TOWARDS A NEUROBIOLOGY OF MUSICAL EMOTIONS

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The functioning of the brain is fascinating. It fascinates for the obvious reason that the brain is the commander of all our actions, thoughts, and motivations. By studying its functioning, we hope to obtain crucial information about the biological basis of human cognition and emotion. Neuropsychology is the discipline concerned with these questions. As its name indicates, neuropsychology aims to relate neural mechanisms to mental functions. It is an old discipline, dating back to the discovery by Broca in (1861) that speech was related to the functioning of a small region of the left brain. Following this discovery, the neural correlates of musical abilities were similarly scrutinized (e.g. Bouillaud, 1865). Although the neuropsychological approach to music is a century old, progress has been slow until recently. Recent advances in brain-imaging techniques (see Chapter 12, this volume), as well as the current trend of viewing most human activities from a biological perspective, has intensified research activities in the field.

As a result of this biological trend, neuropsychology has been recently renamed 'cognitive neuroscience'. This change in terminology reflects the intention to include neuropsychology within the vast domain of neuroscience. Because neuroscience covers a large spectrum of discipline—from the physiological study of single neurons in the turtle retina (Sernagor & Grzywacz, 1996) to the brain organization subserving the sense of humour in humans (Shammi & Stuss, 1999)—'cognitive' has qualified the 'neuroscience' term. The qualifier is unfortunate because 'cognitive' usually excludes emotion. Indeed, cognition is often seen as antithetical to emotion. For example, Kivy (1990) in his influential essay on the meaning of music coined the term 'cognitivist' to refer to the position that holds that music simply expresses emotions without inducing them. The opposite position, called 'emotivist', holds that music induces emotions in listeners.

The antagonism between 'cognitivists' and 'emotivists' is not limited to music psychology. It has a long history starting with Descartes's early separation between emotion and reason. Still today, the majority of experimental psychologists are 'cognitivists' by default. They tend to ignore emotions. This neglect partly reflects the information-processing approach that started in the early sixties (e.g. Neisser, 1967), which used the computer as a metaphor for mental functions. According to this approach, the brain is a machine, devoid of emotions.

Recently, however, neuropsychologists (or neuroscientists) have become more concerned with emotions (e.g. Phelps, 2006). Although neuropsychologists continue to distinguish between emotional and cognitive processes, they no longer reject the emotional part as being too obscure or subjective to be studied scientifically. On the contrary, emotions are now studied for their own sake. In their two popular books published in 1994 and 1996 respectively, Damasio and LeDoux contributed greatly to the rapprochement between cognition and emotion in neuropsychology. Reason is no longer seen as the human-specific activity that controls emotional irrationality. As Damasio (1994) showed, emotional processes are an integral part of decision making and are not confined to subcortical brain structures that humans share with other animals. Emotions recruit portions of the frontal lobes, which are the largest and latest brain structures to develop in the human brain. Thus, neuropsychologists are currently studying emotions just as they study any other mental function worthy of inquiry.

The objective of this chapter is to present current knowledge about musical emotions from a neuropsychological perspective. In doing so, I will adopt a biological perspective. Music, and *a fortiori* musical emotions, are generally *not* regarded as biological functions. Rather, music-related functions are considered as a refined product of human culture. Over the last decade, however, research has yielded a considerable amount of data that suggest that music might be part of human nature (Peretz, 2006). The study of musical emotions plays a crucial role in this biological perspective. Indeed, musical emotions are inherent to experiences of music and may account for its ubiquity. Accordingly, understanding the biological origin of musical emotions may shed light on the biological roots of music processing more generally. Here, I will examine the extent to which musical emotions might be biologically determined. Since the evidence points to biological foundations of musical emotions, I will examine the possibility that music is particularly suited (or designed) to invade emotion circuits that have evolved for emotional vocalizations.

5.1 MUSICAL EMOTIONS: UNIVERSALITY AND PREDISPOSITIONS

Musical emotions are often considered to be too personal, elusive, and variable to be studied scientifically. *A fortiori*, emotions could not be subserved by neuroanatomical

structures and functions shared by all members of the same species. The work of Paul Ekman on human facial expressions has helped to convince the scientific community that the above view is inadequate (see Peretz, 2001, for a review). In music, the recent focus on 'basic emotions' has provided ample evidence that emotional responses to music can be remarkably invariant across listeners of different ages.

'Basic emotions' refer to emotions like happiness, sadness, anger, and fear. Such basic emotions are today the main focus of neuropsychological studies, because these emotions are assumed to be innate, reflex-like circuits that cause a distinct and recognizable behavioural and physiological pattern (e.g. Panksepp, 1998). Although basic emotions may differ from what most adults experience when listening to music (for example, see Zentner, Grandjean, & Scherer, 2008, for a more nuanced range of musically induced emotions), many researchers believe that music can induce happiness, sadness, and fear. These basic emotions are typically the target of film soundtracks, especially those intended for children. Moreover, these basic emotions are among the easiest to recognize and communicate in music (e.g. Gabrielsson & Juslin, 2003; Juslin & Laukka, 2003). Thus, the present chapter will focus on basic emotions.

If musical communication of basic emotions is biologically prepared, similar emotional intentions should be recognized across music cultures. That is, we should be able to infer the emotions expressed by a musical culture to which we have never been exposed (and which has not yet been 'contaminated' by Western music). Conversely, adults from musically isolated cultures should be able to infer the musical emotions of Western music. Curiously, these predictions are tested rarely. The few published cross-cultural studies are encouraging, in showing that Western listeners can easily recognize joy, sadness, and anger in Hindustani ragas (Balkwill & Thompson, 1999; see also Chapter 27, this volume), and that Japanese listeners are able to recognize joy, anger, and sadness from both Hindustani and Western music. Interestingly, Japanese listeners do not perform systematically better on Japanese than on Hindustani music (Balkwill, Thompson, & Matsunaga, 2004). Similarly, Chinese listeners are able not only to distinguish happy from sad music written following Western conventions, but they also exhibit sensitivity to the same structural features (mode and tempo) as do Westeners (see Table 5.1; Rousseau, Peretz, & Dalla Bella, unpublished data). Thus, these findings point to the existence of some invariance in expressing basic emotions across musical cultures. Although non-Western participants may have assimilated the rules of Western music through exposure, it is remarkable how quickly cues to musical emotions, such as mode, which appear to be so culture-specific, can be internalized by listeners of a different culture. This flexibility is suggestive of an underlying universal bias on which listeners build their own cultural variants and assimilate those of distant cultures.

Remarkable invariance across individuals of different cultures is also evident among members of the same culture. For example, ordinary adult listeners need less than a quarter of a second of music (e.g. one chord or a few notes) to classify musical excerpts as happy or sad (Peretz, Gagnon, & Bouchard, 1998; see Bigand, Vieillard, Madurell, Marozeau, & Dacquet, 2005, for similar findings with slightly longer excerpts—1 second—and more emotions). Moreover and more generally, emotional judgements

Table 5.1 The mean ratings (standard deviation) were provided by 48 Chinese participants (mean age: 21 years), born in China and who emigrated to Canada less than 60 months prior to the testing. They rated whether each musical excerpt sounded happy or sad on a 10-point scale, with 1 indicating very sad and 10 very happy. The original versions were 32 classical musical excerpts (e.g. *Adagio* from Albinoni) that were synthesized and transcribed for piano. These versions were modified so that all tempi were set to a unique median value (tempo change), or were transcribed in the opposite mode (mode change), or contained both the tempo and mode change (tempo + mode change; see Peretz, Gagnon, and Bouchard, 1998 for all the details). As can be seen, listeners' ratings depended on the version, with $F(3,141) = 64.23$, $p<.001$ for the interaction between version and happy/sad tone. The ratings did not differ from those obtained by Western students (Rousseau, Peretz, and Dalla Bella, unpublished data).

	Music	
Version	Happy	Sad
Original	7.9 (0.1)	3.9 (0.1)
Tempo change	7.0 (0.1)	4.5 (0.1)
Mode change	7.3 (0.2)	4.9 (0.1)
Tempo + mode change	6.1 (0.1)	5.4 (0.1)

exhibit a high degree of consistency across listeners of the same culture who vary widely in terms of musical training (e.g. Vieillard et al, 2008). These results indicate that the perception of basic emotions in music is natural and effortless.

The universality of expressions of emotions is necessary but not sufficient for us to conclude that they are biologically determined. Universality could also result from common learning experiences. All infants are exposed to the same situations (e.g. pain, being left alone, or reassured) across cultures. Music is typically used in these contexts. Caregivers around the world sing to their infants, with the intuition (or instinct?) that music has the power to regulate the infant's state (e.g. comforting) or the quality of interaction (e.g. attention getting). Caregivers nicely mirror infants' perceptual abilities by singing more slowly, at a higher pitch, with exaggerated rhythm, and in a more loving or emotionally engaging manner when singing to infants than when singing alone (e.g. Trainor, Clark, Huntley, & Adams, 1997). Exposure to maternal singing, however, cannot account for the observation that two-day-old hearing infants, born from congenitally deaf parents (who sign and do not sing or speak), prefer infant-directed singing to adult-directed singing (Masataka, 1999; see Chapter 23, this volume). In short, responsiveness to infant-directed singing appears to be innate.

Caregivers also speak to infants in a sing-song manner called 'baby-talk' or 'infant-directed' speech. Regardless of the language adults speak, they raise their voice to elicit the infant's attention and talk at a much slower rate. Adults mostly communicate emotions in their infant-directed speech (Trainor, Austin, & Desjardins, 2000) and the communication of these emotions appears to be universal (Bryant & Barrett, 2007). Nevertheless, infants seem to prefer infant-directed singing to infant-directed speech. Nakata and Trehub (2004) exposed six-month-old infants to videotaped performances of their own mothers. The infants showed more sustained attention and engagement to mothers' singing episodes than to their speaking episodes. The observation that emotional communication through singing is powerful for infants, even for hearing newborns of deaf parents, is consistent with the proposal of biological preparedness for music (see Section 5.4 for a plausible neurobiological account of this phenomenon).

Predispositions to respond emotionally to music may account for the fact that young children can easily extract emotion intentions from music. By nine months, infants discriminate happy and sad music (Flom, Gentile, & Pick, 2008). By the age of three years, they show the ability to recognize happiness in elaborate art music of their culture, and by the age of six they show adult-like abilities to identify sadness, fear, and anger in music (Cunningham & Sterling, 1988; Terwogt & van Grinsven, 1988, 1991; but see Dolgin & Adelson, 1990, for later emergence). Furthermore, childhood competence is associated with sensitivity to specific musical features. At five years of age, children are able to discriminate between happy and sad excerpts by relying on tempo differences (fast vs. slow). At six, children show evidence of using both tempo and mode (major vs. minor) as adults do (Dalla Bella, Peretz, Rousseau, & Gosselin, 2001). Although these results suggest that sensitivity to tempo precedes sensitivity to mode, it is remarkable that by the age of six, Western children show full knowledge of the rules that govern the happy–sad character of the music of their culture. This ability remains largely unchanged over the lifespan (Adachi & Trehub, 2000; Dalla Bella, Peretz, Rousseau, & Gosselin, 2001; Gerardi & Gerken, 1995; Gregory, Worrall, & Sarge, 1996; Kastner & Crowder, 1990; Kratus, 1993), until old age, when it declines (Laukka & Juslin, 2007).

Thus, the propensity to respond emotionally to music may be innate. This possibility does not mean that experience plays no role. Infants' musical emotions could emerge from an innate propensity to respond to the emotional tone of the voice, as suggested by the innate bias found in hearing newborns of deaf parents. This innate impulse could, in turn, be shaped by the musical regularities of the culture. Indeed, infants have powerful statistical learning capacities. Two minutes of exposure to tones with variable sequential probabilities of occurrence are sufficient for eight-month-old babies to discover the sequential structure (e.g. Saffran, Johnson, Aslin, & Newport, 1999). In a similar manner, infants may capitalize on the statistical regularities in their auditory emotional environment with relatively little effort. For instance, they may quickly discover that a high pitch level and fast tempi are typically used when a caregiver is happy.

Indeed, among adults, there is robust evidence that emotional responses are modulated by experience. As listeners, we tend to like what we already know (see Bornstein,

1989, for a review). In music, we prefer familiar over unfamiliar music even though we may be unaware of this bias (Peretz, Gaudreau, & Bonnel, 1998). The unconscious affective influence of prior exposure to music may account for a vast array of phenomena, such as the preference for consonance over dissonance (Zentner & Kagan, 1996) and the association of the major and minor modes with happy and sad emotions (Peretz, Gagnon, & Bouchard, 1998).

In sum, with consistency and precociousness, musical emotions might be constrained by innate mechanisms, as are basic tastes (sweet, salt, sour, bitter; Steiner, 1979). The origin of this predisposition remains to be determined. In Section 5.4, I will discuss the possibility that musical emotions owe their precociousness and efficacy to an invasion of the brain circuits that have evolved for emotional responsiveness to vocal expressions.

5.2 MUSICAL EMOTIONS: BRAIN ORGANIZATION

The hypothesis that basic musical emotions exhibit universality and innateness is important from a neuropsychological perspective. In this view, brain organization for these emotions would be expected to recruit neural networks that are fixed not only across members of the same culture but across members of different cultures. Since there is as yet no cross-cultural study of the neural correlates of musical emotions, I will focus here on Western listeners and will examine below the specific brain areas that have been identified to date in the processing of musical emotions. Before doing so, it is important to review briefly the evidence suggestive of a neural pathway for processing musical emotions.

5.2.1 An emotional neural pathway

If basic musical emotions recruit a distinct neural pathway, one should be able to find individuals who cannot respond to music emotionally but are able to perceive and memorize it. Conversely, one would expect to find cases who can respond to music emotionally despite having severe difficulties in perceiving music. Such conditions typically occur after accidental brain damage in adults. Indeed, there are musicians who, after a cerebro-vascular accident, retained their musical skills but complained that they lost interest in music because it sounded 'flat' or emotionless (Griffiths, Warren, Dean, & Howard, 2004; Mazzoni et al, 1993; Mazzuchi, Marchini, Budai, & Parma, 1982). Unfortunately, these reports are anecdotal. The emotional losses have not been assessed.

Similarly, autistic individuals are often described as having superior musical skills but atypical or impaired emotions. This is the case for 'musical savants', whose musical performance has been qualified at times as 'mechanical' (Mottron, Peretz, Belleville, & Rouleau, 1999; Sloboda, Hermelin, & O'Connor, 1985). Nevertheless, musical expressiveness has never been studied experimentally. The only two empirical studies that examined recognition of musical emotions in autism did not report impaired emotions processing (Heaton, Hermelin, & Pring, 1999; Khalfa & Peretz, 2007). In both studies, autistic children and young adults could recognize basic emotions from music as accurately as 'normals' did. It may still be the case that autistic individuals decode musical emotions in a qualitatively anomalous manner. For example, autistic children can recognize and imitate facial expressions as normals do, but no mirror-neuron activity is observed in the inferior frontal gyrus (Dapretto et al, 2006).

There is actually little current evidence that *all* musical emotions can be (1) selectively lost after brain damage or (2) never acquired as a consequence a neurogenetic disorder. Nonetheless, there is clear evidence that *specific* emotions can be lost after brain damage. This is the case for the recognition of 'scary', and to some extent, 'sad', music after damage to the amygdala (Gosselin, Peretz, Johnsen, & Adolphs, 2007; Gosselin et al, 2005), and of the preference for consonance over dissonance after lesion to the parahippocampal gyrus (Gosselin et al, 2006). In both of these instances, perceptual processing of the musical selections was found to be spared. These results support the notion that there is a distinct emotional pathway for music processing, and that this neural pathway may differ according to the emotion considered.

Further support for the existence of a distinct neural pathway for emotions is provided by cases of intact emotions despite severe problems in perception and memory. This is the case for IR, a patient who suffers from long-standing bilateral brain damage to the auditory cortex. Her case is remarkable because 15 years after her brain damage, IR still experiences severe difficulties with music while her language abilities and her general intellectual and memory abilities are normal (Peretz, Belleville, & Fontaine, 1997; Peretz & Gagnon, 1999). Despite her severe musical deficits, she reports that she enjoys music and listens regularly to pre-recorded music. In an experimental study, IR was able to classify melodies as 'happy' and 'sad' in a manner equivalent to normal controls, yet she was impaired in classifying these same melodies on the basis of their familiarity. For example, when presented with the melody of 'Happy birthday' without its lyrics, IR would say 'I don't know that tune but it sounds happy.' CN, another patient with bilateral lesions to the auditory cortex and severe recognition problems for melodies that were once highly familiar to her (Peretz, 1996), made a similarly interesting comment. When listening to the famous *Adagio* of Albinoni taken from her own record collection, CN first said that she had never heard the piece before. Suddenly, she said: 'It makes me feel sad . . . the feeling makes me think of Albinoni's *Adagio*' (Kolinsky, personal communication). In short, both IR and CN were unable to recognize melodies that were highly familiar to them before the brain accident, yet they were able to do so via their emotional responses.

In a follow-up study of IR (Peretz, Gagnon, & Bouchard, 1998), we tested her in a series of experiments using the same set of excerpts taken from the classical repertoire

(e.g. Albinoni's *Adagio*). These were selected to convey a 'happy' or 'sad' tone, and they were presented under various transformations and with different task demands. IR was just like normal controls in that she was able to use both the mode and the tempo characteristics to derive the 'happy' or 'sad' tone of the music, and her judgements were immediate. In contrast with her relatively sophisticated emotional processing of the musical excerpts, IR showed impaired performance in her non-emotional assessments. Specifically, she performed well below normal in the discrimination of these musical excerpts in a 'same–different' classification task that was very easy for controls. She also failed to detect most errors purposely inserted on either the pitch or time dimension of the musical excerpts, yet these mistakes were obvious to control subjects. IR was able, however, to use a change of mode (from major to minor and vice versa) to discriminate excerpts. We concluded from these studies with IR and CN that severe deficits in perception and memorization of music can leave emotional judgements of music unimpaired. Such a spectacular isolation of emotional judgements of music suggests the presence of an emotional neural pathway for music. In principle, neural segregation of emotional and non-emotional pathways could be confirmed by functional brain imaging in normal brains. Such a study has not yet been reported.

In summary, brain lesion studies suggest that musical emotions might be subserved by a brain pathway that is separable from that involved in music perception and memory. One attractive possibility, derived from the animal work of LeDoux (1996) and from the theoretical position of Zajonc (1984), is that basic emotions need no cortical mediation. That is, basic emotional responses might function like subcortical reflexes. These emotional responses would be immediate but superficial, because they would not require the additional time taken by elaborate processing of the signal in cortical structures.

5.2.2 Evidence for a subcortical route

There are two plausible levels at which emotion and perception might bifurcate in the processing of music: early on after fast acoustical analysis of the musical input, or later on, after detailed analysis of emotional features. Consider a sudden dissonant chord or crash of cymbals, which may elicit a rapid, reflex-like reaction in the subcortical pathway, in the absence of detailed analysis of the music. This alerting role is probably often exploited in the soundtracks of terror movies. In contrast, the frequent alternation between major and minor keys in Klezmer music is more likely to be mediated cortically.

The subcortical emotional pathway classically reaches the limbic system first (e.g. the amygdala; see Figure 5.1). This system, named '*le grand lobe limbique*' by Broca (1878), corresponds to subcortical structures that appeared early in evolution and are similar across species. The limbic system was designated as the substrate of emotions by Broca a century ago, and later also by Papez (1937). Since then, the concept has gradually developed to include many more regions, both cortical and subcortical (see Damasio, 1994; LeDoux, 1996). In other words, emotions are no longer confined to the functioning of the limbic system, although the limbic system retains a fundamental role.
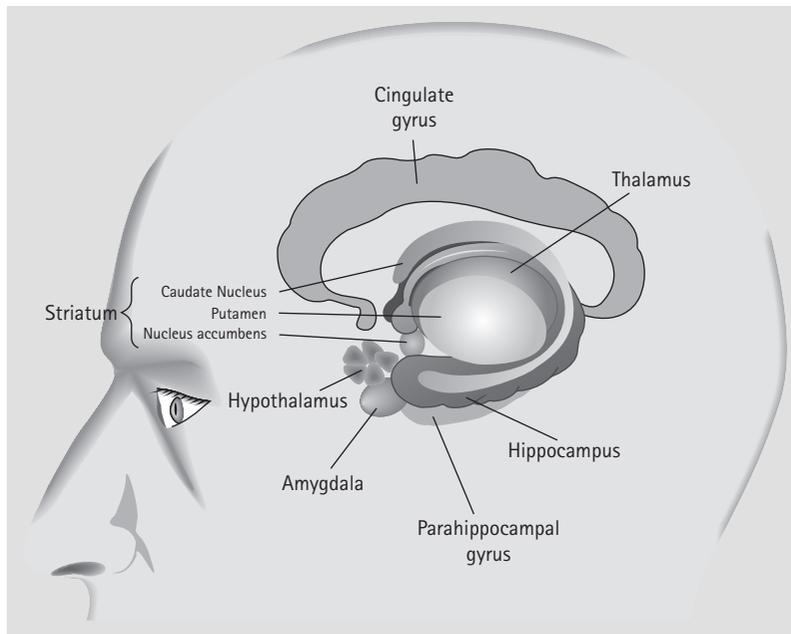
Fig. 5.1 Deep brain structures involved in emotion recognition and represented in a medial inside view of the brain. The limbic lobe includes the hypothalamus, the amygdala, the hippocampus, the thalamus, the cingulate gyrus, and the ventral striatum (which contains the nucleus accumbens).

There is ample evidence that subcortical structures are involved in emotional responses to music (see Figure 5.1 for the localization of these structures). In one early demonstration, Blood and Zatorre (2001) reported cerebral blood flow changes in subcortical neural structures while people experienced musical 'chills' (see also Chapter 21, this volume). They observed increased activation in the ventral striatum (which contains the nucleus accumbens, known to be involved in reward) and *decreased* activation in the amygdala. Similar activation of the nucleus accumbens has been observed while nonmusicians listen to pleasant music (i.e. from recordings) that was either unfamiliar (Brown, Martinez, & Parsons, 2004; Koelsch, Fritz, von Cramon, Müller, & Friederici, 2006) or familiar (Menon & Levitin, 2005; Mitterschiffthaler, Fu, Dalton, Andrew, & Williams, 2007) to the subjects. Some of these regions (especially the nucleus accumbens) have been implicated in response to highly rewarding or motivationally important stimuli (Knutson & Cooper, 2005), including chocolate (Small, Zatorre, Dagher, Evans, & Jones-Gotman, 2001) and drugs of abuse (Breiter et al, 1997). Thus, under certain circumstances, music can access subcortical structures that are associated with primary reinforcers. This neurobiological link between music and the limbic system is

not limited to hedonic mechanisms. The amygdala can also be recruited by scary music (Gosselin et al, 2005, 2007). Thus, music may be as effective as food, drug, and facial expressions (Johnson, 2005) in eliciting subcortically mediated affective responses.

One important question is whether this subcortical involvement responds to top-down influences from the cortex (is cortically mediated) and whether the subcortical relay can modulate the cortical processing of music. Menon and Levitin (2005) observed enhanced functional connectivity between subcortical regions (e.g. the nucleus accumbens) and cortical regions (e.g. the insula and the orbitofrontal cortex), but the nature of this connectivity or its direction cannot be specified with functional neuroimaging. In order to obtain indication of whether the subcortical activations precede, are concomitant, or follow cortical mediation, one needs to use other techniques such as intracranial recordings and lesion studies.

Because many emotional responses are fast, automatic, and can be derived from low-level acoustical analysis of the musical input, three kinds of response are potentially informative in this regard: the startle reflex, avoidance of dissonance, and perception of danger. All three responses are optimal at engaging a fast, feed-forward subcortical system that could in turn feed cortical systems. Each response is examined below.

The startle reflex

The acoustical startle reflex is an automatic defensive reaction to an unexpected loud sound. Its neural pathway is relatively well understood. The expression of the reflex itself is controlled at the brain-stem level (Yeomans & Frankland, 1995), but it can be modulated by subcortical structures, notably the amygdala, during exposure to aversive stimuli (Grillon & Baas, 2003). In such cases, the startle reflex is enhanced compared to a neutral situation. The reflex can also be attenuated by pleasant stimuli, as we have shown in the case of pleasant music (Roy et al, 2009). Animal research suggests that lesions to the nucleus accumbens but not lesions of the amygdala can influence pleasure attenuation of the reflex (Koch, Schmid, & Schnitzler, 1996). Presently, however, we do not know whether modulation of the startle reflex via the subcortical structures, such as the nucleus accumbens, precedes or results from cortical analysis of music. Exploration of this issue is currently in progress in our laboratory.

Sensory dissonance

Sensory dissonance can be created by two simultaneous tones one or two semitones apart. This combination creates beating at the level of the basilar membrane in the inner ear. The overlap in vibration patterns compromises the resolution of pitches of different frequency on the basilar membrane, leading to the perception of roughness. Thus, the unpleasant character of dissonant sounds can be computed by the auditory system before it reaches subcortical structures and, hence, before it reaches the auditory cortex where neurons that respond to dissonance are located (Fishman et al, 2001). The functioning of a fast, reflex-like subcortical pathway might rely on these peripheral mechanisms of the auditory system and account for its effect on human behaviour early in development. Newborns and young infants prefer consonant over dissonant tone

pairs (Trainor & Heinmiller, 1998) and musical passages (Masataka, 2006; Zentner & Kagan, 1996). This preference for consonance appears innate because even hearing newborns from deaf parents prefer consonance over dissonance (Masataka, 2006).

Support for the involvement of subcortical (or paralimbic) structures in response to dissonance comes from functional neuroimaging and brain lesion studies. Neuroimaging studies have identified the parahippocampal gyrus (Blood, Zatorre, Bermudez, & Evans, 1999) and the amygdala (Ball et al, 2007; Koelsch, Fritz, von Cramon, Müller, & Friederici, 2006) as key brain structures. Interestingly, activity in the right parahippocampal gyrus increases with increasing dissonance (Blood, Zatorre, Bermudez, & Evans, 1999). Lesion data have confirmed the critical involvement of the parahippocampal cortex in evaluating the unpleasantness of dissonance. Substantial resections of the left or right parahippocampal cortex gave highly abnormal judgements to dissonant music, which was judged to be pleasant while controls found it unpleasant. This indifference to dissonance was specific and not due to a perceptual disorder. Moreover, the impairment differed from that induced by amygdala damage alone (Gosselin, Peretz, Johnsen, and Adolphs, 2007; Gosselin et al, 2006). Thus, the current evidence points to the parahippocampal cortex, rather than the amygdala, as being a key structure in the emotional evaluation of dissonance. It remains to be determined, however, if this paralimbic contribution is 'direct' or mediated by cortical analysis. A case like IR, who appears to be deaf to dissonance due to damage to the auditory cortex (Peretz, Gagnon, & Bouchard, 1998), could provide indication in this regard.

To test the importance of the auditory cortex in mediating dissonance judgments, IR was asked to rate the pleasantness of the stimuli used in the neuroimaging study with normals (Blood, Zatorre, Bermudez, & Evans, 1999) and in our prior study (Peretz, Gagnon, & Bouchard, 1998), of which half were manipulated so as to create sensory dissonance. IR was deaf to dissonance: she did not judge the dissonant music as unpleasant as every normal does (Peretz, Blood, Penhune, & Zatorre, 2001). Thus, there was no evidence that IR's intact subcortical pathway could give rise to emotional reactions to dissonance. Rather, the results suggest that emotional responses to dissonance are mediated via an obligatory cortical perceptual relay. Because IR was tested with explicit emotional tasks, it remains possible that the functioning of her intact subcortical pathway was not assessed with appropriate methods. In order to assess a rapid, reflex-like subcortical response to dissonance, one could use functional neuroimaging and see if normal activity can be observed in IR's parahippocampal cortex in response to dissonance. Unfortunately, neuroimaging cannot be used with her due to the presence of metallic clips in her brain. Another, less invasive avenue could be to explore whether conditioning and physiological recordings in response to dissonance can be obtained. If IR were to exhibit evidence of sensitivity to dissonance with such indirect measures, it would be the first demonstration of subcortical emotional responses to music without cortical relay. Future work with intracranial recordings in patients who have depth electrodes implanted in the parahippocampal gyrus should also be informative in this regard.

Scary music

Suspense in music is often created by dissonance (think of *Psycho*, the horror film directed by Alfred Hitchcock), but this is not always the case. In our set of musical clips composed with the intention of expressing threat (and inspired by real film soundtracks[1]), some of the stimuli were consonant and musically regular. Moreover, the presence of dissonance, violation of expectancies, and irregularities did not determine listeners' accuracy in judging the music as scary (Gosselin et al, 2005; Vieillard et al, 2008). This is surprising given the recent finding that auditory uncertainty plays an important role in activating the amygdala (Herry et al, 2007; Koelsch, Fritz, & Schlaug, 2008). Music might convey anxiety in a variety of ways, which may, in turn, recruit different perceptual mechanisms.

Nevertheless, our heterogeneous set of 'scary' musical selections was effective in highlighting the role of the amygdala. Using these stimuli, we found that recognition of 'scary' music can be impaired by unilateral medial temporal lobe excision (Gosselin et al, 2005). Patients having sustained such an excision that systematically removes the amygdala, particularly on the right side of the brain, seemed to have lost the knowledge of what signals danger from music, as attested by their aberrant choice of 'peacefulness' or 'happiness' as the intended emotion for the scary music. This atypical behaviour did not seem to arise as a consequence of a poor perceptual system. All patients managed to obtain a fairly high-level performance in an error-detection task that used the same musical selections. The most likely neural locus underlying this disorder is the amygdala. Indeed, SM, who has complete bilateral damage relatively restricted to the amygdala, was selectively impaired in the recognition of 'scary' and 'sad' music. In contrast, her recognition of 'happy' music was normal. SM's impaired emotional judgements occurred in an otherwise intact processing system of musical features that are emotionally relevant (such as mode, tempo, and dissonance). Thus, the amygdala appears to be *necessary* to perceive musical suspense.

Support for this hypothesis has been obtained recently in two neuroimaging studies, in which increased activity in the amygdala was observed when normal subjects were viewing films with scary musical soundtracks (Baumgartner, Lutz, Schmidt, & Jancke, 2006; Eldar, Ganor, Admon, Bleich, & Hendler, 2007). Thus, evidence from lesion and neuroimaging studies highlights the role of the amygdala as a central hub of the two emotional routes mentioned earlier, with a fast and coarse reflex-like circuit that predominantly resides in subcortical structures (Johnson, 2005; LeDoux, 2000), and a slower, more detailed cortically mediated circuit used for recognition and decision making. In the former, the amygdala assigns affective value to incoming stimuli directly. In the latter, the amygdala assigns affective values via its connections with the cortical systems.

It remains to be determined if involvement of the amygdala precedes or follows a cortical perceptual relay. To this aim, one would need to specify the nature of the musical features that may express danger from music. The various candidates that we have tested so far, such as dissonance, rhythmic irregularities, and expectancies, are elaborate musical features that may require cortical mediation. It remains possible that

the amygdala could be triggered by coarser acoustical features, such as high-spectral sounds, highly dynamic sounds, or highly unpredictable sounds. Thus, future work should aim at defining the nature of the musical characteristics that are quickly and effectively picked up by a subcortical pathway to verify if there is a 'short-cut' from music to emotions. The point is not only theoretically relevant, but clinically important as well. For example, direct access to subcortical structures may account for the fact that patients with Alzheimer dementia continue to respond to music despite the existence of vast and diffuse cortical lesions.

5.2.3 The cortical emotional pathway

Cortical systems are neural structures that are evolutionary relatively recent and particularly developed in the human brain. Another characteristic of these cortical structures is that they exhibit functional specialization within and across the two cerebral hemispheres. For example, it is well established that regions of the left hemisphere of the brain are much more essential for speech than the right side of the brain.

Hemispheric specialization

There is a long-held debate involving two alternative views with respect to emotions. One view is that the right hemisphere is specialized for processing *all* emotions by containing all 'modules' for nonverbal affect computation (e.g. Bowers, Bauer, & Heilman, 1993). This position is known as 'the right hemisphere hypothesis'. The opposing view is 'the valence hypothesis,' which posits that the right hemisphere is more involved in negative emotions while the left hemisphere is more engaged in positive emotions (e.g. Davidson, 1992). The first observations related to the emotional competence of each cerebral hemisphere go back to Jackson (1878), who noticed that emotional language is often preserved in aphasic patients. He attributed the source of the preserved affective utterances to the contribution of the right hemisphere. This dissociation between propositional and affective language has been reported often since then. It is difficult to reconcile, however, with another classical pattern in clinical neurology that identifies each hemisphere with a distinct affective style. A lesion in the right hemisphere often produces indifference (anosognosia) and a tendency to joke. In contrast, an injury in the left hemisphere often leads to depressive-catastrophic states. The former is obviously less comprehensible than the latter as a reaction to the brain accident. The two emotional modes of responding have been associated with differences in 'affective styles' of the cerebral hemispheres. The left and right frontal cortex would be mediating approach and avoidance, respectively (Davidson & Irwin, 1999).

   Both hypotheses have been discussed in regard to musical emotions. Support for the valence hypothesis has been obtained in several studies measuring brain electrical activity—the electroencephalogram (EEG)—from scalp electrodes in normal listeners (Altenmuller, Schurmann, Lim, & Parlitz, 2002; Flores-Gutierrez et al, 2007; Schmidt & Trainor, 2001; Tsang, Trainor, Santesso, Tasker, & Schmidt, 2001). Subjects exhibit greater relative left activity to pleasant musical excerpts and greater relative right EEG

activity to unpleasant music. Converging results have been obtained from ear asymmetries in normal listeners (Gagnon & Peretz, 2000). Non-musicians were required to classify tonal and atonal melodies as pleasant and unpleasant in one condition. In a non-affective 'control' condition, the same subjects were required to judge if the melodies sounded conventional or not. Listeners exhibited a left-ear superiority effect, taken to reflect the predominance of the right hemisphere, when judging atonal melodies as unpleasant, but they displayed a slight right-ear advantage when judging tonal melodies as pleasant. This pattern of ear-asymmetries was specific to emotional judgements, because a different pattern was obtained when the same melodies had to be classified for 'correctness'.

Nonetheless, the valence account of cerebral asymmetries is not always supported, and results from some studies are more supportive of the right-hemisphere hypothesis. One measured ear asymmetries in normal subjects who were judging major and minor melodies as expressing positive or negative emotions (Bryden, Ley, & Sugarman, 1982). In that study, an overall left-ear (i.e. right-hemisphere) advantage was observed across positive and negative emotional judgements. In another study by Blood, Zatorre, Bermudez, and Evans (1999), the neural structures activated by pleasant, consonant music were found primarily in the right hemisphere. Moreover, reciprocal activations occurring between particular neural structures and the valence of the musical stimulus were found within the same hemisphere.

Although the nature of each hemispheric contribution to the perception of musical emotions remains to be determined, it is plausible that the cortical contribution is related to both the demands of the task and the nature of the perceptual analysis of the input. For example, it is relatively well established that pitch-based mechanisms are more likely to recruit right-hemisphere structures while hemispheric lateralization of time-based mechanisms is less clear (Peretz & Zatorre, 2005). Thus, there is a need to fractionate the processing components involved in each basic musical emotion in order to understand the principles underlying hemispheric differences.

Orbitofrontal cortex and ventromedial prefrontal cortex

As suggested previously, there is solid evidence that various cortical structures are involved in the emotional processing of music. For example, activity in the orbitofrontal cortex (Blood & Zatorre, 2001; Blood, Zatorre, Bermudez, & Evans, 1999; Khalfa, Schon, Anton, & Liegeois-Chauvel, 2005; Menon & Levitin, 2005), the superior temporal cortex, and the anterior cingulate cortex (Blood & Zatorre, 2001; Blood, Zatorre, Bermudez, & Evans, 1999; Mitterschifffthaler, Fu, Dalton, Andrew, & Williams, 2007; Green et al, 2008) has been reported frequently in relation to musical emotions. Among these structures, the orbitofrontal cortex and the ventromedial prefrontal cortex are key in the emotional cortical pathway. The orbitofrontal cortex has robust reciprocal connections with the amygdala, and both areas have strong connections with cortical representations of every sensory modality, so that they form a functional circuit that integrates sensory information.

Among all these brain areas, it is not always easy to determine if the activity is related to emotional or non-emotional processing of the musical structure. In most studies, the musical stimuli vary widely in structure. For example, Mitterschiffthaler et al (2007)

selected 'happy' and 'sad' musical excerpts from the classical repertoire. These stimuli, such as *Traviata* from Verdi and the *Adagio* of Albinoni, are polyphonic, complex, familiar to a variable degree, and widely different in acoustical and musical structure. While maximizing the ecological value of the study, the use of real pieces of music may introduce substantial confoundings in terms of acoustical, attentional, musical, and memory differences. All of these acoustical and cognitive differences are likely to recruit largely different and distributed neural networks (Peretz & Zatorre, 2005), thereby making the interpretation of the activated cortical areas difficult.

Yet, it is possible to use brain imaging techniques in the study of emotional responses to musical events in a highly controlled manner. For example, Mizuno and Sugishita (2007) presented musicians with major, minor, and ambiguous isolated chords in the scanner. They found that the inferior frontal gyrus (BA 47), the medial thalamus, and the dorsal anterior cingulate cortex were critically involved in the happy–sad judgements of the major–minor mode distinction. This network of neural activations fits nicely with IR's brain lesions, which largely spared these areas (see above). In Mizuno and Sugishita's study, however, happy–sad judgements were not contrasted with a non-emotional control task, such as asking the subjects to judge the pitch level of the chords (as high or low). Thus, it remains to be determined if these regions are part of the emotional pathway or of the non-emotional cortical pathway.

As yet, no lesion study has attempted to identify focal cortical regions that are part of the cortical emotional pathway in music processing. The paradoxical changes of musical tastes seen in cases of frontotemporal dementia (e.g. Geroldi et al, 2000) support the notion that the orbitofrontal cortex and the ventromedial prefrontal cortex are key brain systems in the emotional cortical circuit subserving musical emotions.

5.3 MUSICAL EMOTIONS: DISCUSSION AND GENERAL REMARKS ON BRAIN ORGANIZATION

The available evidence suggests that the musical input may require cortical mediation in the superior temporal gyri. The perceptual output is then relayed to emotional systems in the limbic and paralimbic structures and in more frontal areas, depending on its valence. This two-stage model suggests that emotion and perception are not taking place along two parallel and independent pathways as some models (LeDoux, 2000; Zajonc, 1984) posit. The cortical and subcortical routes would be serially organized in the case of music.

Each pathway may play a distinct function in emotional responses, with different distributed networks underlying different emotions. Just as cognitive neuroscience has demonstrated the necessity to fractionate global functions, such as face processing or music recognition, into more elementary constituents whose neural substrates can be identified, so too modern research in the neuroscience of emotions suggests fractionation of affective processes. This conclusion highlights what is often not obvious to psychologists. It shows why the study of neural correlates in general, and brain

localization in particular, is of importance. Examination of brain correlates can shed light on more general assumptions, by requiring that complex brain functions be decomposed into simpler processes so that components can be localized anatomically and studied in relative isolation. This fractionation into elementary, localized mechanisms can then serve to test current models of emotional functioning or contribute to the development of new models.

From this perspective, brain lesion studies should not be ignored. Though neuroimaging and other brain mapping techniques are of tremendous importance, they have not and cannot replace research with brain-damaged patients. Indeed, brain-mapping techniques cannot disentangle correlation from causation. Emotional processes are distributed across several spatially distinct neural regions that interact in order to implement the function under study. Moreover, the contribution of each component is not fixed but depends on its interactions with other components of the system. 'All of this conspires to make the data that functional imaging studies yield overinclusive' (Adolphs, 2007, p. 426). To causally link a specific neural structure to emotion, we must turn to the effect of brain damage, the 'experiments of nature'. Similarly, intracranial stimulation and newer non-invasive brain stimulation (such as transcranial magnetic stimulation) can causally relate a function and a brain region. In short, all techniques have their strengths and weaknesses, and should be used in combination.

There are a number of issues related to the neural correlates of musical emotions that have not been addressed in this chapter because of insufficient relevant data. This is the case for three of the four basic emotions easily conveyed by music, namely happiness, sadness, and anger. There is as yet no clear indication on how these musical emotions are organized in the brain, although their perceptual determinants are relatively well documented (Chapters 14 and 17, this volume).

Another untackled issue is the possible exploitation of neurochemical correlates of musical emotions. Neurochemicals are neurotransmitters and hormones that alter the response properties of sets of neurons. Music is apparently effective in eliciting such responses, as indicated by the action of the antagonists of endorphins (Goldstein, 1980) and cortisol measures (Khalfa, Dalla Bella, Roy, Peretz, & Lupien, 2003; Suda, Morimoto, Obata, Koizumi, & Maki, 2008; Trehub, 2001; see Chapter 11, this volume). The study of these neurochemicals may provide yet another neuropsychological avenue to a better understanding of the nature and brain organization of musical emotions.

5.4 MUSICAL INVASION OF VOCAL EMOTION CIRCUITS OF THE BRAIN

With limbic mediation, consistency, and precociousness, musical emotions resemble other important classes of emotions, such as facial emotions (Peretz, 2001). As seen above, music recruits key brain regions for processing emotions, such as the striatum,

the amygdala, the orbitofrontal cortex, and the anterior cingulate cortex. These emotion circuits have been associated with basic biological functions, such as sex and food. Music can hardly be compared to such basic needs. There seems to be a much larger cultural learning component to musically induced emotions. Thus, one may wonder how the relations between music and these neurobiological substrates should be conceptualized. One possibility is that music is particularly suited (or designed) to invade or co-opt emotion circuits that have evolved for biologically important sounds.

One likely emotional system for neural invasion (or 'neural recycling', to adopt the terminology of Dehaene & Cohen, 2007) is the systems dealing with emotional vocalizations, such as laughs and screams, and prosody. Communication among humans (and animals) is often carried out using acoustical signals, whose affective value might well be genetically transmitted and supported by specialized brain emotion circuits. Musical emotions might invade these evolved circuits for vocal emotions and adjust them for its particularities. If so, the study of musical emotions might benefit from what has been learned about these other emotions. Brain organization for vocal emotions could constrain brain organization for musical emotions.

5.4.1 Vocal emotions: brain organization

In humans, the expression of emotions through the voice can take two different forms. It can be conveyed by the tone of voice in speaking, or by emotional vocalizations such as laughs, cries, and screams. There has been a greater interest in the first category of vocal expressions, which is usually referred to as *affective prosody*. Despite their importance, and in contrast to the large literature on affective prosody, emotional vocalizations have not been extensively studied. Thus, they will be jointly considered here.

A distinct neural pathway

The most remarkable neuropsychological property of the vocal emotional system is its apparent specificity. First, despite the obvious link between facial and vocal expression of emotions, emotional evaluation of the tones of voices is dissociable from the emotional evaluation of faces. Some patients can infer the emotional tone of vocal expressions but not of facial expressions, whereas others show the opposite pattern (e.g. Hornak, Rolls, & Wade, 1996). This dissociation is not due to differences related to the modality of input, because the patient's ability to process other aspects of faces and voices is typically spared. The neural separability of vocal from facial emotions is not trivial, given that they typically signal the same emotion at any given time. Yet the two modes of expressions seem to be subserved by independent neural systems.

Secondly, within the speech signal, the recognition of vocal cues that are emotionally meaningful is dissociable from the recognition of vocal cues that are semantically informative. As mentioned previously, Jackson (1878) was the first to notice the separability of affective prosody from propositional speech. The distinction has been made several times in perception as well. For example, in a dichotic listening study with normal adults, Ley and Bryden (1982) found a left-ear (i.e. right-hemisphere) advantage

for the perception of the emotional tone of voice, and a right-ear (i.e. left-hemisphere) superiority for the recognition of the actual semantic content of the words from the same set of sentences. Similarly, there are reports of patients who can no longer understand speech, but who are still able to infer the emotion conveyed by vocal cues (e.g. Barrett, Crucian, Raymer, & Heilman, 1999). These findings show that emotional processing of speech signals can take different routes, one determined by semantic content and one determined by vocal form.

Finally, the tone of the voice is not analysed just for affective purposes. Prosodic cues can provide important person-specific information (e.g. identity, age, and sex) and linguistic, non-semantic information (e.g. differentiating a question from a statement). Once again, the use of these non-affective cues is dissociated from their emotional use. Brain lesions can interfere with the identification of vocal emotions of happiness, sadness, and fear, yet spare the identification of prosodic differences marking questions, exclamations, and assertions in spoken sentences (e.g. Heilman, Bowers, Speedie, & Coslett, 1984). Similarly, functional neuroimaging of neurologically intact brains points to the involvement of distinct neural regions for emotion recognition and for speaker identification (Imaizumi et al, 1997). Together, these findings highlight the fine tuning and specialization of the neural system underlying the emotional interpretation of vocal sounds.

What remains to be determined is to what extent the emotional vocal pathway can be dissociated from the musical one. There are some indications that these may dissociate. For example, Griffiths et al (2004) describe a patient with damage to the left insula and amygdala who experienced a deficit in musical emotions, while retaining normal music perception and voice prosody perception. Unfortunately, as mentioned previously, this report is anecdotal. The emotional losses have not been assessed. To my knowledge, the reverse dissociation—that is, impaired vocal emotions in the presence of normal musical emotions—has not yet been reported. Therefore, it remains possible that the emotional pathway of vocal emotions is shared with (and perhaps invaded by, as discussed below) musical emotions.

Subcortical pathway of vocal emotions

Curiously, evidence for the involvement of the amygdala in vocal emotions is inconsistent. Lesions to the amygdala impair the recognition of vocal expressions of fear sometimes (Scott et al, 1997; Sprengelmeyer et al, 1999), but not at other times (Adolphs & Tranel, 1999; Anderson & Phelps, 1998). In the latter cases, patients with selective bilateral damage to the amygdala show preserved recognition of fearful voices while showing evidence of impaired recognition of fearful faces. One such patient is SM, who showed impaired recognition of both fearful facial expression and scary music (Gosselin et al, 2007). Similarly, neuroimaging data show activation of the amygdala in both visual and auditory fearful expressions in some instances (Dolan, Morris, & de Gelder, 2001; Morris et al, 1996; Phillips et al, 1998), but not in others (Imaizumi et al, 1997; Morris, Scott, & Dolan, 1999; Pourtois, de Gelder, Bol, & Crommelinck, 2005; Royet et al, 2000). When there is evidence of amygdala activation, it may encompass positive (pleasure and laughter) and negative vocal sounds (fear and sadness; Fecteau, Belin, Joanette, & Armony, 2007). The latter finding may be related to two recent

findings about the amygdala. First, the amygdala is not a single entity but contains functionally distinct regions that may respond differentially to positive and negative emotions (Ball et al, 2007). Secondly, the amygdala may act more as a 'relevance detector' for biologically meaningful events, independently of their valence (Sander, Grafman & Zalla, 2003).

Nonetheless, tone of voice is as meaningful and biologically important as facial expression. Thus, the current inconsistency in engaging the amygdala through the vocal channel is puzzling. From an evolutionary perspective, one would expect a common pathway. The involvement of subcortical structures in vocal emotions, including the amygdala but also the basal ganglia, remains poorly understood. In a recent review of the literature, Schirmer and Kotz (2006) proposed that subcortical mechanisms are limited to the case of unexpected changes in speaker tone or cases of threat that motivate adjustments to behaviour. In sum, there is so far little support for the notion that musical emotions invade the subcortical brain circuits devoted to vocal emotions.

Cortical pathway of vocal emotions

At the cortical level, vocal emotions are typically associated with the right hemisphere. Several recent neuroimaging studies have suggested, however, that decoding emotional prosody engages both hemispheres (Adolphs, 2002; Schirmer & Kotz, 2006). Studies in patients with focal brain lesions show that recognition of emotional information through prosody engages a distributed network of areas, mostly within the right frontal and parietal lobes. These areas include the temporal cortex, the insula, and the inferior frontal gyrus (e.g. Schirmer & Kotz, 2006). Some of these findings have been integrated in a model proposing that regions in the superior temporal sulcus (STS) and superior temporal gyrus, especially in the right hemisphere, form an emotional 'gestalt', which is then made accessible for higher-order cognitive processing, possibly taking place in the orbitofrontal cortex (Schirmer & Kotz, 2006).

Interestingly, some of these brain regions appear to support the processing of emotional vocalizations in both human and non-human primates. The human right ventrolateral orbitofrontal cortex responds more to negative than to positive vocalizations of other humans as well as of cats and rhesus monkeys (Belin et al, 2008). This region is close to areas that are activated in awake macaques when they are presented with negative and positive monkey vocalizations (Gil-da-Costa et al, 2004). These results suggest that some of these neural systems for processing vocal emotions are shared between humans and primates.

5.4.2 Implications of a brain emotion circuit invasion

Although the evidence in support of common brain organization for vocal and musical emotion is currently scarce, it is theoretically interesting to examine the neurobiological implications of such an hypothesis:

Availability. As brain circuits dedicated to vocal emotions are invaded by music, their prior organization should shape musical emotions early on in infancy. One would

predict, for example, that the ventral striatum and the amygdala should be tuned early on by both music (infant-directed singing) and voice (infant-directed speech), depending on the intended emotion. Similarly, processing in the auditory cortex and perhaps in the superior temporal sulcus might respond to emotionally meaningful inflections of the voice, pitch level, and tempo in both infant-directed speech and songs. It would be particularly informative to examine whether avoidance of dissonance applies to both musical and vocal sounds. Indeed, the increased tension of the vocal chords in infant cries and distress calls introduces many subharmonics in the vocal sounds that otherwise are harmonic signals. These distortions in screams sound unpleasant and are effective in triggering a response in others (who will notice it rapidly and will try to stop it; Fitch, Neubauer & Herzel, 2002). What is needed is a definition of the acoustical correlates of dissonance that can be applied to both musical and vocal sounds (Peretz, 2008).

Reconfigurability. With exposure, the musical invasion scenario might be associated with a re-mapping of the brain emotion circuits via plasticity. An important test of the invasion hypothesis would be to show that there is no creation of domain-specific brain circuits, and that plasticity is expressed by reconfiguring the existing emotional networks. Thus, one might predict different configurations of the same neural circuits to be engaged at different ages. For example, we may expect the neural pathways for musical emotions that are driven by innate mechanisms (e.g. beating and dissonance) to be relatively fixed, whereas musical emotions that are likely driven by (culturally acquired) musical associations (e.g. sadness and minor mode) to be a dynamic process that develops during the first few years of life. Unfortunately, there is as yet no neuroimaging study that has examined musical emotions in infants or during development. Another way to test this prediction is to compare musicians to nonmusicians. For example, Thompson, Schellenberg and Husain (2004) have shown effects of musical lessons on the ability to recognize basic emotions (happy, sad, fearful, or angry) from both speech prosody and tone sequences that mimic this prosody. It would be interesting to see if these effects of musical expertise are due to further specialization of the same brain circuits that are used by non-musicians, or if these effects are due to flexible use of distinct brain circuits.

Efficacy. One interesting possibility is that music invasion of the vocal emotion brain circuitry arises from its efficacy to function as a 'super-stimulus' for the vocal emotion system. Juslin and collaborators (Juslin & Laukka, 2003; Juslin & Västfjäll, 2008) have argued that we process music as if it were a *super-expressive voice*. This idea is analogous to what Sperber and Hirschfeld (2004) propose for facial manipulations. Masks, cosmetics, and caricatures may arise from the nature of face coding in the human brain, which allows these cultural artefacts to function as 'super-stimuli' for the fusiform face area. In other words, music may aim at the vocal emotional systems just as artistic masks target the face recognition system. Music may exaggerate particular nonverbal vocal features that are effective for bonding. From this perspective, the actual domain of the emotional systems is said to be invaded or co-opted. Music could have stabilized in all cultures because music is so

effective at co-opting one or several evolved emotional systems, which have their roots in animal communication. Multiple anchoring in several emotional systems may even contribute to the ubiquity and power of music. As mentioned previously, music appears more effective than stories in attracting infants' attention (Nakata & Trehub, 2004) and in enhancing cognitive recovery after brain damage (Sarkamo et al, 2008).

Clearly, there is a need for comparison between musical and vocal emotions. There are as yet very few studies beyond a meta-analysis of the data obtained in separate experimental settings (Juslin & Laukka, 2003), which indicated that both domains use similar emotional acoustic cues. Partial support for this proposal was provided recently by Ilie and Thompson (2006). They found similar effects on emotional responses by manipulating some acoustical cues such as pitch intensity in both music and speech, but they also found domain-specific effects. Interestingly, music received higher ratings than speech in valence and arousal, suggesting that music may be more engaging than vocal expressions. In sum, there are presently few studies and thus little evidence for the existence of a common channel for conveying emotions through the musical and vocal channels. Future comparisons between domains should not only originate from neuroscience but also from developmental and comparative research, ethnomusicology, and psychology.

5.5 CONCLUSIONS

Although many questions about the neurobiological basis of musical emotions remain unresolved, there is evidence that musical emotions depend on a specialized emotional pathway that recruits various subcortical and cortical structures that may be shared, at least in part, with other biologically important systems. This emotional pathway is not simple. There is not a single, unitary emotional system underlying all emotional responses to music. For instance, most of the neural pathway underlying emotional responses to dissonance has been delineated and involves a complex and distributed system in the brain (Peretz, 2008).

Nevertheless, it is remarkable how much progress has been accomplished over the last decade. As a result, I could not simply update my former review of the field (Peretz, 2001); I had to rewrite it. In this short span of time, research has moved from mere acknowledgment of musical emotions to carefully controlled study in multiple directions. I believe that further major advances will be made by research that involves multiple methods, integrating lesion studies, functional imaging, pharmacology, transcranial magnetic stimulation, psychophysiology, cognitive psychology, comparative psychology, and the emerging fields of behavioural genetics.

The motivation for understanding the biological foundations of musical emotions is currently high in the scientific community. There is increasing awareness of the social

and clinical value of music, particularly with respect to its effectiveness in communicating emotions. Today, music plays an even more powerful and unique role in human life than ever, with wide-ranging effects on many aspects of functioning besides its obvious social function. Music has become such a key element in the human behavioural repertoire that it might be considered as a defining human attribute. In fact, music is so highly valued that very few people are willing to acknowledge a lack of emotional responsiveness to music.[2] Much work remains to be done but there is every reason to welcome advances in the biological foundations of musical emotions. We cannot change the way our brain is built, but we can better understand its functioning and adjust musical practices to its biological limitations.

Notes

1. The musical selections can be downloaded at the Internet from: www.brams.umontreal.ca/plab/publications/article/96
2. I am grateful to Glenn Schellenberg, Sylvie Hébert, Nathalie Gosselin, Eckart Altenmüller, and two anonymous reviewers for offering insightful comments. The research summarized in this chapter has been supported by research grants from the Natural Sciences and Engineering Research Council of Canada and the Canadian Foundation for Innovation.

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