. This would explain why damage to superior temporal or frontal cortices can wipe out both musical perception and emotion, but damage to other emotion-related structures only affects emotional and not perceptual musical abilities.

19.3.2. NEUROIMAGING

Neuroimaging studies of musical emotion extend the picture provided by clinical studies and also allow a relatively direct examination of the neural substrates that may be involved in healthy individuals. As with any technique, however, attention to experimental design is critical and converging evidence from other sources is also essential. One critical design issue which is especially important in neuroimaging is the need to validate the emotional experience of the person being studied. Not all imaging experiments have determined whether the listeners being scanned in fact experienced the intended emotion, which would seem an essential element for understanding the observed findings. But obtaining judgments of emotions from listeners is not easy, because evaluating one's affective response may itself change the nature of the emotion felt. Such judgments may also be easily biased, as there may be a demand characteristic in the experiment, leading to participant responses based on their expectations or normative conventions, rather than their actual experience of a given emotion. In this respect, the psychophysiological measures mentioned in the next section are especially useful as providing both an objective and reliable way to determine emotion without conscious intervention from the individual (it is difficult, for instance, to "fake" changes in skin conductance at will). But since psychophysiological measures are relatively non-specific, some type of subjective behavioral appraisal will almost certainly still be necessary in most circumstances.

One of the first studies to apply functional imaging to musical emotion was carried out by Blood et al. (1999), who examined changes in regional cerebral blood flow elicited by varying degrees of pleasant and unpleasant music (Figure 19.1). Pleasantness was specifically modulated by parametric manipulations of dissonance. The study uncovered a pattern of reciprocal brain activity in paralimbic and neocortical areas as a function of changes in dissonance, and hence pleasantness, as measured via behavioral ratings. Specifically, increased pleasantness was associated with recruitment of subcallosal and orbitofrontal cortex, whereas increasing dissonance, leading to unpleasant evaluations, resulted in parahippocampal cortical activity (Figure 19.1c). The latter structure has strong connections to, and strong functional connectivity with, the amygdala (Stein et al. 2007) and has been found to be active during unpleasant visual stimulation (Lane et al. 1997), although with less consistency than the amygdala. As noted above, the study by Gosselin et al. (2006) indicates that the parahippocampus is critical for dissonance-induced unpleasant emotion, as patients with lesions in this area fail to show the normal subjective response to dissonant music despite intact musical perception. Blood et al.'s

observation that the ventromedial prefrontal regions are active in association with pleasant responses is also consistent with a large body of evidence from neuroimaging studies that indicate higher activation in ventromedial regions during processing of positive vs. negative stimuli or outcomes (Kringelbach and Rolls 2004). It may be noted that this pattern of positively valenced responses is not completely universal across stimulus modalities or ventromedial subregions (e.g., see Gottfried et al. 2006), but it is striking in its frequency. The reciprocal coupling between blood flow increases in ventromedial prefrontal cortex and decreases in the parahippocampal gyrus in the study by Blood et al. (1999) suggests the presence of a functional network, such that pleasant or unpleasant stimuli simultaneously influence brain activity in opposite directions in different regions.



FIGURE 19.1

(See Color Insert)Changes in regional cerebral blood flow during unpleasant (dissonant) and pleasant music. (a and b) Blood oxygenation signal increases associated with listening to unpleasant dissonant music: activation was detected in the hippocampus, (more...)

The essential findings of Blood et al. (1999) were replicated in a subsequent fMRI neuroimaging study by Koelsch et al. (2006), who reported very similar patterns of reciprocal brain activity using a set of stimuli in which unpleasantness was also generated by dissonance (Figure 19.1a, b). A particularly interesting finding of this latter study is that neural responses associated with both pleasant and unpleasant music tended to increase over time, indicating that there is a certain time course to the affective response. Unlike Blood et al. however, Koelsch and colleagues also observed significant modulation of the amygdala, such that there was relative activation of this structure for unpleasant stimuli, coupled with relative deactivation for pleasant music. A subsequent paper from this group extended this result by demonstrating that the amygdala is activated not only by dissonance, but also by unexpected consonant chords when they are perceived as unpleasant due to the harmonic context (Koelsch 2008b, 2008c); these findings are consistent with this region's general sensitivity to negatively valenced stimuli (see Zald 2003 for review).

Although the above studies intended to examine both pleasure and displeasure, the nature of the stimuli used makes it more likely that they primarily probed the unpleasant side of the response pattern, since the consonant stimuli used to elicit pleasure were not selected specifically so as to maximize the individual listeners' pleasure. In these studies, listeners rated the consonant music as more pleasant than the dissonant music but this does not mean that they were experiencing a high state of pleasure as such. This brings us to a critical aspect of music which is sometimes overlooked: individual differences in preferences. It is sometimes difficult to elicit strong and consistent emotions if musical pieces are selected in advance for a study without taking into account different tastes amongst listeners (Carter, Mintun, and Cohen 1995; Thaut and Davis 1993). Among the individual factors that are important to consider in eliciting musical pleasure are age, musical acculturation, personality, and musical training (Grewe et al. 2007b), to say nothing of social factors that no doubt influence musical pleasure. Although listeners can broadly agree that certain musical excerpts exhibit certain emotions (Vieillard et al. 2008), unanimity in emotion elicited by music is not at all guaranteed (Gabrielsson 2001). What evokes musical bliss in one person may be another (readers of this chapter are invited to compare their musical recording collection to that of their parents or to that of their children, for an informal confirmation of this hypothesis).

One way to take individual tastes into account is to allow participants of a study to select their own favorite music that they know elicits strong emotional reactions. This approach is not without difficulties, since individual responses may be contaminated by associations and memories. Furthermore, when listening to familiar music it is more difficult to dissociate anticipatory reactions from more direct reactions. Nonetheless, it provides a way to probe intense pleasure, and this was the aim of a PET study by Blood and Zatorre (2001), who examined the neural substrates associated with musical chills. Blood and Zatorre had participants select music that they knew to elicit chills, excluding any with verbal content or explicit associations that may have contributed to their emotional impact. Taking advantage of the fact that one person's favorite music leaves another one cold, they paired their subjects so that the chills-inducing music used in one person became the control for the other, and vice versa. This manipulation ensured that across the entire sample none of the differences measured in the neural response could be driven by physical differences in the stimuli used (a recurring problem in many of the above-cited studies). A number of changes in psychophysiological variables (heart rate, respiration, muscle tension) were observed when listeners heard their own music, but not control music, thus validating their subjective reports of the occurrence of chills during several of the scan periods. The study revealed a widespread pattern of blood flow changes in the brain associated with the presence of chills. Activity increases were found in several neocortical sites (insula, supplementary motor area, anterior cingulate, orbitofrontal cortex), as well as in subcortical areas, including notably the ventral striatum (Figure 19.2a) and dorsomedial midbrain. Deactivations were also noted in the amygdala (Figure 19.1d) and adjacent hippocampus, as well as in ventromedial prefrontal cortex.

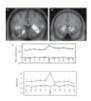


FIGURE 19.2

Neural and physiological changes as a consequence of chill-inducing music. (a) Coronal section showing increased cerebral blood flow response in left ventral striatum (arrow) during highly pleasurable music that elicits chills. (Modified from Blood, A.J., (more...)

Given the importance of the nucleus accumbens and other striatal regions in reward and motivation, these findings suggest that music may resemble biologically rewarding stimuli in its ability to engage similar neural circuitry. Indeed, the pattern of brain activity associated with intensely pleasurable music is similar in many respects to that seen with other relevant stimuli, such as consumption of chocolate (Small et al. 2001) and even administration of cocaine (Breiter et al. 1997). The neocortical changes also parallel some of the responses seen with these other emotion-inducing paradigms, although it is difficult to know which brain responses are specific and which ones are general, to the extent that they are all simultaneously present. Indeed, this question remains an important issue for future studies to work out, particularly as arousal-related vs. pleasure-related responses are hard to dissociate with this type of experimental design.

Of particular interest are the decreases in amygdala and hippocampus that accompanied the chills, similar to those observed subsequently by Koelsch et al. (2006). This interaction may suggest that the euphoric feeling associated with pleasant music is mediated via gating of behaviorally antagonistic approach/withdrawal mechanisms, given the important role for the amygdala in negative emotional experience, and other aversive emotions. Thus the pleasure of music may be due both to positive engagement of brain areas related to reward and inhibition of areas mediating negative affective states. In considering this hypothesis, we note that many sensory stimuli that are experienced as intense, and even positively arousing, can also lead to activation of the amygdala, such that some investigators interpret amygdala activations in regards to salience rather than valence per se (see Zald 2003 for review). To date, positive music remains

one of the only examples of a positively arousing stimulus capable of decreasing amygdala activity. This suggests that music may be unusual in its ability to downregulate the amygdala (although the exact meaning of deactivations in neuroimaging studies remains open to interpretation).

Engagement of the ventral striatal area during music listening is unlikely to be linked exclusively to the experience of chills. Although simple consonant music such as used by Blood et al. (1999) is evidently not sufficient to recruit this system, more naturalistic music may do so even in the absence of chills, as shown by several studies (Koelsch et al. 2006; Brown, Martinez, and Parsons 2004: Menon and Levitin 2005: Mitterschiffthaler et al. 2007). These studies all find activity within the ventral striatum during presentation of music that is enjoyable, or happy, although it is difficult to be certain that it is the enjoyment, as opposed to some other feature of the music (attentional engagement, arousal, etc.) that is relevant if one only compares music to a "resting state" (Brown, Martinez, and Parsons 2004), or compares normal music to scrambled music (Menon and Levitin 2005), because such analyses are nonspecific. There is also the related problem of comparing conditions in which the stimuli differ in terms of physical parameters, so that it is difficult to dissect out whether a given effect is stimulus-driven, or related to the emotion; this could be why three of these studies (Brown, Martinez, and Parsons 2004; Koelsch et al. 2006; Mitterschiffthaler et al. 2007) report changes in auditory cortex in response to pleasurable music, even though it is unlikely that auditory cortex itself mediates the emotional responses of interest. Alternatively, this modulation of auditory cortex may reflect a top-down influence of emotion on early sensory cortical areas, as a similar modulation of visual cortex is seen when individuals view emotional pictures (Lang et al. 1998).

There is also some uncertainty about whether the measured brain response to music in these studies reflects experienced pleasure, a happy emotional experience congruent with the valence of the music (Mitterschiffthaler et al. 2007), or an absence of experienced displeasure when consonant music is contrasted with the unpleasantness of dissonant (Koelsch et al. 2006) or scrambled music (Menon and Levitin 2005). As discussed in more depth below, the distinction between experienced pleasure and the emotional valence expressed in the music is likely critical to interpreting the observed activations in these studies. Humans frequently take pleasure in music that is negatively valenced. This dissociation between pleasure and valence is particularly striking for sad music (Levinson 1990). Indeed sad musical pieces induce pleasurable chills even more often than happy music (Panksepp 1995), despite their negative emotional valence. While the precise interpretation of ventral striatal activations will require further investigation, it seems likely that the ventral striatal response is directly related to some aspect of positive emotion or pleasure elicited during music listening. Menon and Levitin (2005) further observe significant functional connectivity between the ventral striatum and the dopamine midbrain region, as well as hypothalamus, orbitofrontal cortex, and insula, which supports the idea that the striatal response is part of a network associated with emotion processing.

The findings of these studies all point to the mesolimbic reward system as important for music-induced pleasure, leading to the hypothesis that the dopamine system may be mediating the affective response. This hypothesis was recently tested and confirmed by Salimpoor et al. (in press). Using raclopride as a dopamine-specific PET radioligand, these investigators showed that there was dopamine release in both ventral and dorsal portions of the striatum while listeners experienced highly pleasurable pieces of music that induced chills (Figure 19.2b), as compared to control music, which was rated as neutral and that did not produce chills. These data provide direct support for the hypothesis that dopamine is released in the mesolimbic reward system while listening to pleasurable music.

In a complementary investigation (Salimpoor et al. in press) the same participants were tested with the same stimuli using fMRI. A functional dissociation in BOLD activations was observed

between ventral and dorsal striatal regions. The dorsal striatal BOLD response was associated with time periods prior to the occurrence of chills, when listeners were anticipating maximum pleasure, while the ventral striatal BOLD response was found during the epochs in which chills were reported, and hence represent the highest pleasure moments. Finally, BOLD activity in dorsal and ventral regions also differentially predicted behavioral responses: number of chills experienced correlated with dorsal BOLD activity, whereas intensity of chills correlated with ventral striatal activity, in keeping with the idea that dorsal responses are related to expected events, while ventral responses are related to the experience of pleasure. Because the PET data do not provide temporal information, the precise relationship between dopamine release as measured with PET and these dissociable BOLD responses is uncertain, but to the extent that they are related (see Knutson and Gibbs 2007; Buckholtz 2010 for a discussion of this issue), the fMRI data raise the possibility of two phases of dopamine release, or topographically specific effects of dopamine release during highly rewarding music listening: one associated with musical expectancies and the other to resolution. We return to the importance of temporal features in understanding music reward below.

In summary, the extant data indicate that music activates key meso-corticolimbic areas that have previously been implicated as biological substrates of reward and emotion, and that this activity involves dopaminergic neural responses (cf. Chapters 4 and 11 in this volume). This knowledge is critical in understanding the neurobiological basis of musically mediated emotion, because it links the mechanisms involved in emotion associated with music to those associated with biologically relevant stimuli. However, the specific mechanisms through which these areas become activated remain largely unexplored. That is to say, the findings do not provide information on why organized combinations of sounds modulate the brain areas in question.

19.3.3. Psychophysiology

There are a number of studies of the effects of music on psychophysiological indices, such as skin conductance, heart rate, and respiration. These studies generally agree that music can modulate these markers of physiological and mood states quite dramatically and consistently. Furthermore, there are strong relationships between subjective ratings of various affective states and accompanying physiological responses, which is important as a validation of behavioral report relative to an objective index of internal state. One of the first to study the psychophysiological responses to music conveying different emotions was Krumhansl (1997). who showed that music rated as happy, sad, or fearful gave rise to different patterns of electrodermal, cardiac, and temperature measures. Consistent with these findings, Rickard (2004) demonstrated that skin conductance in particular could be a sensitive indicator of the intensity of affective responses to musical excerpts. Skin conductance is among the most widely used psychophysical measures as it provides a robust index of arousal. Similarly, Steinbeis et al. (2006) and Koelsch et al. (2008) observed that electrodermal changes occurred when unexpected chords were presented in a harmonic sequence. Similar reactions were reported by Grewe et al. (2007a) in response to unfamiliar music, particularly at points where a new voice or section was introduced. These responses suggest a specific arousal or orientation response to music when it is unknown or deviates from expectancies.

One of the interesting features of music is that it generates expectancies based both on veridical knowledge of a piece of music (i.e., when one has heard the piece before) and implicit knowledge of the rules of the musical system that one has learned (Huron 2006; Meyer 1956). The latter may be likened to knowledge of syntax in language. The fact that psychophysiological changes are elicited by chord sequences that are not in themselves specifically emotion-inducing (e.g., dissonant) (Koelsch 2008), and also by unfamiliar music heard for the first time, suggests that physiological responses are generated in part by abstract knowledge of how musical

antecedents lead to conclusions. These data provide an initial clue of the importance of expectancies in how we respond to music. We will return to the issue of expectancies later in this chapter, but note here that such expectancies play a prominent role in current theories of why music is rewarding.

Turning to the emotional states associated with pleasure, a number of studies have examined the psychophysiology associated with the experience of musical "chills," which is a useful marker of highly arousing and strongly positive emotion that appears to be qualitatively distinct from other emotional responses (Panksepp 1995). Several studies using electrophysiological and other techniques have specifically focused on the chills phenomenon. One of the first papers to probe this effect was carried out by Goldstein (1980), who tested the hypothesis that endogenous opioids might mediate musically induced chills by administering naloxone, an opiate blocker, prior to exposure to music. The results were inconclusive, however, as only three of ten listeners reported reduction of chills from this manipulation, and it is unclear whether this was a specific or more general effect. Several more recent studies (Craig 2005; Rickard 2004; Guhn, Hamm. and Zentner 2007; Grewe et al. 2007b; Salimpoor et al. 2009) have probed the psychophysiology associated with episodes when listeners report they are experiencing chills. The most consistent finding from these studies is that chills are accompanied by increases in skin conductance, along with heart rate and respiration, and that they are elicited at relatively consistent points in the music for any given listener, though not necessarily in a consistent manner across individual listeners (Figure 19.2c). In fact, Salimpoor et al. (2009a) showed that individual psychophysiological responses can be independent of psychoacoustical factors, and instead are strongly linked to listeners' experience of pleasant emotion. Such findings validate via an objective measurement that individual subjective reports of chills are indeed reflective of a distinct emotional response, although, as mentioned above, skin conductance changes are also elicited to surprising stimuli that do not necessarily induce pleasure. More importantly, these psychophysiological measurements implicate the autonomic nervous system in a physiological response which is no doubt mediated centrally, hence motivating studies on the neural basis of these reactions.

19.4. WHY IS MUSIC REWARDING?

A truly comprehensive discussion of the reasons music is rewarding is beyond the scope of this chapter as there are likely multiple complementary answers to this question and we cannot do each of these mechanisms justice. The question is closely related to the larger topic of whether music induces "true" emotions and what mechanisms allow this to happen. (See Juslin and Vastfiall 2008 and related commentaries for a larger discussion of these issues.) Nevertheless, a useful starting point is to consider what sort of positive feelings are induced by music. Zentner, Grandjean and Scherer (2008) recently reported the results of a confirmatory factor analysis of mood ratings induced by music. Seven primary positive factors were defined: (1) Wonder (including terms such as happy, amazed, and moved); (2) Transcendence (including terms such as inspired and feelings of spirituality); (3) Tenderness (with terms such as love, affectionate, and sensual); (4) Nostalgia (with terms such as sentimental and dreamy); (5) Peacefulness (with terms such as calm and relaxed); (6) Power (with terms such as energetic and triumphant); and (7) Joyful Activation (with terms such as stimulated, joyful, and animated). The first 5 primary factors loaded on a second-order factor, which the author labeled Sublimity, while Power and Joyful Activation loaded on a second order factor of Vitality. Based on these self-report findings, it is easy to speculate that there are several different mechanisms leading to pleasure in music, ranging from being impressed by the skill of the composer or musicians (Wonder), to reductions of tension (Peacefulness), and engagement of energy (Vitality).

19.4.1. AROUSAL

The induction of vitality and peacefulness by music is notable in that these states are closely tied to arousal. This sort of generalized up- or down-regulation of arousal is widely seen in how people use music to aid alertness, to help propel activities (such as during exercise), or to calm or soothe (e.g., lullabies). As others (Berlyne 1971; North and Hargreaves 1997) have previously speculated, gross changes in arousal may be explained through a brainstem (ascending reticular activating formation) mechanism. This arousal mechanism may be modulated by limbic structures, in particular the amygdala, which sends significant projections to the brainstem (Silvestri and Kapp 1998). Given the apparent up- and down-regulation of amygdalar activity by music, we speculate that the amygdala plays a critical role in this process of arousal manipulation.

The modulatory ability of music over ascending projection systems may also be related to its ability to act as an analgesic. It has been known for some time (Gardner, Licklider, and Weiss 1960) that music can be effective in reducing or controlling pain in people undergoing various types of medical treatments (e.g., Voss et al. 2004; Nilsson, Unosson, and Rawal 2005). A recent behavioral study has demonstrated that this effect is not due to generalized arousal, and is specific to pleasurable music, as no pain reduction is seen with music not judged to be pleasant (Roy, Peretz, and Rainville 2008). Moreover, in a recent study, Zhao and Chen (2009) found that pain reduction was similar for happy and sad music of similar perceived pleasantness, thus indicating that the pleasantness rather than the specific mood of the music is most significant in inducing analgesia (and further highlighting the idea that pleasure can be induced from either sad or happy music). Given these facts, it is tempting to conclude that the music-induced pleasure response, which we know to include both upregulation of dopaminergic reward circuitry and, perhaps especially relevant, downregulation of amygdala, may also cause a modulation of ascending nociceptive information. The details by which this interaction occurs will no doubt be a topic of intense future study.

The relationship of peacefulness and vitality to other mood states warrants special attention, because they provide a direct link to broad models of mood. Vitality is part of positive affect, which is marked by terms such as active and interested (Watson and Tellegen 1985), and comprises one of the two higher-order factors of mood. As such, the induction of vitality may be viewed as a direct modulation of positive affect. Peacefulness has a more complicated relationship to the general structure of mood. Tellegen originally suggested that peaceful calm states represented the low end of negative affect, as they reflect an absence of negative states such as anxiety or distress. Work carried out by Zald (unpublished) suggests that calm cannot be simply viewed as the low end of negative affect, as ratings of calm correlate more highly with positive affect terms than negative affect terms. Regardless of their specific position in affective space, it is clear that humans highly value feelings of vitality and feelings of peacefulness. Indeed, humans across cultures show a willingness to pay money for foods, herbs, medicines, illegal drugs, and sensory experiences that increase feelings of calm and vitality.

Yet, manipulation of arousal is almost certainly just one of several features that contributes to music's appeal. For instance, it is difficult to explain feelings of wonder, nostalgia, or transcendence through an arousal mechanism. Indeed, in reviewing these sorts of experiences, it is difficult to link such states to either arousal or the larger literature on affect and mood, in that most studies of mood do not include terms tapping these types of traits. There are only a few studies that have attempted to understand the neural substrates of these types of experiences, and as of yet, we would argue that the data are too limited to suggest a model of their neural substrates. Indeed, the literature on the neural substrates of awe is essentially nonexistent. Several methodological features will also make these domains difficult to capture using musical stimuli, leading us to suspect that it will be some time before we have a handle on each of the domains described by Zentner, Grandjean and Scherer (2008).

19.4.2. EMOTIONAL COMMUNICATION AND CONTAGION

Another avenue for exploring music's rewarding properties arises from the simple idea that music is a form of communication, which like nonverbal vocal cues can provide information to the listener about the emotional or motivational state of the person making the sounds. Although there has long been speculation about the parallels between nonverbal vocal and musical communication (see for instance Spencer 1857), it is only relatively recently that empirical research has addressed this issue. Much of this work is summarized by Juslin and Laukka (2003), who observe that music and vocalizations have similar decoding accuracy for individual emotions, use similar acoustic features to convey specific emotions, and show similar developmental trajectories. Based on these similarities, Juslin and Laukka argue that the development of music in humans is a specific outgrowth of adaptive advantages that were gained by being able to encode and decode emotions through vocalizations.

In treating music as a mode of emotional communication, it is useful to consider the concept of emotional contagion, through which the expression of an emotion leads to the experience of the same emotion in an observer. This concept has been primarily applied in relation to the effects of emotional facial expressions, where it has repeatedly been found that viewing emotional facial expressions induces similar emotional experiences in the viewer (Preston and de Waal 2002; Wild, Erb, and Bartels 2001). This process happens even in response to faces that are presented quite briefly (Lishner, Cooter, and Zald 2008), at time spans far shorter than a typical musical passage. Much less attention has been given to emotional contagion in the vocal sphere, but it is clear that vocalizations elicit subjective emotional responses in listeners. For instance, the sound of voiced laughter robustly induces positive affect in the listener (Bachorowski and Owren 2001).

To the extent that music uses similar acoustic cues as nonverbal vocalizations, it may tap into similar contagion-like features. This leads to a set of specific hypotheses, namely, that the experience of reward or other emotions from music will lead to activation of the same regions as when the person experiences that emotion in a natural setting, or when the emotion is invoked by an emotion contagion-like process from another sensory modality such as facial expressions. Thus, for instance, since exposure to happy facial expressions tends to engage the ventral striatum (particularly in those with high empathy; Chakrabarti, Bullmore, and Baron-Cohen 2006), we would predict similar engagement by happy music. As discussed earlier in the chapter, this hypothesis finds support in the small but increasing literature on emotion and music. For example, Mitterschiffthaler et al. (2007) report that happy music engages the ventral (and dorsal) striatum. This is an intriguing convergence, although we would caution against treating the striatal activations as necessarily reflecting the experience of happiness, per se. Interestingly, unlike some of the above-described studies which have emphasized pleasantness rather than mood (e.g., happy, sad) in relation to the engagement of the striatum, the data of Mitterschiffthaler and colleagues indicate that sad music did not produce a similar activation in the striatum. However, since no ratings of pleasantness were provided, it is unclear whether the pieces were perceived as highly pleasant.

If, as Juslin and Laukka (2003) argue, music is closely tied to nonverbal vocal communications, we would predict that the neural correlates of emotions induced by music would be particularly similar to those arising from nonverbal vocalizations that are not musical in nature. A few neuroimaging studies have examined neural responses to nonverbal emotions (Fecteau et al. 2007; Johnstone et al. 2006; Pourtois et al. 2005). Although multiple areas showed activation in response to happy or positive emotional vocalizations, there is a decided absence of striatal activations in these studies, making it unlikely that striatal activations during music can be directly related to pathways evolved to detect emotional features in vocalizations. A stronger argument may be made linking affective vocalization and music processing in portions of

temporal cortex, as both modalities cause widespread temporal cortical activations, although studies utilizing both types of affective auditory information in the same subjects are needed to determine the degree of specific convergence that occurs. Some evidence also emerges for convergence in the amygdala, where Fecteau et al. (2007) observed significant bilateral activations for both positive and negative vocalizations. We note, however, that this contrasts with the data presented above in which chills were associated with deactivation of the amygdala.

There is also an important caveat in attempting to extend the emotional contagion concept to music. Specifically, the emotional contagion paradigm has largely been explored in regards to discrete emotional expressions. For instance, a study may expose someone to a fearful face for a matter of a few seconds. In contrast, the conveyance of emotion in music is typically played out over a more extended period of time. This difference in temporal dynamics may limit the generalizability of the empirical literature on emotion contagion to music. Nevertheless, the idea that moods, and not just discrete emotions, are contagious seems reasonable, and thus emotional contagion remains a viable explanation for at least some of the rewarding properties of music conveying happiness.

Several theorists have argued that emotional contagion is at least partially mediated by sensorymotor interactions. This idea converges with recent work on the so-called mirror neuron system. which describes neural activity in premotor cortex as a mechanism for translating observed actions into motor responses. The role of this system in perception of emotion, empathy, and social cognition in general has been discussed by several investigators (for review see de Gelder 2006), the basic idea being that the interpretation of sensory signals is mediated at least in part by the mirror neuron system, as it provides a way of modeling the intended outcome of the motor actions of others. If music taps into a similar system, it stands to reason that modeling or mimicking of emotions expressed by music may be one way in which music may induce emotion (Juslin 2005; Jackendoff and Lerdahl 2006; Molnar-Szakacs and Overy 2006). For example the acoustical features of sad or subdued music (e.g., slow tempo, low intensity, sustained tones, smooth transitions between tones) are compatible with the physical movements associated with sadness or depression (slowed action, low intensity of movements and vocalizations, etc.). Conversely, music typical of happiness or excitement tends to be loud, fast, with abrupt changes, and is associated with rapid, high-energy movements. These motor features are explicitly expressed in dance, but can also impact the tempo and vigor of other physical activities such as walking and running. Sensory-motor interactions as mediated by auditory and premotor regions may provide the link between listening and moving, since premotor cortices are often recruited during music perception in the absence of overt movement, just as rhythmic motor actions can elicit auditory cortex activity (Zatorre, Chen, and Penhune 2007). In turn, this interaction may enhance or even create an affective response because of the close relationship between emotions and their motor manifestations. The psychophysiological changes associated with music listening reviewed above might also provide afferent feedback to this same system, thereby further augmenting the affective state.

19.4.3. THE PROBLEM OF UNHAPPY MUSIC

Regardless of the method through which music invokes emotion, it is easy to see why individuals would select music that induces a happy mood. However, people frequently report enjoying music that induces negative affective states. Zentner, Grandjean, and Scherer (2008) suggest the presence of two primary factors that capture negative affect in music: Tension and Sadness. Why would someone actively choose to listen to music that causes tension or sadness, when such mood states are generally viewed as unpleasant or even aversive? No empirical literature really addresses this issue. However, some attempts have been made to explain this on theoretical grounds. Scherer (2004) proposes a distinction between aesthetic and other "utilitarian"

emotions, and suggests that aesthetic emotions are experienced in a manner that is detached from urgency or pragmatic, self-oriented concerns. Lacking this urgency, feelings induced by music may be experientially strong, but nevertheless lack the full physiological arousal that would arise when these emotions are induced by events that would directly impact the person in day-to-day life. This type of aesthetic emotion is not limited to music, but also occurs in various types of arts and literature. Such emotions may be experienced as rewarding because they augment our engagement with the art form, and allow us to focus our attention on the art form and away from other real-world distractions. Yet, there is still something unsatisfying about such an explanation in that we often listen to music without any specific aim of escapism. We suspect that if you asked people buying a compact disc or a ticket to a concert, few would suggest the purchase was based on a desire to escape or a desire to experience emotions. Something else must act as a reinforcer here.

19.4.4. EXPECTANCY AND PREDICTION CONFIRMATION

Among the many different mechanisms postulated to explain the reward of music, one of the most refined ideas involves the rewards associated with expectancy and prediction confirmation. This approach argues that the reward of music does not need to arise through the specific induction of mood states or discrete emotions, but rather music is rewarding because of properties intrinsic to how we process sequential events. In his classic book, Emotion and Meaning in Music. Leonard Meyer (1956) argued that music's ability to evoke emotion primarily derives from expectations. In the more recent book, Sweet Anticipation, David Huron (2006) expands on this idea, arguing for the presence of five components (labeled by the acronym ITPRA) that link expectations in music to reward. These include imagining responses, tension responses, prediction responses, reaction responses, and appraisal responses. Imagining responses refer to situations where we complete music in our imagination (ahead of the music's actual completion). Tension responses refer to the pre-outcome preparation (motoric and perceptual) that occurs in anticipation of music's next step or resolution. Prediction responses involve the results of a comparison between the person's prediction and the actual outcome of the music: when the music is accurately predicted it is experienced as rewarding (for the sake of clarity, we will refer to this as prediction confirmation, and use the term prediction more generically to refer to the act of forecasting future or subsequent events). Reaction responses reflect a quick response to the actual outcome, be it positive or negative. Finally, appraisal responses reflect the slower conscious determination of the meaning of the outcome.

The idea that prediction confirmation is rewarding is well supported. Indeed, psychological studies have strongly demonstrated that confirmation of predictions leads to positive affect (Mandler 1975). While such studies have rarely examined musical prediction, the structure of music lends itself well to predictions. Sections and phrases of music often have clear beginnings, middles, and ends, with the beginning and middle sections often providing clear clues as to how the section or phrase will end. Thus, music provides a series of micro- (note to note and phrase to phrase) and macro- (section to section) level outcomes. If you are asked to sing "Happy Birthday to ___," most people will not stop at the "to," but include the outcome "you." In this way music is filled with successive streams of micro- and macro-level events, each of which provides an opportunity to predict where the music will go and subsequently provides an opportunity to verify whether those predictions are met or not.

Once one is familiar with a particular musical tradition, it is possible to make reasonable predictions about multiple features of music, even if one has never heard the specific piece of music before. One need not be consciously aware of these predictions. Rather, there are statistical (actuarial) features within music traditions that direct the expectations of a listener without the listener necessarily being aware of these statistical properties and lead to implicit knowledge of

musical rules, or "syntax." For example, in Western music, one can predict frequent pitch changes of two semitones, since these are far more common than other pitch changes (for a review of the statistical properties of music see Huron 2006). The size of steps also can be predicted based on whether the melody is ascending or descending (descending uses smaller steps). The direction of the next pitch change can be predicted based on the size of the current pitch change, with small intervals typically followed by changes in the same direction and large intervals more frequently followed by movement in the opposite direction (melody regression). If you hear a first step in a melody descend, there is a 70% probability that the next step will also descend. Melodies frequently follow an arch-shaped pattern, rising in the middle and returning at their end. The total distribution of tones relative to the root can be predicted for the whole piece: even limiting notes to a given scale, certain tones, such as fifths, occur much more frequently than sixth and sevenths. Similarly, in many musical styles, chord progressions often have fairly set sequences, such as 12-bar blues, or resolutions to the tonic. While the typical listener is probably not consciously aware of most of these statistical properties, they nevertheless are likely to shape their expectations. In many regards, this is equivalent to the implicit pattern learning that develops during exposure to serially presented visual stimuli, which can be learned through repetition, even without the participants' explicit awareness of a pattern (Nissen and Bullemer 1987). In the visual realm, such implicit learning develops for both sequences of visual stimuli, as well as configurations of stimuli (Chun 2000) (also see Chapter 5 for further discussion of sensory configurational learning). While psychological research has focused more on the visual sphere, empirical studies make evident that implicit learning also occurs in the auditory domain (Dennis, Howard, and Howard 2006; Tillmann and McAdams 2004; van Zuijen et al. 2006). Because speech and music unfold over time, such implicit learning of sequences may be particularly critical, as the information must be perceived in sequence to have accurate meaning. Indeed, this sort of statistical learning of patterns and sequences lies at the heart of models of language acquisition, and appears to play a similarly prominent role in infants' acquisition of music (Saffran 2003).

As a consequence of the statistical properties of music, clear expectancies emerge. Such expectancies have motivating properties. We innately want to complete sequences. Singing "Happy birthday to ___," not only leads to a prediction of "you," but produces a desire to complete the phrase. Try to play an ascending major scale, but leave out the octave at the top of the scale. Perhaps even more dramatically, play the same scale in descending order but end on the second rather than the root. If you are like many people, there is an urge for completion. The resolution of this tension is experienced as pleasurable (this formulation is similar to drive theories [and even Freudian ideas about catharsis—see Chapter 2], in which need states are experienced as tension, and the removal of the need is experienced as rewarding). The need for completion is certainly weaker than our basic physiological needs, but it may nevertheless be experienced quite powerfully. Urges for sequence completion can be so great that they lead to clinically significant problems. This is most clearly seen in patients with obsessive-compulsive disorder, who become extremely distressed when unable to complete a behavior satisfactorily. The need for completion may reflect the nature of information storage. We often store information (or actions) in chunks, such that once started, the rest of the sequence is triggered automatically. This chunking often happens with no conscious effort (Bower and Winzenz 1969). Indeed, it may only be with conscious effort that the remainder of a well-learned sequence can be suppressed. Because of the sequential nature of music, such chunking is essential, since the memorization of a piece of music involves hundreds or even thousands of notes in sequence. which far outstrips the roughly seven pieces of information that we can typically hold on-line in short-term memory (Miller 1956).

To the extent that the desire for completion is motivating, it can be manipulated by a delay or obstruction of the predicted outcome. Composers frequently take advantage of this feature by

inserting extra chords or notes before the resolution. Similarly, slowing the tempo can delay the expected resolution. Such manipulations can heighten the motivation for completion, and increase the pleasure of the prediction confirmation when the expected closure finally happens.

19.4.5. DOPAMINE EXPECTATION AND PREDICTION

Studies of brain systems involved in reward have long emphasized the critical role of the dopamine (DA) system. Reinforcing drugs of abuse such as cocaine and amphetamine engage this system, and animals will perform repetitive operant responses to the exclusion of meeting other basic needs in order to stimulate DA projections (Wise 1998). For many years animal studies emphasized DA release simply as a neural substrate for reward. Consistent with such a model, the rapid buildup of DA caused by many drugs of abuse induces euphoria. However, over the last two decades a number of critical insights into DA functioning have emerged that point to DA's critical role in processes that are linked to prediction and anticipation.

DA cells show two types of firing (Grace 1991). The first is a tonic pacemaker-like firing, which provides a general statewise level of DA in target areas. This statewise activity may produce prolonged effects, such as determining the amount of motivated responding an individual is willing to make to obtain a reward. The second type of DA cell firing involves phasic bursts (brief trains) of firing. This second type of firing appears exquisitely tuned to the prediction of rewards. These cells fire when a reward is unpredicted, or underpredicted (Mirenowicz and Schultz 1994: Schultz 1998). By contrast, the cells do not fire in response to the receipt of fully predicted rewards, but rather fire to the cues that predicted its occurrence (further details provided in Chapter 14). For instance if a bell sound always precedes a reward (the bell is a conditioned stimulus), the cells will fire when the bell occurs, rather than firing for the actual rewarding outcome (Schultz, Apicella, and Ljungberg 1993). Critically, the pattern of DA cell firing fits a temporal difference learning model, in which learning occurs when there is an error in the prediction of an outcome (Schultz and Dickinson 2000). A positive prediction error occurs whenever the outcome is better than expected, while a negative prediction error occurs when an outcome is worse than expected. The phasic firing of DA neurons corresponds closely to a positive prediction error that is transmitted to multiple target brain regions simultaneously. Functional MRI studies have demonstrated that activity in the midbrain (presumably in DA neurons) conforms to this type of positive prediction error (D'Ardenne et al. 2008). This DA release is ramified in the ventral striatum, which consequently shows responses that also track positive prediction errors (Yacubian et al. 2006).

If we accept the basic tenet that music is rewarding at least in part due to its opportunity to provoke and confirm predictions, then DA is likely to be released during the learning process, especially when the listener is in the early process of becoming familiar with the piece. A person who is learning or relearning a piece of music will be able to successfully predict more aspects of the music. As such, initial parts of a sequence will take on the positive reward value that was previously associated just with the sequence's completion. In other words, when initially hearing the music, the biggest DA surge would likely arise from the closure of a phrase or a section, whereas with repetition, the beginning of the phrase will provoke more of the DA release. To be clear here, we are not suggesting that knowledge of the piece leads to a lack of pleasure in the piece or motivation to hear the piece through. However, knowledge of the piece will dramatically alter the motivational and rewarding experience of the music and the temporal features of these experiences.

19.4.6. DISSOCIATING POSITIVE PREDICTION ERRORS AND PREDICTION CONFIRMATION

There is a major paradox that arises when trying to integrate a temporal difference learning model with the idea that prediction confirmation is rewarding. Specifically, if prediction

confirmation drives reward, the more the person is able to predict the music, the more they should like it. By contrast, temporal difference models suggest that with too much learning, there will be little positive prediction error, and therefore DA release will decrease and perhaps be limited to just the first few notes of a section or a piece (just enough to identify the piece, since the rest would be highly predictable) (see Figure 19.3). There are at least three situations that provide a test of whether greater prediction confirmation leads to more or less reward. These include prior exposure, conventionality/prototypicality, and musical fluency.

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FIGURE 19.3

The contrasting effects of repeated exposures on the strength of positive prediction errors and prediction confirmation.

Prior exposure to a piece of music makes it more predictable. Thus, if accurate prediction is rewarding, one would expect music that is familiar to be better liked or enjoyed than music that is not familiar. This contention is supported by mere exposure effects in which the prior exposure to a stimulus increases preferences for that stimulus (Zajonc 1968). This effect was originally described in the visual domain, but subsequent studies have confirmed its presence for melodies (Wilson 1979). That is, the mere repetition of a melody makes it more preferred and pleasant. Such mere exposure effects can work both at the level of a total piece (listening to the piece performed on multiple occasions) or within a piece of music. Most music traditions include repetitions or repetitions with modest variations within the same piece of music. Thus, even if one has never heard a piece before, a motif, melody, or chord progression may be repeated multiple times, such that by the later parts of the piece, the key themes have become more familiar. When the variations are modest, the expectations may be fairly explicit and the listener may be consciously aware of the repetition. With more dramatic variations, the repetition may be less transparent, but nevertheless the aspects that have not changed (for instance the underlying chord progression, bass line, or rhythmic pattern) will still provide an implicit basis for prediction based on the previous exposures to the section.

On first listening, music that is more conventional/prototypical will also be easier to predict than music that strays from a musical tradition. Thus, pieces that conform to standard statistical features will be perceived positively. The flip side to this axiom is that music that grossly defies conventions will at least initially be viewed as unappealing because of its prevention of accurate predictions. The classic tale of the disastrous 1913 debut of Stravinsky's *Rite of Spring* is a case in point: the audience, unable to properly predict the music and unsettled by the unorthodox choreography, appeared to despise the piece. And yet, with repetition and exposure to its innovations, the piece has taken its place as one of the triumphs of its period.

Finally, fluency (i.e., the person's level of musical listening skill) should influence people's musical enjoyment, with individuals with greater musical fluency finding it easier to predict the music. The issue of fluency ties into a larger issue in general aesthetics. Reber, Schwarz, and Winkielman (2004) emphasize the idea that stimuli that are fluently processed are inherently pleasant, leading to increased positive affect. In music, this is partially supported. Musical novices tend to prefer simple, easier to predict, pieces over more challenging pieces (Smith and Melara 1990), which is consistent with a fluency view.

There are however limits to some of these prediction confirmation effects. While changes in preference ratings remain high after multiple exposures, they often asymptote after multiple repetitions (Bornstein 1989). Thus, at a certain point there is little further gain. Repetition of pieces close in time (for instance within a single extended session) leads to reductions in liking after as few as eight repetitions (Schellenberg, Peretz and Vieillard 2008), suggesting a cap on

the benefits of repetition. There appears an inverted *U*-shaped curve related to familiarity, in which repetitions producing greater familiarity produce increases in liking, but this effect peaks after multiple exposures and can be antagonized by a countervailing process related to over-familiarity, if repetitions occur too frequently after initial learning.

Similarly, fluency can lead to reduced liking of pieces that are too easy. Individuals with greater musical fluency take less pleasure from easy musical pieces relative to more challenging (less easy to predict) pieces (Smith and Melara 1990). If prediction confirmation alone were driving reward and preference, the appreciation of the simpler pieces should remain high even in the musically fluent. These data suggest that there is not a singular relationship between prediction and musical pleasure. Rather, the experience of pleasure more likely represents a summation or weighted integration of correct prediction and positive prediction error, with the relative weighting varying based on the extent of prior exposure to the musical piece or genre.

An additional feature of DA coding may lead to its greater engagement early in learning. Specifically, the DA system has long been recognized to play a role in responses to novelty. Novel stimuli trigger SN/VTA firing (Ljungberg, Apicella, and Schultz 1992). Several recent fMRI studies observed blood oxygen level-dependent (BOLD) responses in the SN/VTA region when healthy humans anticipated or viewed novel pictures or associations (Bunzeck and Duzel 2006; Wittmann et al. 2007). Kakade and Dayan (2002) suggest that this type of novelty-induced phasic firing of DA neurons provides a motivating "exploration bonus" that encourages exploration of stimuli or environments. In the context of music, this may produce a signal boost towards pursuing new musical experiences, which like positive prediction errors partially counteracts mere exposure effects in determining musical preferences. In most individuals this signal boost is probably weaker than the effects of expectancy and prediction, and generally limits individuals willing to explore radically different musical genres than ones that they already know. However, personality factors such as novelty seeking, and breadth of musical exposure, may lead some individuals to gain a greater novelty bonus for musical exploration.

19.4.7. Music, Pleasure, and Wanting

In the above discussion, we have frequently emphasized the experience of pleasure that arises from listening to music. We have also emphasized DA-striatal reward circuitry as an important substrate for affective aspects of music. However, it is critical to distinguish between different aspects of reward processing, which can be divided into reward learning, reward wanting, and reward liking. In addition to its role as a phasic reward learning cue, current models of DA function emphasize its role as a substrate for motivating behavior to obtain rewards. These models argue that DA firing itself does not underlie the subjective experience of pleasure, but rather provides a basis for the subjective experience of wanting (Berridge and Robinson 1998). For instance, manipulations of the DA system (particularly those involving the ventral tegmental area's projections to the nucleus accumbens) will alter the amount an animal is willing to work for a reward, but not its apparent consummatory pleasure (liking) of the reward (Salamone, Cousins, and Snyder 1997). By contrast, Berridge and Robinson argue that the experience of pleasure (i.e., liking) is linked instead to the endogenous opioid system.* To the extent that rapid increases in nucleus accumbens DA leads to euphoria, it is argued to arise secondary to its ability to stimulate beta-endorphins (Roth-Deri, Green-Sadan, and Yadid 2008).

Wanting and liking reflect different temporal phases of reward processing, with wanting corresponding to an anticipatory, appetitive phase, and liking corresponding to a consummatory phase. This anticipatory-consummatory temporal relationship parallels the repeated prediction-confirmation phases of music. It also parallels the fMRI findings of the study by Salimpoor et al. (in press) in which separate dorsal and ventral striatal activations emerged respectively in the anticipation of chill-inducing sections of music, and during the maximally pleasurable chill

period itself. Although PET imaging of DA release lacks the temporal resolution to distinguish these two phases, the observation of temporally discrete fMRI activations in the same locations as DA release suggests a potential biphasic dopaminergic response. The topography of these findings is intriguing in that recent addiction research has suggested greater dorsal striatal involvement in anticipation (craving) and greater ventral striatal (nucleus accumbens) engagement during intoxication (euphoria) (Koob and Volkow 2010).* We note in this regard music can have an almost compulsive-addictive feel to it, as the motivation to hear the music once started can be enormous. Indeed, for music fans, just imagining a few bars of a piece of music may produce a significant desire to experience the music.

19.4.8. DOPAMINE AND UNCERTAINTY

We have already noted that factors such as fluency, conventional/prototypicality, and repeated exposure will influence the degree of positive prediction errors and influence phasic dopamine firing. Music that is highly conventional, too easy, too repetitive, or that has been heard too many times will not produce positive prediction errors. There has to be a chance of being wrong.

Uncertainty of outcome brings us to another aspect of DA cell firing. Specifically, DA cells have been observed to show a distinct response related to unpredictability. In an electrophysiological study with monkeys (Fiorillo, Tobler, and Schultz 2003), it was observed that 29% of SN/VTA cells demonstrated firing which increased from the time a conditioned stimulus was presented to the time at which the outcome of the trial was given (i.e., the reward was or was not received). This sustained increase was maximal when probability was at 50% chance of reward or no reward, and was larger when the value of the potential reward was increased (or when the size of the difference between two potential rewards was increased). This extended period of firing may have two effects. First, given dopamine's motivational role, it may increase wanting or desire for the possible outcome. Such effects may contribute to numerous behaviors, such as gambling and watching sports, both of which produce substantial engagement of motivation when the outcome is unknown. Second, it may produce a state in which the subjective reward of the outcome is enhanced when it occurs (perhaps by priming the opioid system). Not all rewards are experienced equally; winning money produces greater reward than getting money that you knew was coming. Indeed, people will be more excited about winning a small amount of money than getting a larger amount of money that they already knew was coming. A win by one's favorite sports team over another team will be far more enjoyable when the outcome was not assured.

In the same manner, we suspect that uncertainty plays a major role in music appreciation, both increasing the motivation for the desired outcome and priming the subjective reward of prediction confirmation. Indeed, there may be ways of preventing 100% predictability even in a known piece of music. We noted previously that delaying a resolution may increase an urge for the resolution; the function of an appoggiatura in music is the perfect illustration of this phenomenon. Similarly, by inserting extra notes before a resolution, a composer may provide some uncertainty over whether the progression will end or go some place different; this phenomenon perhaps finds its extreme realization in the device common in nineteenth-century Western music known as a cadenza, which can extend a simple cadence sometimes for many minutes. Perhaps even more strikingly, the composer can insert notes that in the majority of other pieces lead in a different direction. In other words, the specific experience of the piece may run counter to a larger actuarial store of information about music, such that even if the piece is fully known, there is conflicting actuarial data on how the music should proceed. A common example of this effect is provided by the so-called deceptive cadence, in which a dominant chord, which would typically lead to a resolution back toward the tonal center or tonic chord, leads instead to a different chord (the submediant, in music-theoretic parlance), which is not expected, but is still perceived as an acceptable option. This situation sets up a tension between the implicit

knowledge of musical syntax rules learned from many prior exposures to the typical chord progression, and the veridical long-term memory trace associated with the piece itself that one may have heard on multiple occasions (see <u>Huron 2006</u> for additional discussion). In live performance situations, the music may become even more unpredictable as the performance is slightly different every time, and the performer has considerable leeway to emphasize some events over others, to introduce delays at particular moments, or in some cases to improvise entirely new musical passages.

The type of DA firing that occurs with uncertainty behaves in a temporally distinct manner from the positive prediction error signaling. Whereas the positive prediction error signal is brief and punctate, occurring when an outcome is better than expected (or a not fully expected cue occurs). the firing of DA neurons during unpredictability is maintained until the outcome is known. Thus its effects may be far more sustained and powerful. It also provides a focus not just on whether the outcome occurs, but when the outcome occurs. The longer the delay, the greater the motivation for reaching the resolution. Musically, such heightening can occur by extending the number of notes before a resolution, slowing the tempo, or even coming to a full rest before providing the expected outcome. In his 2006 treatise on music and prediction. David Huron never mentions issues of DA coding. However, his characterization of when individuals experience tension or desire for resolution appears highly consistent with the present formulation, as he describes that tension may be particularly large when statistical characteristics lead to a strong prediction of an outcome, but do not directly move to that outcome. He notes that it is in these situations where listeners often express the most clear motivation or desire when listening to music, using terms such as "yearning," which is certainly in the same subjective arena as the "wanting," "craving," or "compelled" experiences that are often described in relation to DA functioning.

Interestingly, tension and resolution lie at the heart of aesthetic theory. Dewey (1934) argued that aesthetics come from a conversion of resistance and tensions towards a resolution. There has to be some tension and movement towards resolution for a piece to be valued. A piece that is totally conventional in its movement to resolutions will lack impact. Rather, some degree of ambiguity or unpredictability is necessary to create tension. This may be at the essence of why expert fluent listeners may not particularly enjoy pieces that are too simple and easy. The rewards associated with correct prediction appear to be minimal if there was no risk of being wrong. Thus, there may be a threshold of uncertainty or difficulty that must be surpassed before prediction confirmation provides a reward. A similar process likely occurs with media other than music: books and TV shows aimed at young children are often unappealing to older children and adults (we suspect most readers who were ever forced as adults to watch an episode of the children's TV show *Teletubbies* are nodding their heads in agreement while reading this).

Armstrong and Detweiler-Bedell (2008) make a distinction between the types of rewards associated with fluency and those associated with works that provide greater challenges. They suggest that fluency alone may be associated with a piece of art being perceived as pretty, whereas true beauty in art emerges when greater levels of processing must be invested to understand (resolve) the piece. In other words, there has to be an ambiguity in order to reach a high reward. To the extent that music can provide both uncertainty and repeated opportunities for resolution and prediction confirmation, it is capable of moving beyond the simply pretty to the arena that Armstrong and Detweiler-Bedell refer to as beauty.

19.5. CONCLUSIONS

We have articulated several routes through which music may be experienced as rewarding, including the manipulation of arousal and emotional contagion, the engagement of "aesthetic emotions," and by tapping mechanisms involved in coding predictions and uncertainty. Thus,

rather than proposing a singular mechanism through which music becomes rewarding, we suggest that there are multiple mechanisms that enter into the process. These different mechanisms rely on several different neural circuits, including those involved in regulating arousal, motivation, and reward prediction. We have particularly emphasized mesolimbic and paralimbic processes as central to the experience of reward in music. These areas are of course also present in mammals in general. Yet, music does not appear to act as a reward for any other species. We suspect that these species lack the cortical auditory processing architecture that would allow them to organize, learn, anticipate, and predict long sequences and combinations of tones and timbres in a manner that produces inherent reward. Hence, we would once again emphasize that musical pleasure arises from an interaction between biologically ancient reward mechanisms and much more recently evolved cortical systems which are highly modifiable by individual experience and culture.

An observant reader may note that in presenting a model of musical reward that focuses on anticipation and prediction, we have provided little data from studies that were designed to directly test these models. However, if, as we argue, features related to anticipation, prediction confirmation, and uncertainty in music engage dopaminergic, limbic, and paralimbic mechanisms, and their associated cortical loops, then it should be possible to test these ideas by manipulating these features with appropriate neuroimaging, electrophysiological, and neuropsychological paradigms. Such studies would move the field beyond a simple statement that music engages areas involved in emotion, to a more comprehensive assessment of the neural mechanisms that underlie our continued desire for, and pleasure from, sequences of tones.

REFERENCES

- 1. Armstrong T., Detweiler-Bedell B. Beauty as an emotion: The exhilarating prospect of mastering a challenging world. Review of General Psychology. 2008;12:305–29.
- Bachorowski J. A., Owren M. J. Not all laughs are alike: Voiced but not unvoiced laughter readily elicits positive affect. Psychological Science. 2001;12:252–57. [PubMed: 11437310]
- 3. Berlyne D. New York: Appleton-Century Crofts; Aesthetics and Psychobiology. 1971
- 4. Berridge K. C., Robinson T. E. What is the role of dopamine in reward: Hedonic impact, reward learning, or incentive salience? Brain Research. Brain Research Reviews. 1998;28:309–69. [PubMed: 9858756]
- Blood A. J., Zatorre R. J. Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. Proceedings of the National Academy of Sciences. 2001;98:11818–23. [PMC free article: PMC58814] [PubMed: 11573015]
- 6. Blood A. J., Zatorre R. J., Bermudez P., Evans A. C. Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions. Nature Neuroscience. 1999;2:382–87. [PubMed: 10204547]
- 7. Bornstein R. F. Exposure and affect: Overview and meta-analysis of research, 1968–1987. Psychological Bulletin. 1989;106:265–89.
- 8. Bower G. H., Winzenz D. Group structure coding and memory for digit series. Journal of Experimental Psychology Monographs, 1969;80:1–17.
- Breiter H. C., Gollub R. L., Weisskoff R. M., Kennedy D. N., Makris N., Berke J. D., Goodman J. M., et al. Acute effects of cocaine on human brain activity and emotion. Neuron. 1997;19:591–611. [PubMed: 9331351]
- 10. Brown S., Martinez M., Parsons L. Passive music listening spontanelously engages limbic and paralimbic systems. NeuroReport. 2004;15:2033–37. [PubMed: 15486477]
- 11. Buckholtz J. W., Treadway M. T., Cowan R. L., Woodward N. D., Benning S. D., Li R., Ansari M. S., et al. Mesolimbic dopamine reward system hypersensitivity in individuals

- with psychopathic traits. Nature Neuroscience. 2010;13:419–21. [PMC free article: PMC2916168] [PubMed: 20228805]
- 12. Bunzeck N., Duzel E. Absolute coding of stimulus novelty in the human substantia nigra/VTA. Neuron. 2006;51:369–79. [PubMed: 16880131]
- 13. Carter C. S., Mintun M., Cohen J. D. Interference and facilitation effects during selective attention An (H2O)-O-15 PET study of Stroop task performance. Neuroimage. 1995;2:264–72. [PubMed: 9343611]
- 14. Chakrabarti B., Bullmore E., Baron-Cohen S. Empathizing with basic emotions: Common and discrete neural substrates. Social Neuroscience. 2006;1:364–84. [PubMed: 18633800]
- 15. Chun M. M. Contextual cueing of visual attention. Trends in Cognitive Science. 2000;4:170–78. [PubMed: 10782102]
- Craig D. G. An exploratory study of physiological changes during chills induced by music. Music Scientiae. 2005;9
- 17. D'Ardenne K., McClure S. M., Nystrom L. E., Cohen J. D. BOLD responses reflecting dopaminergic signals in the human ventral tegmental area. Science. 2008;319:1264–67. [PubMed: 18309087]
- Darwin C. The Descent of Man and Selection in Relation to Sex. John Murray: London. de Gelder, B. 2006. Towards the neurobiology of emotional body language. Nature Reviews Neuroscience. 1871;7:242–49.
- 19. Dennis N. A., Howard J. H., Howard D. V. Implicit sequence learning without motor sequencing in young and old adults. Experimental Brain Research. 2006;175:153–64. [PubMed: 16788812]
- 20. Dewey J. New York: Penguin Group; Art as Experience. 1934
- 21. Dubé L., LeBel J. L. The content and structure of laypeople's concept of pleasure. Cognition and Emotion. 2003;17:263–295. [PubMed: 29715723]
- 22. Fecteau S., Belin P., Joanette Y., Armony J. L. Amygdala responses to nonlinguistic emotional vocalization. Neuroimage. 2007;36:480–87. [PubMed: 17442593]
- 23. Fiorillo C. D., Tobler P. N., Schultz W. Discrete coding of reward probability and uncertainty by dopamine neurons. Science. 2003;299:1898–1902. [PubMed: 12649484]
- 24. Fitch W. T. The biology and evolution of music: A comparative perspective. Cognition. 2006;100:173–215. [PubMed: 16412411]
- Gabrielsson A. Oxford: Oxford University Press; Emotions in Strong Experiences with Music. 2001
- 26. Gardner W., Licklider J., Weiss A. Suppression of pain by sound. Science. 1960;132:32–33. [PubMed: 13826543]
- 27. Geissmann T. Duet songs of the siamang, Hylobates syndactylus: I. Structure and organisation. Primate Report. 2000;56:33–60.
- 28. Goldstein A. Thrills in response to music and other stimuli. Physiological Psychology. 1980:8:126–29.
- 29. Gosselin N., Peretz I., Johnsen E., Adolph R. Amygdala damage impairs emotion recognition from music. Neuropsychologia. 2006;129:2585–92.
- Gosselin N., Peretz I., Noulhiane M., Hasboun D., Beckett C., Baulac M. Impaired recognition of scary music following unilateral temporal lobe excision. Brain. 2005;128 [PubMed: 15699060]
- 31. Gottfried J., Small D., Zald D. H. The chemical senses. Zald D. H., Rauch S. L. Oxford University Press; The Orbitofrontal Cortex. 2006:125–72.
- 32. Gould S. J., Lewontin R. C. The spandrels of San Marco and the panglossian paradigm: A critique of the adaptationist programme. Proceedings of the Royal Society of London Series B. 1979;205:581–98. [PubMed: 42062]
- 33. Grace A. A. Phasic versus tonic dopamine release and the modulation of dopamine system responsivity a hypothesis for the etiology of schizophrenia. Neuroscience. 1991;41:1–24.

- [PubMed: 1676137]
- 34. Grewe O., Nagel F., Kopiez R., Altenmuller E. Emotions over time: Synchronicity and development of subjective, physiological, and facial affective reactions to music. Emotion. 2007a;7:774–88. [PubMed: 18039047]
- 35. Grewe O., Nagel F., Kopiez R., Altenmuller E. Listening to music as a re-creative process —Physiological, psychological and psychoacutical correlates of chills and strong emotions. Music Perception. 2007b;24:297–314.
- Griffiths T., Warren J., Dean J., Howard D. 'When the feeling's gone': A selective loss of musical emotion. Journal of Neurology, Neurosurgery & Psychiatry. 2004;75:344–45.
 [PMC free article: PMC1738902] [PubMed: 14742630]
- 37. Griffiths T. D., Rees A., Witton C., Cross P. M., Shakir R. A., Green G. G. Spatial and temporal auditory processing deficits following right hemisphere infarction. A psychophysical study. Brain. 1997;120:785–94. [PubMed: 9183249]
- 38. Guhn M., Hamm A., Zentner M. R. Physiological and muscio-acustic correlates of the chill response. Music Perception. 2007;24:473–83.
- 39. Habib M., Daquin G., Milandre L., Royere M., Rey M., Lanteri A. Mutism and auditory agnosia due to bilateral insular damage role of the insula in human communication. Neuropsychologia. 1995;33:327–39. [PubMed: 7791999]
- 40. Huron D. Cambridge, MA: MIT Press; Sweet Anticipation: Music and the Psychology of Expectation. 2006
- 41. Jackendoff R., Lerdahl F. The capacity for music: What is it and what's special about it? Cognition. 2006;100:33–72. [PubMed: 16384553]
- 42. Johnstone T., van Reekum C. M., Oakes T. R., Davidson R. J. The voice of emotion: An FMRI study of neural responses to angry and happy vocal expressions. Social Cognitive and Affective Neuroscience. 2006;1:242–49. [PMC free article: PMC1905858] [PubMed: 17607327]
- 43. Juslin P. N. From mimesis to chatarsis: Expression, perception, and induction of emotion in music. Miell D., MacDonald R., Hargreaves D. New York: Oxford University Press; Musical Communication. 2005:85–115.
- 44. Juslin P. N., Laukka P. Communication of emotions in vocal expression and music performance: Different channels, same code? Psychological Bulletin. 2003;129:770–814. [PubMed: 12956543]
- 45. Juslin P. N., Vastfjall D. Emotional responses to music: The need to consider underlying mechanisms. Behavioral and Brain Sciences. 2008;31:559–75. [PubMed: 18826699]
- 46. Kakade S., Dayan P. Dopamine: Generalization and bonuses. Neural Network. 2002;15:549–59. [PubMed: 12371511]
- 47. Khalfa S., Roy M., Rainville P., Dalla Bella S., Peretz I. Role of tempo entrainment in psychophysiological differentiation of happy and sad music? International Journal of Psychophysiology. 2008;68:17–26. [PubMed: 18234381]
- 48. Knutson B., Gibbs S. E. Linking nucleus accumbens dopamine and blood oxygenation. Psychopharmacology (Berl). 2007;191:813–22. [PubMed: 17279377]
- 49. Koelsch S., Fritz T., Cramon D., Muller K., Friederici A. D. Investigating emotion with music: An fMRI study. Human Brain Mapping. 2006;27:239–50. [PMC free article: PMC6871371] [PubMed: 16078183]
- 50. Koelsch S., Kilches S., Steinbeis N., Schelinski S. Effects of unexpected chords and of performer's expression on brain responses and electrodermal activity. PLoS One. 2008;3 [PMC free article: PMC2435625] [PubMed: 18612459]
- 51. Koob G. F., Volkow N. D. Neurocircuitry of addiction. Neuropsychopharmacology. 2010;35:217–38. [PMC free article: PMC2805560] [PubMed: 19710631]
- 52. Kringelbach M. L., Rolls E. T. The functional neuroanatomy of the human orbitofrontal cortex: Evidence from neuroimaging and neuropsychology. Progress in Neurobiology.

- 2004;72:341-72. [PubMed: 15157726]
- 53. Krumhansl C. L. An exploratory study of musical emotions and psychophysiology. Canadian Journal of Experimental Psychology. 1997;51:336–53. [PubMed: 9606949]
- 54. Lane R. D., Reiman E. M., Bradley M. M., Lang P. J., Ahern G. L., Davidson R. J., Schwatz G. Neuroanatomical correlates of pleasant and unpleasant emotion. Neuropsychologia. 1997;35:1437–44. [PubMed: 9352521]
- Lang P. J., Bradley M. M., Fitzsimmons J. R., Cuthbert B. N., Scott J. D., Moulder B., Nangia V. Emotional arousal and activation of the visual cortex: An fMRI analysis. Psychophysiology. 1998;35:199–210. [PubMed: 9529946]
- 56. Levinson J. Music and negative emotions. Levinson J. Ithaca: Cornell University Press; Music, Art and Metaphysics: Essays in Philosophical Aesthetics. 1990:306–35.
- 57. Lishner D., Cooter A. B., Zald D. H. Addressing measurement limitations in affective rating scales: Development of an empirical valence scale. Cognition and Emotion. 2008:22:180–92.
- 58. Ljungberg T., Apicella P., Schultz W. Responses of monkey dopamine neurons during learning of behavioral reactions. Journal of Neurophysiology. 1992;67:145–63. [PubMed: 1552316]
- 59. Mandler G. New York: John Wiley; Mind and Emotion. 1975
- 60. McDermott J., Hauser M. D. Nonhuman primates prefer slow tempos but dislike music overall. Cognition. 2007;104:654–68. [PubMed: 16935277]
- 61. Menon V., Levitin D. J. The rewards of music listening: Response and physiological connectivity of the mesolimbic system. NeuroImage. 2005;28:175–84. [PubMed: 16023376]
- 62. Meyer L. B. Chicago: University of Chicago Press; Emotion and Meaning in Music. 1956
- 63. Miller G. A. The magical number seven, plus or minus two: Some limits to our capacity for processing information. Psychological Review. 1956;63:81–97. [PubMed: 13310704]
- 64. Mirenowicz J., Schultz W. Importance of unpredictability for reward responses in primate dopamine neurons. Journal of Neurophysiology. 1994;72:1024–27. [PubMed: 7983508]
- 65. Mitterschiffthaler M. T., Fu C. H., Dalton J. A., Andrew C. M., Williams S. C. A functional MRI study of happy and sad affective states induced by classical music. Human Brain Mapping. 2007;28:1150–62. [PMC free article: PMC6871455] [PubMed: 17290372]
- 66. Molnar-Szakacs I., Overy K. Music and mirror neurons: From motion to 'e'motion. Social Cognitive & Affective Neuroscience. 2006;1:235–41. [PMC free article: PMC2555420] [PubMed: 18985111]
- 67. Nilsson U., Unosson M., Rawal N. Stress reduction and analgesia in patients exposed to calming music postoperatively: A randomized controlled trial. European Journal of Anaesthesiology. 2005;22:96–102. [PubMed: 15816586]
- 68. Nissen M. J., Bullemer P. Attentional requirements of learning: Evidence from performance measures. Cognitive Psychology. 1987;19:1–32.
- 69. North A. C., Hargreaves D. J. Liking, arousal potential, and the emotions expressed by music. Scandinavian Journal of Psychology. 1997;38:45–53. [PubMed: 9104103]
- 70. Panksepp J. The emotional sources of "chills" induced by music. Music Perception. Music Perception. 1995;13:171–207.
- 71. Patel A. D. Oxford University Press; Oxford, U.K: Music, Language and the Brain. 2007
- 72. Patel A. D., Iversen J. R., Bregman M. R., Schuiz I. Experimental evidence for synchronization to a musical beat in a nonhuman animal. Current Biology. 2009;19:827–30. [PubMed: 19409790]
- 73. Peretz I., Blood A., Penhun V., Zatorre R. Cortical deafness to dissonance. Brain. 2001;124:928–40. [PubMed: 11335695]
- 74. Pinker S. New York: Norton; How the Mind Works. 1997

- 75. Pourtois G., de Gelder B., Bol A., Crommerlinck M. Perception of facial expressions and voices and of their combination in the human brain. Cortex. 2005;41:49–59. [PubMed: 15633706]
- 76. Preston S. D., de Waal F. B. Empathy: Its ultimate and proximate bases. Behavioral and Brain Sciences. 2002;25:1–20. [PubMed: 12625087]
- Reber R., Schwarz N., Winkielman P. Processing fluency and aesthetic pleasure: Is beauty in the perceiver's processing experience? Personality and Social Psychology Review. 2004;8:364–82. [PubMed: 15582859]
- 78. Rickard N. S. Intense emotional responses to music: A test of the physiological arousal hypothesis. Psychology of Music. 2004;32:371–88.
- 79. Roth-Deri I., Green-Sadan T., Yadid G. beta-Endorphin and drug-induced reward and reinforcement. Progress in Neurobiology. 2008;86:1–21. [PubMed: 18602444]
- 80. Roy M., Peretz I., Rainville P. Emotional valence contributes to music-induced analgesia. Pain. 2008;134:140–47. [PubMed: 17532141]
- 81. Saffran J. R. Statistical language learning mechanisms and constraints. Current Directions in Psychological Science. 2003;12:110–14.
- 82. Salamone J. D., Cousins M. S., Snyder B. J. Behavioral functions of nucleus accumbens dopamine: Empirical and conceptual problems with the anhedonia hypothesis.

 Neuroscience & Biobehavioral Reviews. 1997;21:341–59. [PubMed: 9168269]
- 83. Salimpoor V., Benvoy M., Longo G., Cooperstock J., Zatorre R. The rewarding aspects of music listening are related to degree of emotional arousal. PloS One. 2009;4:1–14. [PMC free article: PMC2759002] [PubMed: 19834599]
- 84. Salimpoor V. N., Benovoy M., Larcher K., Dagher A., Zatorre R. J. Anatomically distinct dopamine release during anticipation and experience of peak emotion to music. Nature Neuroscience. In press. [PubMed: 21217764]
- 85. Schachner A., Brady T. F., Pepperberg I. M., Hauser M. D. Spontaneous Motor Entrainment to Music in Multiple Vocal Mimicking Species. Current Biology. 2009;19:831–36. [PubMed: 19409786]
- 86. Schellenberg E. G., Peretz I., Vieillard S. Liking for happy- and sad-sounding music: Effects of exposure. Cognition and Emotion. 2008;22:218–37.
- 87. Scherer K. R. Which emotions can be induced by music? What are the underlying mechanisms? And how can we measure them? Journal of New Music Research. 2004;33:239–51.
- 88. Schultz W. Predictive reward signal of dopamine neurons. Journal of Neurophysiology. 1998;80:1–27. [PubMed: 9658025]
- 89. Schultz W., Apicella P., Ljungberg T. Responses of monkey dopamine neurons to reward and conditioned stimuli during successive steps of learning a delayed response task.

 Journal of Neuroscience. 1993;13:900–13. [PMC free article: PMC6576600] [PubMed: 8441015]
- 90. Schultz W., Dickinson A. Neuronal coding of prediction errors. Annual Review of Neuroscience. 2000;23:473–500. [PubMed: 10845072]
- 91. Silvestri A., Kapp B. Amygdaloid modulation of mesopontine peribrachial neuronal activity: Implications for arousal. Behavioral Neuroscience. 1998;112:571–88. [PubMed: 9676974]
- 92. Small D. M., Zatorre R. J., Dagher A., Evans A. C., Jones-Gotman M. Changes in brain activity related to eating chocolate From pleasure to aversion. Brain. 2001;124:1720–33. [PubMed: 11522575]
- 93. Smith J. D., Melara R. J. Aesthetic preference and syntactic prototypicality in music Tis the gift to be simple. Cognition. 1990;34:279–98. [PubMed: 2328564]
- 94. Spencer H. The origin and function of music. Fraser's Magazine. 1857;56:396–408.

- Stein J. L., Wiedholz L. M., Bassett D. S., Weinberger D. R., Zink C. F., Mattay V. S., Meyer-Lindenberg A. A validated network of effective amygdala connectivity. NeuroImage. 2007;36:736–45. [PubMed: 17475514]
- 96. Steinbeis N., Koelsch S., Sloboda J. The role of harmonic expectancy violations in musical emotion. Journal of Cognitive Neuroscience. 2006;18:1380–93. [PubMed: 16859422]
- 97. Stewart L., von Kreigstein K., Warren J. D., Griffiths T. D. Music and the brain: Disorders of musical listening. Brain. 2006;128:2533–53. [PubMed: 16845129]
- 98. Thaut M. H., Davis W. B. The influence of subject-selected versus experiment-chosen music on affect, anxiety, and relaxation. Journal of Music Therapy. 1993;30:210–23.
- Tillmann B., McAdams S. Implicit learning of musical timbre sequences: Statistical regularities confronted with acoustical (dis)similarities. Journal of Experimental Psychology-Learning Memory and Cognition. 2004;30:1131–42. [PubMed: 15355141]
- 100. van Zuijen T. L., Simoens V. L., Paavilainen P., Naatanen R., Tervaniemi M. Implicit, intuitive, and explicit knowledge of abstract regularities in a sound sequence: An event-related brain potential study. Journal of Cognitive Neuroscience. 2006;18:1292–1303. [PubMed: 16859415]
- 101. Vieillard S., Peretz I., Gosselin N., Khalfa S., Gagnon L., Bouchard B. Happy, sad, scary and peaceful musical excerpts for research on emotions. Cognition and Emotion. 2008;22:720–52.
- 102. Voss J., Good M., Yates B., Baun M., Thompson A., Hertzog M. Sedative music reduces anxiety and pain during chair rest after open-heart surgery. Pain. 2004;112:197–203. [PubMed: 15494201]
- 103. Watson D., Tellegen A. Toward a consensual structure of mood. Psychological Bulletin. 1985;92:426–57. [PubMed: 3901060]
- 104. Wild B., Erb M., Bartels M. Are emotions contagious? Evoked emotions while viewing emotionally expressive faces: Quality, quantity, time course and gender differences. Psychiatry Research. 2001;102:109–24. [PubMed: 11408051]
- 105. Wilson W. R. Feeling more than we can know: Exposure effects without learning. Journal of Personality and Social Psychology. 1979;37:811–21.
- 106. Wise R. A. Drug-activation of brain reward pathways. Drug and Alcohol Dependence. 1998;51:13–22. [PubMed: 9716927]
- 107. Wittmann B. C., Bunzeck N., Dolan R. J., Duzel E. Anticipation of novelty recruits reward system and hippocampus while promoting recollection. Neuroimage. 2007;38:194–202. [PMC free article: PMC2706325] [PubMed: 17764976]
- 108. Yacubian J., Glascher J., Schroeder K., Sommer T., Braus D. F., Buchel C. Dissociable systems for gain- and loss-related value predictions and errors of prediction in the human brain. Journal of Neuroscience. 2006;26:9530–37. [PMC free article: PMC6674602] [PubMed: 16971537]
- 109. Zajonc R. B. Attitudinal effects of mere exposure. Journal of Personality and Social Pychology. 1968;9:1–27.
- 110. Zald D. H. The human amygdala and the emotional evaluation of sensory stimuli. Brain Research Reviews. 2003;41:88–123. [PubMed: 12505650]
- 111. Zatorre R. J., Chen J. L., Penhune V. B. When the brain plays music: Auditory-motor interactions in music perception and production. Nature Reviews Neuroscience. 2007;8:547–58. [PubMed: 17585307]
- 112. Zentner M., Grandjean D., Scherer K. Emotions evoked by the sound of music:
 Characterization, classification, and measurement. Emotion. 2008;8:494–521. [PubMed: 18729581]
- 113. Zhao H., Chen A. C. Both happy and sad melodies modulate tonic heat pain. Journal of Pain. 2009;10:953–60. [PubMed: 19595640]

Footnotes

- * Although, as discussed in Chapter 13, opioid processes in the basolateral amygdala may also help mediate incentive learning and the encoding of incentive value, casting a slightly different light on the opiate "liking" hypothesis.
- * A different perspective is provided in <u>Chapter 14</u>, where it is argued that ventral and dorsal striatum are involved in Pavlovian and instrumental conditioning, respectively.

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