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Chapter VI

NEUROSCIENCE OF MUSIC AND EMOTION

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ABSTRACT

The chapter discusses recent studies of neural representations of musical emotions. Despite an increasing number of empirical studies on the emotional effects of music, there is paucity of brain research that has identified the underlying neural networks. It is argued that the representation of musical emotions might be based on similar structures as compared to emotions in other domains. Consequently, it is hypothesized that musical emotions recruit networks of emotion processing that are known to be involved in both visual and auditory (speech) perception and that are responsible for psychological as well as physiological responses to emotional stimuli. Beside the provision of theoretic and empirical accounts, the review addresses methodological issues of current imaging techniques that may be particularly detrimental for the study of neural correlates of musical emotions. However, research findings so far support the assumption of largely overlapping networks required for the processing of both general and music-specific emotions. They also corroborate the notion of closely interconnected networks for cognitive and emotional processing even within the same neural structures. Specifically, emotional processing of music most likely involves limbic and paralimbic structures that include amygdala, hippocampus, parahippocampal gyrus, insula, temporal poles, ventral striatum, orbitofrontal cortex, and the cingulate cortex. It is further assumed that the behavioral distinction between perceptual and experiential (or feeling) aspects of musical emotions might be established within these neural structures. More research is needed, for example, to address the generation of musical emotions in the performer as well as developmental aspects and individual differences in neural representations of musical emotions.

MUSIC, EMOTION, AND THE HUMAN BRAIN

Emotions are critical to our understanding of music. They have long been the subject of debate among philosophers, artists and scientists in Western culture and other musical traditions around the world. According to the Greek philosophers, for example, music listening could influence the physiology and character of an individual and even affect subsequent behavior (e.g. Freeman, 2000). These authors not only stressed the therapeutic and educational power of music, but also warned against the negative consequences of musical malpractice for individuals and society.

Since the end of the 19th century, research methods in psychology and physiology have been able to elucidate philosophical speculations. For once, the relationship between musical structure and emotional expression has proved a viable approach. Music is thought to convey emotional information via an interactive, communicative process involving composer, performer and listener. It has been shown that the structural cues in musical scores that reflect the intentions of the composer interact with the cues that are under the control of the performer to shape the emotional expression that is communicated to the listener. For example, the expression of ‘sadness’ in a piece of music conveyed by the slow tempi and soft timbres indicated by the composer can be enhanced by the deliberate choices of articulation and nuances of timing made by the performer (e.g. Juslin, 2001).

Until recently, the plethora of research on musical emotions has been directed towards the effects of listening to music. More active musical behaviors such as singing, playing musical instruments, or dancing may produce different kinds of emotional response. For example, the extent to which and how emotional experiences might interfere with performance *per se*, has long been debated, since performers are also listening to themselves, in the first place.

This chapter focuses on neuroscientific approaches to music and emotion, which has become an important domain of interdisciplinary research (Juslin & Sloboda, 2001; Kreutz, *in press*). This relatively new field draws from the philosophical and behavioral research traditions rooted in the social sciences on one hand, and the advances of modern neuropsychological and imaging techniques emerging from the natural sciences on the other. The question arises as to the structure and function of neural correlates in the perception and experience of musical emotions. Some might belong to the auditory modality in the sensory-motor system, while others are neither specific to auditory processing nor the processing of music.

Whether the neural basis of emotional appraisal of music is innate or rather acquired through acculturation is subject to ongoing discussion (Peretz & Sloboda, 2005). Beside the nature-nurture problem, there are more puzzling phenomena in relation to musical emotions. For example, on the one hand, the reliable recognition of emotions, unlike the perceptual processing of music *per se*, appears independent of musical training and occurs in time windows so short that such experiences qualify as *reflexes* (Peretz, Gagnon & Bouchard, 1998; Bigand, Filipic & Lalitte, 2005). On the other hand, emotions are often seen as dynamically unfolding processes, in which physiological (Krumhansl, 1997) as well as brain activation changes occur over time (Koelsch, Fritz, v.Cramon, Müller & Friederici, 2006). These dynamic changes appear to be associated with the experienced intensity of emotions, sometimes culminating in pleasant sensations such as “chills” (Grewe, Nagel, Kopiez & Altenmueller, 2005; Panksepp, 1995) that may indicate the release of endorphins (McKinney, Tims & Kumar, 1997).

In another vein, repeated exposure to complete pieces of music often modulates appreciation, giving rise to so-called *exposure effects* (Samson & Peretz, 2005). Note that recognizing and experiencing musical emotion are different: not only do they involve different temporal aspects of processing, but they also might reflect different modes of processing that interact with time, situation, context, and the musical biographies of individual listeners.

Many researchers argue that emotional responses to music should be at least partially similar to emotional responses in other domains such as, for example, vision and speech (Peretz, 2001). To this end, introspective and behavioral approaches as well as peripheral physiological measurements of hemodynamic, respiratory, galvanic skin responses, and other parameters of bodily function have been used (Bartlett, 1996). The precise relationships between subjective experience and physiological concomitants during the processing of emotions are largely unknown. However, it is likely that brain research will provide important new information to reduce the amount of unexplained variances in psychophysiological studies of emotion in general and musical emotion in particular. Moreover, studying musical emotions from a neuroscientific perspective seems particularly promising with respect to the time course and dynamics of human emotion processing (Koelsch, 2006; Grewe et al., 2005; for a review of continuous measurement techniques used in behavioral studies see Schubert, 2001).

A recurrent observation is that the same brain structures may serve different roles in functional architectures within and across domains. Features of the brain such as plasticity as the result of learning and its ability to reorganize neural functions in the case of physical damage or disease suggest that any modeling of brain function needs to account for this flexibility. Thus the neuroscientific perspective on music and emotion necessitates interdisciplinary approaches, in which general models and theories of emotion, music theory, and brain research combine (Peretz, 2001). Although the implications of this approach to learning and education will be dealt with in the last chapter at the end of this book, it can be stated from the outset, that emotions – as a means rather than an end – appear to play a major role in modulating human learning processes. Investigating the underlying neural structures and the functions of musical emotion might thus be an important step towards understanding human learning processes within and beyond the domain of music.

In the remainder of this chapter, we will first deal with the neural structures that have been implicated in emotion processing. Then we will address empirical evidence relating to the neural correlates of musical emotion. The final goal of this chapter is to summarize our current knowledge of brain structures and functions related to the emotional processing of music, as well as to suggest some possible topics for future research.

NEURAL CORRELATES OF EMOTION PROCESSING

Historically, emotion in the human brain has been considered with respect, first, to hemispheric differences, and, second, to the distinction between high-level cortical structures and deeper-level limbic structures. In fact, as early as 1912, Mills suggested that cognition and emotion were functionally specified and separated, postulating an analytic-cognitive dominance for the left and an emotional dominance for the right hemisphere (Mills, 1912). Later in the first half of the 20th century, McLean (1949) proposed the idea of a structure-function relationship between the limbic system and the generation of emotions (for an overview of the historical development of this hypothesis, see LeDoux, 1996).

Whereas the traditional view on brain processing differentiates the cognitive and emotional domains (Drevets & Raichle, 1998), there are other approaches that integrate the two. Recent studies provide evidence of a substantial overlap between the neural structures involved in both cognition and emotion. Indeed, cognitive and emotive systems might be far more interconnected and indistinct at neuronal levels (Wager & Feldmann Barrett, 2004). Some researchers contend that emotion even precedes cognition as the former is critical to motivating some cognitive and behavioral processes such as decision-making or executing movements. Specifically, the origins of attention control are difficult to conceive of in the absence of affect. According to this view, emotions arise from cognitive appraisals of situations, some of which are relevant to survival (Lazarus, 1991). However, emotion and cognition may interact in more complex ways. For example, Schachter and Singer (1962) observed that after participants received injections of epinephrine, their specific interpretation of a ‘felt’ emotion depended on contextual information rather than the physiological state of arousal induced by the drug. From this view, it would be less plausible to assume that experiences of emotions are more or less hard-wired cognitive interpretations of physiological states as implicated, for example, by the classic theory by William James (1890).

The idea of emotion as preceding cognition has also emerged from theories of the evolution of the human brain. The basic affective experience that arises when a self-relevant event occurs has been termed *core affect* (Russell & Barrett, 1999). Wager and Feldman Barrett (2004) suggest that with this core affect “… arise the physiological and motivated response tendencies that have been shaped over the course of our evolution to promote adaptive cognitions and behaviors. Thus, in this view, emotion and cognition are not opponents in a zero-sum tug of war. Rather, they are synergistic partners in the game of adaptive self-regulation, each shaping the direction of the other” (Wager & Feldman Barrett, 2004).

To conclude, the idea of a clear separation between cognition and emotion on the basis of structure-functional differentiation appears inadequate. Therefore, broader concepts of one or possibly several emotion-related neural systems at deeper levels in the brain interacting with the high-level cortical structures that are engaged in processes such as, for example, perception, decision-making, or motor-control, are favored by most researchers (Damasio, 1998; LeDoux, 1996).

1. Valence and Arousal

One important proposal for distinguishing emotions has been the concept of so-called *valence*. The valence of a given stimulus indicates whether it is likely to induce an approach towards or a withdrawal from that stimulus. In neural terms, the left frontolimbic areas should represent positive, the right negative emotional content (Davidson, 1984). However, appetitive/aversive stimuli might not always induce approach/withdrawal behaviors. The precise relationship between the antecedents and consequences of emotional experiences are often modulated by a variety of interfering cognitive processes. The present view of emotional processing, therefore, is moving away from "thinking in terms of an integrated neural system that codes all emotional processes towards thinking in terms of individual neural systems coding distinct dimensions of emotion or different affect programs" (Murphy, Nimmo-Smith & Lawrence, 2003, p. 208).

Emotions differ not only with respect to their valence, varying from negative to positive, but also in their *arousal potential*, varying from low to high. The idea is that these dimensions are considered independent of each other, which suggests that they can be conceptualized as orthogonal in a two-dimensional space (Russell, 1980). While some emotions, such as sadness and peacefulness, are low in associated levels of activity, other emotions, such as anger and happiness, are considered highly activating. On the basis of these two dimensions, valence and arousal, the psychological literature most commonly differentiates between a small number of basic emotions: fear, anger, disgust, happiness, surprise and sadness (Ekman & Friesen, 1982). Research on facial expressions has shown that these basic emotions are communicated across, as well as within, various ethnicities and have been found to be associated with psychophysiological changes (Ekman, Levenson, & Friesen, 1983).

Multivariate analysis of verbal responses to emotional stimuli has shown that most of the variance in descriptions of emotions can be explained by valence and arousal (Mehrabian & Russel, 1974). Moreover, verbal reports and peripheral physiological responses are significantly and differentially correlated along the two dimensions of valence and arousal (Greenwald, Cook & Lang, 1989). In particular, startle reflex amplitudes, for example, increase with negative valence and decrease with positive valence (for a comprehensive review see Bradley and Vrana, 1993), whereas skin conductance response (SCR) increases with subjective arousal, independently of emotional valence. Note that the latter observation has been confirmed recently in studies using music stimuli (Khalfa, Peretz, Blondin & Manon, 2002). Nyklicek, Thayer, and van Doornen (1997) observed in their study using impedance cardiography (ICG) that a respiratory component was significantly related to subjective arousal, while other cardiovascular measures (inter-beat-interval and left ventricular ejection time) decreased for all emotions except for happiness, which the authors interpreted as a possible indication of physiological response related to valence. In another ICG-study, Kreutz, Bongard, and von Jussis (2002) found that the 'happy' or 'sad' tone of music excerpts was differentiated in both expert musicians and non-musicians by a weaker sympathetic influence on the hemodynamic response in the latter group.

Neuroscientific approaches to identifying networks associated with valence and arousal have partially corroborated the view of a dimensional representation of emotion (e.g., Lang, Bradley, Fitzsimmons et al., 1998). For example, Anders et al. (2004) conducted a correlation analysis between activity in different brain areas and individual emotional valence and arousal responses. They found that responses along the valence dimension were positively correlated with activity in the insular cortex, and arousal was correlated with thalamic activity. The second important finding of this study was the functional segregation of brain structures underlying the peripheral physiological responses and verbal reports: startle reflex augmentation was associated with amygdala activity and skin conductance responses with frontomedial activity (Critchley, Elliott, Mathias, & Dolan, 2000).

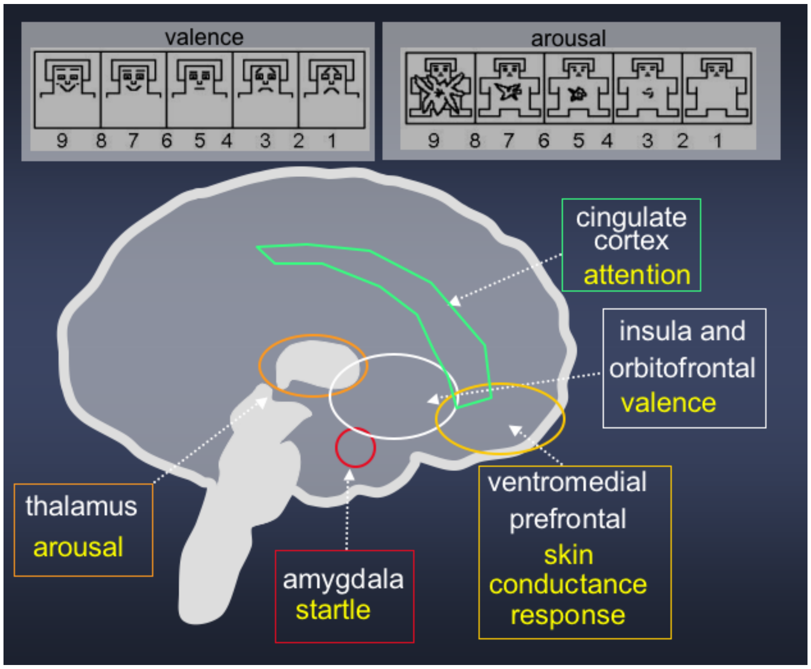

Figure 1. By using correlation analyses interactions between fMRI-activation and other measures used for quantifying the emotional intensity perceived can be detected. These are peripheral physiological measures such as skin conductance response (sweat) or startle amplitude (eye blink increase) but also ratings along the dimensions of valence and arousal. Anders et al. (2004) showed that fMRI-activation in the thalamus correlated positively with arousal, in the amygdala with the startle response, in the ventromedial prefrontal cortex with the skin conductance response and in the insula (and the adjacent orbitofrontal cortex: Wildgruber, Hertrich, Riecker et al., 2004; Lotze, Heymans, Birbaumer et al., 2006b) with the valence perceived. Additionally, activation in the anterior cingulate cortex is associated with attention to the stimulus that is more cognitive in the dorsal and more emotional in the ventral part (Bush, Luu & Posner, 2000).

2. Lesion and Imaging Studies

Recent studies of impaired emotional processing in patients with circumscribed lesions of the bilateral amygdala suggest impairments of the recognition and experience of facial expressions of fear in these patients (Adolphs, Gosselin, Buchanan, Tranel, Schyns & Damasio, 2005). By contrast, lesions of the insula and the surrounding basal ganglia lead to problems in the recognition of expressions representing disgust (for a review see Calder, Lawrence and Young, 2001). Interpretations of lesion studies in the context of studies of emotion (or otherwise) are restricted, because their sites often extend beyond the specific areas of interest. To bypass this problem, repetitive Transcranial Magnetic Stimulation (rTMS) has been recently developed as a method to artificially induce temporary lesions in healthy participants to allow investigations of the functional relevance of confined cortical areas for a given task (Cohen, Celnik, Pascual-Leone et al., 1997; Lotze, Markert, Sauseng et al., 2006a). Therefore, the focalized stimulation capacity of this method overcomes some of the limitations that arise from lesion studies. However, additional tools are needed to explore emotion processing so as to account for potential interactions between networks distributed across the brain.

3. Methodological Issues in Brain Imaging

Functional imaging techniques have been introduced to observe patterns of activation across the entire brain. These methods usually involve measuring changes in electric, magnetic, or metabolic activity over time and across cerebral regions that, depending on the location and size of area investigated, involve thousands to millions of individual nerve cells. These spatiotemporal changes of activity are then often correlated with behavioral as well as peripheral physiological measures. Note that the observed patterns of activation only indirectly represent underlying neural processing and, more importantly, are not necessarily *caused* by (correlated) behavioral information, or vice versa. Instead, relationships between brain activation on the one hand, and subjective or peripheral measures on the other, could well be mediated by intervening processes.

One useful method to identify structure-function associations is characterized as the subtractive approach. Activation patterns represented in so-called brain maps are obtained in different experimental conditions. Then, activation values taken during each condition are subtracted using either brain map as reference. The remaining activation might be interpreted as related to the specific experimental condition. This strategy has been applied in studies of the perceptual and emotional processing of visual materials. It has been shown, however, that disentangling the different functions of neural networks in different brain maps is particularly difficult when studying emotional processing (Murphy et al., 2003). For example, certain patterns of activation might well reflect aspects of visual processing that are induced by the attentional or emotional content of the perceived stimulus rather than being attributable to the emotion circuit (Lang et al., 1998). In other words, interpretations from the subtraction approach are clearly limited, because it is often difficult to associate the observed patterns of activation in the brain with specific functions in stimulus processing.

The methodological problems just mentioned extend to a more conceptual level. It must be noted that the theoretical separation of brain functions appears somewhat artificial given the extreme overlap of different elements of processing in real life situations. For instance, performing and listening to music involve multiple affective processes that are difficult to differentiate. These include, for example, perceiving and feeling the expression of a piece, interacting with others, memorizing and performing music from memory, analyzing music, being motivated to learn an instrument and much more.

Moreover, functional imaging techniques such as Positron Emission Tomography (PET) and functional Magnetic Resonance Imaging (fMRI) are problematic for reasons of experimental economy. Due to disadvantageous signal-to-noise ratios, effect sizes are usually small, while scanning protocols and data evaluation are subject to highly elaborate – and for the participant, uncomfortable – procedures. Furthermore, scanning noise produced by fMRI may have a deleterious effect on auditory processing, if the focus of the study includes music.

Another common problem, related to the low signal-to-noise ratio just mentioned, may arise when there are so few participants in a study that researchers are forced to use low activation thresholds (i.e. when observed patterns of brain activation are deemed significant). In such circumstances, increased blood oxygenation in one hemisphere may be wrongly interpreted as a specialization of this hemisphere for the given task. Obviously, cross-validation by replication is impaired if inadequate activation threshold levels are used.

A final methodological problem in the context of emotion studies arises from the neuroanatomical construction of the limbic system. Measurements of this system are subject to substantial artifacts based on the different densities of adjacent structures: there are air cavities next to the basal forebrain. Differences in lateralization of the amygdala, for example, might therefore result from certain scanning parameters, which can vary from study to study (Robinson, Windischberger, Rauscher & Moser, 2004).

4. Emotion-Related Neural Structures as Revealed by Imaging Studies

The most recent review articles on studies focusing on the functional specificity of areas related to the emotional processing system suggest no hemispheric lateralization of activation during the processing of basic emotions (Phan, Wager, Taylor, & Liberzon, 2002; 2004a; Murphy et al., 2003). Instead, after entering results from 106 imaging studies into meta-analytical procedures, almost none of the hypotheses on localization of emotional processing were upheld. Neither was emotion processing found to be restricted to classical limbic areas, nor did hemispheric lateralization of emotional valence emerge (Murphy et al., 2003). However, a further review of 55 neuroimaging studies on emotional processing converged in identifying a number of emotion-related neural circuits that were located in the bilateral amygdala, the bilateral insula (especially its anterior part: AI), the anterior cingulate cortex (ACC), and the medial and lateral ventral prefrontal cortex (mPFC/vPFC) (Phan et al., 2002).

Converging evidence from lesion and imaging studies suggests that fear and disgust are processed in different areas. Whereas fear activated the bilateral amygdala, disgust activated most strongly the insula and the basal ganglia (pallidum) (Murphy et al., 2003). By contrast, the same meta-analysis suggests that happiness and sadness did not reliably activate distinct representation sites. Finally, the processing of anger appeared to be associated with activation in the lateral orbitofrontal cortex. In sum, the available imaging (and lesion) data point towards a neural system of emotion processing that is far more complex than that which had been envisaged by some earlier proposals.

The meta-analyses mentioned above (Phan et al., 2002, Murphy et al., 2003) also suggest the amygdala to be associated particularly with the processing of fear, while specific patterns of activation were also observed in response to other emotions with both positive and negative valence. These findings converge with results from lesion studies of animals (Hitchcock & Davis, 1986, 1991), in that fear-related activations in the amygdala in humans are highly correlated with the startle response (Anders et al., 2004). Note that bilateral simultaneous activation of this structure and the parahippocampus is also associated with the perception of non-pleasant musical material (Blood, Zatorre, Bermudez & Evans, 1999) and is negatively correlated with the perception of intensely pleasurable episodes, so-called *chills*, while listening to music (Blood & Zatorre, 2001).

In the search for neural correlates during highly violent computer gaming the amygdala as well as the anterior cingulate cortex (ACC) were found to be deactivated (Mathiak et al., 2006). Aggression may decrease activation in areas associated with fear, but it increases activation in areas associated with the cognitive and attentional load during affective tasks, such as the more dorsal part of the cingulate gyrus (Bush et al., 2000). The ACC is closely interconnected with the amygdala and the mPFC (Devinsky, Morrell, & Vogt, 1995). Both the ACC and mPFC are highly correlated with changes in SCR and arousal. Whereas Murphy et al. (2003) found no indication that ACC plays a specialized role in emotion processing, Phan, Wager, Taylor and Liberzon (2004a) reported that in most studies ACC-activation was associated with a feeling of sadness. This report is corroborated by the findings from a study involving depressed patients who had recovered from their condition following pharmacological therapy (Mayberg, Brannan, Mahurin et al., 1997) and demonstrated altered ACC-activation from before to after the treatment.

A functionally relevant connection between ACC-activation and the intensity of subjectively experienced pain has been shown using fMRI-feedback methods. In particular, decreasing activation in the ACC correlated with a decrease in perceived pain (deCharms, Maeda, Glover et al., 2005). As the possibility that increases in ACC activity increased pain can be ruled out, rather than *vice versa,* such studies suggest ways of investigating potential causal links between sensory stimulation and activation in specific regions of interest. This method is already used for studying the modulation of one particular emotion: fear (Veit et al., 2006).

The insula and surrounding operculum contain primary cortical representations of smell and taste (Rolls, Critchley & Treves, 1996), somatosensory and viscero-sensation (Lotze, Wietek, Birbaumer et al., 2001), and pain perception (Apkarian, Bushnell, Treede, & Zbieta, 2005). For this reason, it has been termed the "limbic sensory cortex", and it is associated with the subjective feeling of emotional states. The anterior insula seems especially to reflect the self-conscious aspect of the rated intensity of a given emotion as observed for the visual modality in a parametric activation study. This technique involves regression analyses of brain maps using, for example, the subjective valence values induced by emotional pictures as predictors (Anders et al., 2004). In one particular study, the valence attributed to observed expressive gestures correlated with the activation of the anterior insula and the adjacent lateral orbitofrontal lobe (Lotze et al., 2006b). Whereas the anterior insula is associated with emotional valence, the dorsal part of this structure is more active during cognitive tasks (for a meta-analysis, see Wager & Feldmann Barrett, 2004). It seems that cognitive and emotional aspects of higher-level stimulus processing are represented in tightly adjacent regions in the insula.

Interactions between cognitive and emotional processing have also been observed in the mPFC. Activation of the *dorsal* mPFC has been observed during the cognitive regulation of emotional behavior (Ochsner, Ray, Cooper et al., 2004a), and when participants made judgments about other people's emotional states (Ochsner, Knierim, Ludlow et al., 2004b). In contrast, activity in the *ventral* mPFC has been associated with monitoring one's own feelings (Phan, Taylor, Welsh et al., 2004b) and the physiological changes that accompany particular emotional responses (Damasio, 1996). With respect to music, the modulation of emotions in the *dorsal* mPFC might be especially important since suppression of any emotional feeling during musical perception is most likely to be related to activation in this area. Activity in the *ventral* mPFC, however, is assumed to be associated with bodily responses such as shivers, sweating, and increases of heart rate during intensely pleasurable music (Blood & Zatorre, 2001).

The nucleus accumbens, located in the inferior part of the striatum, is active when individuals are rewarded with a pleasant odour (Gottfried, O'Doherty, & Dolan, 2002) but also when they experience revenge in a social interactive procedure after being cheated (Singer, Seymour, O'Doherty et al., 2006). The nucleus accumbens is often associated with self-rewarding processes (Menon & Levitin, 2005) and might to play some role in the motivation for learning to play musical instruments. Recently, activations of the nucleus accumbens were observed in emotional responses during listening to pleasant music (Blood & Zatorre, 2001; Kreutz, Ott & Wehrum, 2006).

In sum, investigations of emotion processing across specific domains suggest higher specialization of some areas than the meta-analyses are able to demonstrate. These studies also corroborate the view that cognitive and emotional networks are closely interconnected even within the same anatomical regions.

EMPIRICAL RESEARCH ON NEURAL CORRELATES OF MUSICAL EMOTION

1. Binaural Listening Tasks

Peretz et al. (1998) investigated musical judgments in affective and non-affective tasks, while participants listened monaurally to tonal and atonal melodies. The authors observed that tonal melodies were found more pleasant when processed in the left hemisphere, whereas atonal melodies were found more unpleasant when processed in the right hemisphere. These asymmetries were not present when listeners rated the correctness of melodies (Peretz et al., 1998). By contrast, Leichner and Bröscher (1999) concluded from their study using a similar research method, that valence was primarily evaluated by the right hemisphere. The authors used pre-selected examples of classical music to represent four categories, namely positive activating, positive calming, negative activating, and negative calming. Valence ratings were similar for both positive and negative music when stimuli were presented to the left hemisphere (right ear), and dissimilar, when the music was presented to the right or both hemispheres. Moreover, ratings on the ‘activating-calming’ dimension were markedly different for positive and negative music depending on mode of presentation. When presented to the right hemisphere or both hemispheres, negative music was found less activating (i.e. more calming) than positive music. However, when the same excerpts were presented to the left hemisphere, judgments were reversed in the sense that, although not significantly different, positive music was found less activating and negative music was found more activating (i.e. less calming). The authors speculate that there is a hemispheric dominance for some surface features of music that are relevant to emotional processing (Leichner & Bröscher, 1999).

2. Aphasia and Amusia

Broca’s area is an extremely important region of the brain, in the vicinity of the auditory cortices; it has traditionally been implicated in speech production. Consequently, patients with lesions in this area, particularly in the left hemisphere, often suffer from impaired speech production. However, it is note-worthy that some patients with *aphasia* are less affected in their musical abilities. Moreover, singing the lyrics of a song is easier for them than speaking the same words (Kaplan & Gardner, 1990). By contrast, lesions in the right hemisphere are more likely to impair the representation of melody contours (Peretz, 1990) and pitch processing (Murayama, Kashiwagi, Kashiwagi & Mimura, 2004), a condition that has been termed *amusia* (see also chapter 9).

Thus there seems to be some dissociation between the representation of speech and music that emerges from the laterality of cortical processing. Lesion studies are informative in this dissociation. Amusia may involve problems with perceptual processing as well as other skills such as memory for music. Importantly, however, amusia cannot – in most cases – be attributed to general sensory, attentional, or working memory impairments. Only rarely are characteristics of amusia such as *tone-deafness* observed in healthy people (Foxton, Dean, Gee, Peretz & Griffiths, 2004; Sloboda, Wise & Peretz, 2005)

Amusia has been found specifically in patients with bilateral anterior temporal lesions (Satoh, Takeda, Murakami et al., 2005). Other patients show deficits in the retrieval of musical material after right hemisphere posterior medial stroke including the inferior right frontal gyrus, the posterior temporal lobe and the inferior parietal lobe (Schön, Lorber, Spacal & Semenza, 2003). Peretz (1990) summarized a sequence of studies addressing music and emotion processing in a female “patient IR, who suffers from a longstanding bilateral brain damage to the auditory cortex” (Peretz, 1990, p. 116). Interestingly, IR shows normal speech, intelligence and memory capacities, while being unable to recognize familiar tunes or learn novel melodies. One of the most remarkable aspects of her musical deficits is that the recognition of the emotion conveyed by a given melody or musical excerpt is spared. For example, in one task, IR was asked to rate the ‘happy’ or ‘sad’ emotional tone in one half of a set of melodies while judging the degree of ‘familiarity’ in the other half, using the same response format for each scale. The results indicated that IR recognizes musical emotions just like healthy control participants, while being unable to recognize, discriminate, or learn to identify any of the tunes. Samson and Peretz (2005) studied patients suffering from temporal lobe lesions; their findings suggest that right temporal lobe structures play a critical role in priming and recognition memory for melodies as reflected by the absence of an exposure effect. In sum, these studies suggest cortical contributions to musical preference and liking judgments (Samson & Peretz, 2005).

Griffiths, Warren, Dean, and Howard (2004) observed a double dissociation between musical cognition and emotional processing in a 52-year-old patient – a radio announcer – who suffered from a focal lesion in the left insula, hippocampus and amygdala after a stroke. He retained most of his speech and motor functions, and his hearing had returned to normal 12 months later. However, he did not recover the particular pleasure he had previously experienced while listening to Rachmaninov preludes. Yet when he was tested for amusia by means of a standardized test battery, his perceptual abilities were found to be normal. The authors concluded that unilateral lesions in three structures of the limbic system resulted in a specific impairment for the feeling of pleasure elicited by music in this patient (Griffiths et al., 2004).

3. Brain Imaging Studies on Music Listening

Brain imaging studies on emotional responses to music have addressed a variety of research questions related to both the effects of music as well as the influences of individual differences on emotional responses. Some studies looked at brain activations while listening to music differing in emotional valence (Blood et al. 1999; Blood & Zatorre, 2001; Koelsch & Fritz, 2003), emotional tone, e.g. ‘happy’ or ‘sad’ (Kreutz, Russ, Bongard & Lanfermann, 2003), and in structural characteristics giving rise to emotional processing (Koelsch, Fritz, Schulze, Alsop & Schlaug, 2005; Pallesen, Brattico, Bailey et al. 2005). In recent studies, participants listened to music while viewing emotionally standardized pictures (Baumgartner, Esslen, & Jaencke, 2005; Spreckelmeyer, Kutas, Urbach et al., 2006). Few studies so far have investigated the influence of long-term individual differences such as musical training on brain responses to musical emotions (Koelsch et al., 2005; Pallesen et al., 2005).

Blood and Zatorre (2001) had their participants listen to music of their own choice, while peripheral cardiovascular and electrodermal activity as well as regional Cerebral Blood Flow (rCBF) changes were recorded using Positron Emission Tomography (PET). The purpose of using participant-selected music was to induce (pleasurable) *chills* reliably while listening. Subjective chill responses were then correlated with physiological measures. Participants’ responses while listening to a self-selected piece were compared with responses while listening to the favorite piece of another participant. Musical chill-related brain responses were identified in a number of regions including ventral striatum, midbrain, amygdala, orbitofrontal cortex, and ventro medial prefrontal cortex (VMPF). These structures are implicated in reward and emotion by previous research based partially on animal models (see Figure 2).

In their PET study Brown, Martinez and Parsons (2004) investigated the effects of unfamiliar music on a group of listeners who appeared to enjoy the experimenters’ choice of music. Again, increased rCBF was found in limbic and paralimbic structures, specifically the anterior cingulate cortex (ACC). The anterior insula, posterior hippocampus, superior temporal poles and nucleus accumbens, part of the ventral striatum, were activated when listening to music but not in a rest condition.

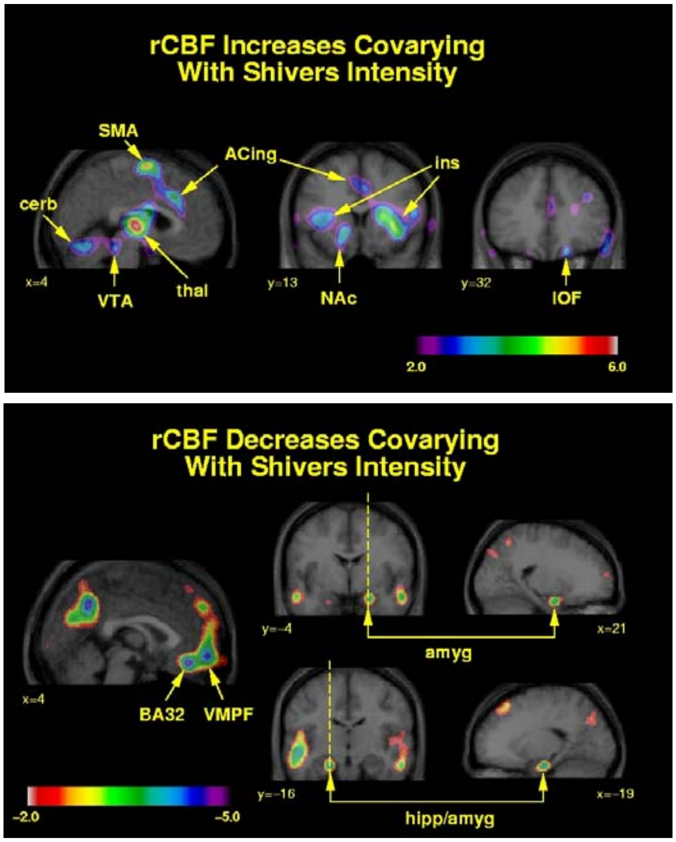

Figure 2. Neuroanatomical regions demonstrating significant rCBF correlations with chills intensity ratings. Regression analyses were used to correlate rCBF from averaged PET data for combined subject-selected and control music scans with ratings of chills intensity (0 to 10). Correlations are shown as t-statistic images superimposed on corresponding average MRI scans. The t-statistic ranges for each set of images are coded by color scales below each column, corresponding to *a*–*c* (positive correlations with increasing chills intensity), and *d*–*f* (negative correlations). *a* (sagittal section, x = 4 mm) shows positive rCBF correlations in left dorsomedial midbrain (Mb), right thalamus (Th), AC, SMA, and bilateral cerebellum (Cb). *b* (coronal section, *y* = 13 mm) shows left ventral striatum (VStr) and bilateral insula (In; also AC). *c* (coronal section, *y* = 32 mm) shows right orbitofrontal cortex (Of). *d* (sagittal section, *x* = 4 mm) shows negative rCBF correlations in VMPF and visual cortex (VC). e (sagittal section, *x* = 21 mm) shows right amygdala (Am). *f* (sagittal section, *x* = -19 mm) shows left hippocampus/amygdala (H/Am) (Figure 2 from PNAS, 98(20), p.11821, copyright (2001) National Academy of Sciences, U.S.A.).

Blood et al. (1999) addressed the valence dimension (pleasantness/unpleasantness) of emotion in a PET-study in which music stimuli with systematically varied degrees of dissonance were used. This variation resulted from the tonal relationship between a melody and its chord accompaniment. If the melody and accompaniment were in the same tonality, they were perceived as more consonant and more pleasant than when melody and accompaniment were derived from different tonalities, or when pitches with no harmonic relationship to the melody were included in the accompaniment. Parametric analyses of brain activation modulated by perceived pleasantness suggested that increasing unpleasantness activated the right parahippocampal gyrus and the precuneus, whereas increasing pleasantness correlated with activation in frontopolar, orbitofrontal regions and the ACC.

Notably, increases of rCBF in the orbitofrontal cortex, the temporal pole, and the superior frontal gyrus were observed in perceptual responses to positively valenced visual, auditory, and olfactory stimuli across all three modalities (Royet, Zald, Versace et. al., 2000). Although non-musical environmental (including speech) sounds were used to test the auditory modality, these results suggest links between music and the emotion-related patterns of activation in specific cortical and limbic structures. This particular link between auditory, music, and emotion processes appears most evident in the activation of the temporal poles (Brown et al., 2004; Kreutz et al., 2003; Royet et al., 2000), which may well be an important structural gateway between limbic and cortical areas.

Brain responses to manipulations of the harmonic structure of chord sequences (Koelsch et al., 2005), rather than of the degree of consonance as in the study by Blood et al. (1999), are believed to include areas of emotional processing, specifically the orbital frontolateral cortex (OFLC), which has been implicated in the evaluation of the emotional significance of sensory information (see Koelsch, 2005, p. 414). The study appears to lend some support to Leonard Meyer's theory of musical emotion as arising from violations of expectancy in the progress of musical sequences (Meyer, 1956). Note that brain activations including amygdala, retrospinal cortex, brain stem, and cerebellum were observed even when responses to isolated dissonant and minor chords were compared with responses to major chords (Pallesen et al., 2005). It seems possible that single musical events followed by silence suffice to induce expectations that might be felt as disrupted, leading to emotional responses (Bigand et al., 2005; Peretz et al., 1998).

Instead of computerized sounds, as in the study by Blood et al. (1999), Koelsch et al. (2006) used commercial recordings as basic materials in their fMRI-study. Excerpts were taken from instrumental dance music, e.g. *Tango Argentino*. From these excerpts, dissonant versions were constructed by digitally manipulating the sound files to introduce massive distortions while maintaining the overall physical time and amplitude characteristics of the music. Contrasts of brain activation in response to the original versus dissonant music showed that the original music activated extensive structures in the inferior frontal gyrus, anterior superior insula, ventral striatum, Heschl's gyrus and Rolandic operculum. Dissonant music, however, activated the amygdala, hippocampus, parahippocampal gyri and temporal poles. All of these sites, except for the hippocampus, were found to be more strongly activated after comparing BOLD signals from the first and the last 30 seconds of the music stimulation, which suggests dynamically changing activations over time. The authors conclude that activation of the amygdala during distorted music is corroborated by a previous report of impaired responses to music representing 'fear' in patients with amygdala resections (Gosselin, Peretz, Noulhiane et al., 2005). They also point out that, according to their own review of the literature, the same neural structures activated during dissonant music are also involved in the processing of pleasant stimuli, including the study by Blood and Zatorre (2001) mentioned above.

Kreutz et al. (2006) presented 25 classical music excerpts representing ‘happiness’, ‘sadness’, ‘fear’, ‘anger’, and ‘peace’, to listeners who rated each excerpt for emotion, valence and arousal. Ratings were entered into a parametric modulation analysis of activations in the entire brain. Results showed that valence as well as positive emotions were associated with activations in cortical and limbic areas including the anterior cingulum, basal ganglia, insula, and nucleus accumbens. Subsequent analyses of activation in other regions of interest largely supported these findings. Negative emotions, however, did not yield significant activations at group level (Kreutz et al., 2006).

Several EEG studies using various sets of musical stimuli (Altenmueller, Schuermann, Lim, & Parlitz, 2002; Schmidt and Trainor, 2001; Tsang et al., 2001) provide support for the hemispheric specialization hypothesis for emotional valence (Heilman, 1997), while. That is, music stimuli, which are judged positive or negative in valence, elicited asymmetrical frontal EEG activity. For example, Schmidt and Trainor (2001) found that music expressing joy and happiness elicited relatively greater EEG activity in the left fronto-temporal lobe, whereas music expressing fear and sadness elicited more activity in the right hemisphere. Moreover, faster tempi and the major mode produced greater responses in the left hemisphere, whereas slower tempi and minor mode were associated with greater responses in the right hemisphere (Tsang et al., 2001). Using a related technique (direct-current EEG), Altenmueller et al. (2002) played 160 music excerpts from four different genres to 16 right-handed students, who provided valence judgments for each stimulus. Positively valenced stimuli elicited bilateral fronto-temporal activations with preponderance of the left hemisphere, whereas negatively valenced stimuli elicited bilateral activations predominantly in the fronto-temporal right hemisphere. Females showed greater valence-related differences than did males. The authors conclude that the emotional responses observed in the EEG-patterns are independent of fine-grained musical structure. In consequence, the frontal temporal lobes seem to be involved in emotional evaluation and judgment rather than the perceptual analysis of emotional information (Heilman, 1997). Significant increases of frontal cortical activity as reflected in the 4-8 Hz power band of the EEG were observed over the first year of life in a developmental study on infants’ responses to affective music (Schmidt, Trainor & Santesso, 2003). Music excerpts, varying in valence and arousal (happy, sad, fear), were also found to induce significant decreases in overall activity between groups of 3-month-old versus 12-month-old children. The authors suggest that taken together their findings, which showed an emerging asymmetry of activation in the presence of an overall decrease of EEG-power, indicate maturation of cortical music processing as well as a “calming” influence of music by the end of the first year of life (Schmidt, Trainor & Santesso, 2003).

Goydke, Altenmueller, Moeller, and Muente (2004) conducted event-related potential (ERP) experiments to investigate the preattentive discrimination of emotions in instrumental timbres. ERPs derive from EEG measures usually in time windows shorter than one second in duration. More specifically, these authors used a particular component of the ERP signal, the so-called mismatch negativity (MMN) as an index of the brain’s capacity for identifying more or less subtle changes of sound. Non-musician listeners were presented with ‘happy’ and ‘sad’ versions of violin and flute sounds of 600 milliseconds duration, which also varied in pitch. The key finding was that emotional tone, like changes in pitch and timbre, triggered MMN. However, it is not clear, why the authors characterize the difference between ‘happy’ and 'sad' tones as more subtle than differences in pitch or timbre. It may be that MMN indexed not the perception of emotion *per se*, but rather – as it usually does – mere changes in the structural features of sound. These in turn feed into emotional processing at deeper levels of the brain. However, this does not preclude the possibility that cortical processing is essential to emotional experience (Damasio, 1998).

4. Brain Imaging Studies on Music Performance

Performing music – whether by singing, playing musical instruments, or dancing – is one of the most complex areas of human engagement in general. One might imagine that emotion in music performance must be based on similar neural processes to those involved in listening, on the grounds that performers listen to themselves. However, there are at least two hypotheses as to how the emotional effects of music performance might differ from those experienced in relation to less active musical behaviors such as listening. On the one hand, it may be assumed that cognitive processes interfere with emotional processes at both preattentive and attentive levels. Thus monitoring and integrating motor-sensory, tactile, kinesthetic, visual and auditory information, attentional and memory processes, etc., might *reduce* the intensity of emotional experiences. On the other hand, it could be argued, conversely, that similar perceptual and cognitive processes *enhance* emotional experiences during performance, because performance gestures appear to be partially conveying emotional information as one of their functions. However, to date it appears that investigations of the neural correlates of emotion in music performance are not nearly as advanced as, for example, research on cognitive processes in this domain.

Notably, psychological research on professional performance has emphasized the role of negative emotions in music performance such as performance anxiety (for a recent review see Steptoe, 2001), whereas a surprisingly small amount of research has addressed (or confirmed) potentially more positive emotional influences on musical activities (e.g., Kreutz, Bongard, Grebe, Rohrmann & Hodapp, 2004). It should be assumed that making music is associated with high levels of motivation and self-reward in order to be sustained as a lifetime commitment for many professional as well as amateur musicians. Indeed, social psychological research suggests that musicians often experience particular emotional states as characterized in the concept of *flow* (Csikszentmihalyi, 1990). In all accounts, however, emotional brain responses to music performance appear to be mediated by a range of factors including individual differences and situational context.

Singing is an obvious activity in which speech and music combine. There are musical aspects of speech, as reflected in so-called *prosody* (Bostanov & Kotchoubey, 2004; Mitchell, Elliott, Barry et al., 2003). Briefly, speech prosody is defined by the (intentional and unintentional) variation of fundamental pitch, intensity, and spectral information during speech production. Prosody is thought to influence the emotional tone of any given utterance. Imaging studies have shown that recognition and perception of prosody appears to be lateralized to the right hemisphere and is associated with activity in the lateral orbitofrontal lobe (Wildgruber et al., 2004). This area seems also important bilaterally for the recognition of valence in visual stimuli (Lotze et al., 2006b).

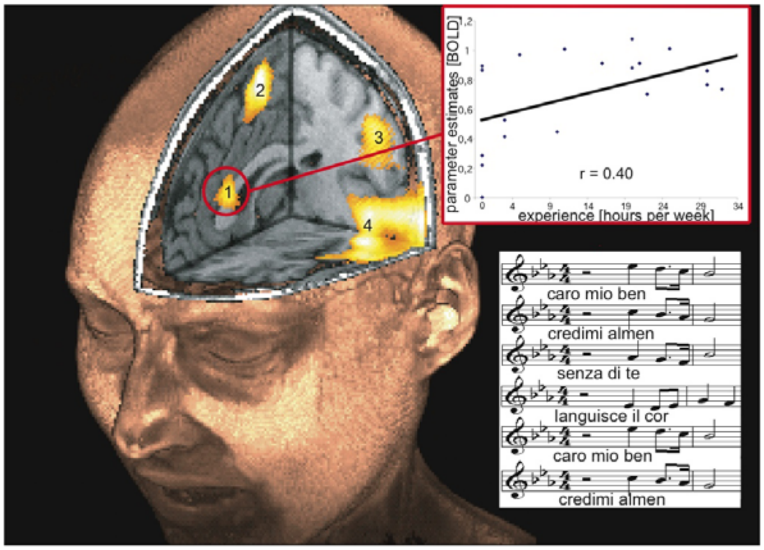

Figure 3. Functional map of a group of 25 participants with different experience in singing during singing an Italian ‘aria antiche’ (“caro mio ben”). Group statistical map was coregistered and then projected on an individual head. During singing the anterior cingulate cortex (1), the SMA (2), the bilateral sensorimotor cortex (3, only seen on the left side) and the primary and secondary auditory cortex (4) showed activation. Interestingly, activity in the anterior cingulate correlated positively ($r = 0.40$; $p < 0.05$) with the amount of practice per week. Some subjects were naïve but some (n=15) were professional singers (8 singing students and 7 opera singers) who performed singing up to 30 hours a week.

Figure 3 depicts patterns of brain activation in 25 participants while singing an Italian bel canto aria. Note that activation in the ACC depends on levels of singing expertise. Significant increase in ACC activation was shown in experienced singers, while naïve participants who had not received singing training (n = 5) showed no such increased activation. When interpreting these findings, it is worth noting that the ACC is also involved in the recall of emotions (Phan et al., 2004a), a capacity that might be crucial to the conveying of emotional expression in professional singing.

CONCLUSIONS

In music psychology, cognitive approaches to music listening and performance dominated during the last third of the 20th century, while research on musical emotion was scarce (cf. Dowling & Harwood, 1986; Lerdahl & Jackendoff, 1983). Nevertheless, over the course of the last decade emotion has now become an established topic. Some authors speculate, with regard to unsolved issues concerning the cognitive processing of music that “there is an even deeper mystery within brain organization to which all these cognitive issues are subservient” (Panksepp & Bernatzky, 2002, p. 134).

Experimental research on emotion is often designed to include measurements of subjective, brain imaging and peripheral physiological responses within single protocols (for a theoretical discussion, see Peper & Lüken, 2002). Investigations of the psychophysiological correlates of musical emotion follow this general trend. However, behavioral approaches in themselves (without or in combination with simultaneous physiological recordings) are of continued importance for several reasons. First, introspection is a key motivation for addressing the biological underpinnings of musical experiences and to ascertain the deep emotional impact of music on potentially every human (e.g. Gabrielsson, 2001). Second, behavioral information, which can be verbal or non-verbal, appears crucial in the generation and construction of research hypotheses and the development of experimental designs that include imaging methods. Third, subjective responses are indispensable when interpreting the physiological concomitants of human emotions (Panksepp & Bernatzky, 2002).

Hypothesis-driven approaches clearly have advantages over exploratory studies, as the former often lead to more precise interpretations. Inevitably, a much wider empirical basis is needed for using brain-imaging methods in the context of musical behavior and emotion. It appears that our current knowledge of neural correlates of musical emotions is based on very few studies each with very few participants. Therefore, in addition to those methodological problems discussed in section 2 of this paper, the interpretation of findings in the field of music appears even more constrained than that of findings from other domains such as vision or speech/language, for which a much larger body of research exists.

It appears that the richness and subtlety of emotional experiences of music stand in sharp contrast to current research on emotion, which has often only focused on, for example, broad categories of so-called basic emotions, or music of drastically different degrees of valence and arousal potential. Similarly, there is a dearth of empirical evidence relating to biographically or culturally mediated influences on musical emotions. To be sure, music might not always induce positive responses in our daily lives. Instead, loud music, for instance, is a prominent stressor with potentially hazardous health implications to the nervous system. However, it is worth noting, as Koelsch (2005) argues, that music is among the very few stimuli that can reliably elicit (strong) *positive* emotions in the laboratory, even across a wide range of listeners, including amusics (Peretz et al., 1998). Moreover, the findings of studies seem to converge in suggesting the involvement of “limbic and paralimbic structures (such as amygdala, hippocampus, parahippocampal gyrus, insula, temporal poles, ventral striatum, orbitofrontal cortex, and the cingulate cortex)” (Koelsch, 2005, p. 412) in musical emotion processing. Note that none of these structures appears to be specialized exclusively for music. However, the existence of music-specific modules for emotion processing remains a plausible hypothesis for future research (Griffiths et al., 2004).

To summarize, the view of musical affect as subordinate to cognition is challenged by the results of investigations into the neural correlates of musical experience that explicitly address emotion. Whether emotional responses precede cognitions, or vice versa, or if music (including aspects of emotion processing) represents an independent modality, are matters of ongoing debate (Peretz & Zatorre, 2005). In any case, music seems an “excellent paradigm to explore the interactions between neocortically mediated cognitive processes and subcortically mediated affective responses” (Peretz & Sloboda, 2005, p. 410).

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