

Emotion investigated with music of
variable valence – neurophysiology
and cultural influence

Emotion investigated with music of variable valence - neurophysiology and cultural influence

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Preface

Motivation and outline of the current thesis

Traditionally emotions were regarded to be the ‘antithesis of human cognitive abilities’ (Mithen, 2005). This picture has changed a great deal during the last decade, showing that emotion modulates a multitude of processes attributed to human cognition. Although emotion research has become a hot topic in cognitive research, the neurophysiology of emotion is still largely ambiguous, especially with regard to positive emotions that are not trivial to elicit in experimental situations.

Music above all other means of perceptual stimulation is exceptional for its capacity to evoke emotional responses in the perceiver. It has popularly been characterized as a “language of emotions” (Bonds, 2006; Michaelis, 1800; Pratt, 1948; Seashore & Metfessel, 1925), and has been suggested to be a method that has evolved to express and induce emotion. Thus, the neurology of music perception appears to be an ideal system to investigate the physiology of emotion and the influence of emotion on auditory perceptual processes.

An important concept in systematic emotion research is the investigation of emotion by means of dimensional emotion models. This concept is based on the assumption that the emotional impact of a sensual stimulus can be qualitatively characterized on various continuous dimensions and that each dimension can be investigated discretely. The valence dimension ranging from unpleasantness to pleasantness is a common denominator between most dimensional emotion

models and has proven to be a parameter that can be reliably varied in psychological experiments.

Music is a powerful and reliable means to stimulate the percept of both intense pleasantness and unpleasantness in the perceiver. However, everyone's social experiences with music suggest that the same music piece may elicit a very different valence percept in different individuals. A comparison of music from different historical periods suggests that enculturation modulates the valence percept of intervals and harmonies, and thus possibly also of relatively basic feature extraction processes. Strikingly, it is still largely unknown how much the valence percept is dependent on physical properties of the stimulus and thus mediated by a universal perceptual mechanism, and how much it is dependent on cultural imprinting.

The current thesis investigates the neurophysiology of the valence percept, and the modulating influence of culture on several distinguishable sub-processes of music processing, so-called functional modules of music processing, engaged in the mediation of the valence percept.

A brief summary of each chapter will ensue, including an outline of the experiments and the main respective findings.

Chapter 1 (What is emotion?) addresses a comprehensive review of the theoretical background necessary to position the present work in the context of previous and current emotion research. Distinguishing characteristics of emotion are outlined, with an emphasis on valence as a fundamental component of emotion. Anatomical and functional qualities of putative neural substrates of emotion are described, with a special emphasis on the amygdala. It is addressed why a better understanding of emotion is beneficial for cognitive science, and it is suggested by which means the investigation of emotion is currently approached most effectively.

Chapter 2 From music perception to valence percept addresses how music processing can be investigated in a theoretical framework composed of functional modules which allows for a differentiated elaboration of several relatively separate sub-processes.

The concept of modular theory as portrayed by Fodor is introduced and abandoned in favour of a more recent derivative of modular theory that takes into account criticism about various module features laid out in the original theory such as domain specificity and innateness. Our current knowledge on the neural basis of the perceptual modules ‘feature extraction’, ‘structure building’, and ‘a-referential meaning’, and their currently known relation to the valence percept are described.

The concepts of musical and sensory consonance/dissonance are introduced, and one component of sensory consonance/dissonance, ‘roughness’, is described in detail.

Chapter 3 Methods describes fundamentals of the methodologies applied in the current thesis. *Chapter 3.1 Ethnomusicological cross-cultural comparison* summarizes principles of ethnomusicological cross-cultural investigation, and lists design features of music. The basics of functional magnetic resonance imaging are outlined in *Chapter 3.2 Functional magnetic resonance imaging*.

The data acquired in Experiment 1 is analysed to address two distinct questions: “What is the neural correlate of the valence dimension?” (*Chapter 4.1 The neurology of the valence dimension as investigated with pleasant and unpleasant music*), and “Does our auditory system privilege the processing of musical sound with low harmonic roughness (high harmonicity)?” (*Chapter 4.2 Opening up to consonance – an amplification mechanism in the auditory pathway dependent on harmonic roughness*).

The neurology of the valence dimension as investigated in *Chapter 4.1* has not yet been intelligibly exposed. The putative workings of the amygdala in the mediation of both positive and negative valence percept remains especially puzzling. The design of Experiment 1 is optimized to investigate the engagement of amygdala subregions during variable valence percepts mediated by musical stimuli with 3T fMRI. It is shown that two separate amygdala subregions are involved in the orchestration of response to stimuli of positive and negative valence. The functional connectivity network of each of these regions is investigated, revealing that each behaves synchronously with a corresponding putatively largely valence-specific network. It was furthermore investigated whether certain brain regions may behave rather in accord with positive and negative valence as independent dimensions (Lewis et al., 2007), instead of valence as a single continuous scale from unpleasantness to pleasantness. Two separate parametric analyses conducted for independent positive and negative valence dimensions showed that a putatively dopaminergic system responded only to alterations in the positive valence spectrum, showing no significant response when a continuous valence dimension from unpleasantness to pleasantness was assumed.

Chapter 4.2 addresses, whether the valence percept in response to consonance and dissonance is hardwired in the auditory perceptual pathway, or an effect of late cognitive processing. Another analysis of the fMRI data investigated in *Chapter 4.1* identifies a neural network sensitive to dissonance that determines how much musical sound engages the auditory cortex dependent on its harmonic roughness. These findings are interpreted in terms of a perceptual gating mechanism in the auditory domain that involves several levels of the auditory pathway and the amygdala to regulate information flow into the auditory cortex.

Experiment 2 addresses the questions “Are violations of music syntactic expectancy perceived as unpleasant?”, “What is the corresponding neural substrate?”, and “How does the neural response to violations in music differ

between Western listeners with varying degrees of musical expertise which corresponds to various degrees of music cultural knowledge?" (*Chapter 5 Is the neurology of aversive response to violations of expectancy in chord progressions modulated by musical expertise?*). Chord sequence paradigms with harmonically regular and irregular chords are often used to investigate the processing of 'musical syntax'. However, these investigations may to some extent be confounded by emotional responses systematically triggered by unexpected chords. Experiment 2 examines the valence percept mediated by music-syntactically regular and irregular chords in non-musicians and musicians behaviourally and with fMRI, showing that the regularity of the chords corresponds to the valence percept they mediate and the degree of amygdala response in the listener.

Furthermore, Experiment 2 investigates how cultural imprinting in terms of musical education modulates the valence percept mediated by the presented chords of variable music-syntactic regularity, and its underlying neural substrate. Evidence is provided that behaviourally non-musicians rated irregular chords as more unpleasant than musicians, which corresponded to a stronger amygdala engagement in non-musicians during the perception of the irregular chords. It will be argued that this likely resembles a music cultural effect.

Experiments 3 and 4 elaborate even more strongly and comprehensively the effect of cultural imprinting on the valence percept mediated by music listening, as well as universals of music appreciation (*Chapter 6 Universal preference for consonance over dissonance and forward over backward in music*). It is still unclear which aspects of music perception are universal and which are developed only after exposure to a specific musical culture. Experiments 3 and 4 are cross-cultural studies with participants from a native African population (Mafa) and Western participants, both groups naïve to the music of the respective other culture. Effects of spectral and temporal distortions on the appreciation of Mafas and Westerners listening to both Western music (Experiment 3) and music from the Mafa culture (Experiment 4) are

investigated. It will be demonstrated that preference for consonant as opposed to dissonant music, as well as preference for music played forward as opposed to music played backward, are based on perceptual mechanisms that are universal, although the impact of the respective distortion is modified by the listeners' music cultural imprinting.

Experiment 5 addresses the modulating influence of a capacity to decode emotional expressions (a form of a-referential semantic information) from Western music on the appreciation of Western music and its manipulated counterparts in Mafa listeners entirely naïve to Western music (*Chapter 7 Recognition of emotional expression in unknown music of another culture modulates the valence of the music percept*).

The experiment consists of two sections: First, it is investigated how good Mafa listeners naïve to Western music (and a Western control group) recognize the emotional expressions happy, sad and scary in Western music. Note that there is evidence that a decoding of such emotional expressions depends on referential information, namely culturally learned musical clichés, but that until today it is not evident if the decoding of such emotional expressions engages universal perceptual processes. Section one of Experiment 5 provides first evidence for such universal perceptual processes underlying the decoding of emotional expressions from music.

In a second section, the emotion expression recognition performance of those Mafa individuals who had also participated in Experiment 3 was correlated with their indication of appreciation of Western music and its counterparts as indicated in Exp. 3. It is shown that the capability to decode emotional expressions from Western music pieces modulates the Mafa listeners' valence percept of the Western music excerpts and their temporally corrupted counterparts. It will be argued that correspondingly the capacity to decode emotional expressions from Western music entails its increased appreciation.

Chapter 8 summarizes and discusses the findings from the experiments conducted, addressing their integration for the benefit of a more holistic understanding of the investigated association of music processing and valence percept. Furthermore, future research questions arising from the present work are pointed out.

I

Theoretical background

Chapter 1

What is emotion?

Etymology: The term emotion originates from the French *émotion*, which derives from *émouvoir*, 'excite' which is based on Latin *emovere*, from *e-* (variant of *ex-*) 'out' and *movere* 'move' (adapted from Kluge, 2002).

1.1 Lack of a comprehensive definition

“Everyone knows what an emotion is, until asked to give a definition” (Fehr & Russell, 1984) (p.464).

Apparently innumerable scholars in philosophical and psychological science have addressed the question “what is emotion?” Why do we still ask this question at present? The answer is obvious: Albeit considerable advances in the field, we still don't exactly know what emotion is. However, today we have new tools and methods at hand to promote an approach towards emotion research from a neuropsychological perspective (affective neuroscience (Daggleish, 2004)), and we hope to put together pieces of the puzzle that have either been missing or seemed discrepant.

Although since the early days of functional human brain imaging in the 1990s, the research of emotion has become an important topic in the field of cognitive science, there has not been reconciliation on a common denominator of what emotion is¹. According to Carroll Ellis Izard the explanation for this is to be found in the complexity and manifold functional integration of emotions, and he states that a definition of emotion must take into account the following three components (Izard, 1971): a.) the experience or conscious feeling of emotion, b.) the processes that occur in the brain and nervous system, and c.) the observable expressive patterns of emotion. The difficulty of this task has led to a large diversity of emotion definitions that add to the ambiguity of the term. The diversity of emotion definitions was investigated by Kleinginna & Kleinginna who aimed at quantifying the number of distinct emotion definitions in the literature, accumulating an impressive number of 92 thereof until 1991 (Kleinginna & Kleinginna, 1981).

Such ambiguity of the term has likely contributed to a negation of a scientific investigation of emotion in the second half of the 20th century, especially during behaviourism (e.g. neither Skinner (Skinner, 1953), nor Duffy (Duffy, 1941) believed that emotion possessed characteristics distinguishing it from other behaviour).

In the course of scientific emotion research there have indeed always been considerable differences in the interpretation of what emotion is.

¹ The significance of the challenge to achieve a common denominator of what emotion is can be illustrated by an introductory statement to "The emotional motor system" (Holstege, Bandler, & Saper, 1996), a book based on a conference focussing on emotionally controlled features of the motor system: "... *there was considerable difference of opinion among the conferees, and no single definition was universally accepted. The key issue appeared to be the view that emotion is an internal state, distinct from other aspects of cognition, and therefore perhaps not definable in terms of cognitive functions*". The vagueness of this account also characterizes a multitude of other emotion definitions, often emphasizing the large variety of processes where emotion is involved. Examples: "*What we refer to as emotion is a constellation of sundry functions. These include subjective experience as well as its evaluation and expression via prosodic, gestural and lexical communicative channels*" (Anderson & Phelps, 2000); "...*emotions are made up of component functions (subjective experience, stimulus evaluation, physiological responses, feedback, elicited behaviours, voluntary behaviour, etc)*" (Armony & LeDoux, 2000).

Correspondingly, several research traditions in favour of different theoretical approaches toward emotion research have developed over the past 150 years. Cornelius (Cornelius, 1996) traced these back to concepts of major influence, differentiating a “Darwinian Perspective”², “Jamesian Perspective”³, “Cognitive Perspective”⁴ and “Social Constructivist Perspective”⁵. The list of research perspectives proposed by Cornelius needs to be complemented,

²Which in the second half of the 19th century originated as a plea against the at that time prevailing concept of special creation and is based on the idea that emotions are mechanisms that have established an increased survival value and have been selected for during species-evolution. “As such, we should see the same emotions, more or less, in all humans. In addition, since humans share an evolutionary past with other mammals, we should expect to observe similarities in the emotions of closely-related species” (Cornelius, 1996).

³This line of research was influenced by the work of William James, who is one of the two namesakes of the James-Lange theory of emotion, which he formulated independently of Carl Lange in the 1880s. He suggested that “bodily changes follow directly the perception of the exciting fact, and... our feeling of the same changes as they occur is the emotion” (W. James, 1884) (p. 189-190). This idea implies that emotions never occur without an alteration of bodily states (visceral, postural, or facially expressive) and that these alterations are a precondition for an emotion. James assumed that each emotion is accompanied by a unique pattern of bodily responses and accordingly suggested that “the nervous system of every living thing is but a bundle of predispositions to react to certain features of the environment” (p. 190).

⁴The “Cognitive Perspective” reflects the view that thought and emotion are inseparable processes and that emotional responses are reliant on preceding or accompanying cognitive assessment procedures that have been subsumed under the term “appraisal” (Arnold, 1960). According to a popular model according to this view, emotion arises from a combination of physiological arousal and cognitive interpretation (e.g. the “two factor theory of emotion”). A prominent and early example of such a theory is the Singer-Schachter theory (Schachter & Singer, 1962). It was the resume of experiments where the authors varied the arousal of the participants by administering different levels of adrenaline and then confronting them with social situations that had been put in scene. The combination of whether participants received adrenaline or a placebo and the appraisal of the situation determined the emotional response evoked in the participants. “Appraisal theories”, which fall into the “Cognitive Perspective” differ with respect to their emphasis on automatic and unconscious or controlled and deliberate assessment processes (Roseman & Smith, 2001; K. R. Scherer, 2001), and the number and quality of other processes involved in the assembly of an emotion. Ortony & Turner for example argued that further elements of an emotion besides appraisal and physiological arousal may be action tendencies, desires, and feelings (Ortony & Turner, 1990). They emphasized appraisal as a constituent element of emotion by means of the following example: Cold-distress (the state of feeling cold) is not regarded as an emotion, although it is negatively valenced and its associated physiological response is hardwired, merely because the shivering and numbness of cold are not the result of the appraisal that one is cold, but only of the body’s automatic reaction to low ambient temperature.

⁵Quasi the counter thesis to the theory of hardwired basic emotions. This research tradition corresponds to the view that emotional mechanisms are entirely acquired during socialization (Armon-Jones, 1986a, 1986b). They may therefore at least to some degree be culturally relative (Levy, 1984; Lutz, 1988; Rosaldo, 1980; Russell, 1991; Shweder, 1985). It is possible to draw parallels between a common social constructivist approach and William James’ view that we feel an emotion as a result of interpreting our bodily state (W. James, 1884), with the important difference that social constructivists assume that the physiological reactions (as well as their interpretation/appraisal) correspond to psychological manifestations learned in a cultural

however, by another theoretical approach, the “dimensional emotion model” introduced by the physiologist and first experimental psychologist Wilhelm Wundt (Wundt, 1896). This approach is of considerable relevance to the present work and will thus be set out in detail in *Chapter 1.1.4*.

Although the different theoretical perspectives vary with respect to their concept of emotion, several authors (Cornelius, 1996; Juslin & Västfjäll, in press) emphasize that these differences largely derive from the fact that the various approaches to the investigation of emotion are unequal with respect to their thematic focus and the mechanisms they investigate. Darwin for example was predominantly concerned with the role played by the expression of emotion, while James was largely concerned with explaining the subjective experience of emotion. Along these lines, it has even been proposed that the best strategy to address a definition of emotion is in terms of conflicting theories (English & English, 1958). It has become clear that we may only comprehensively approach defining emotion by integrating the various research perspectives on emotion. This is an ongoing process, driven by the renaissance of emotion research that has occurred since the early 1990s, largely corresponding to methodological progress in neuroscience.

The present chapter aims at outlining distinguishing characteristics of emotion, touching on why emotion research will be beneficial to the cognitive science community, and suggesting means by which its investigation may be currently addressed best.

1.2 Functions

One possibility to derive a definition of emotion is to outline its characteristics in terms of its functionality, and thus the advantage it provides for an organism

in natural selection. Emotion as a mechanism enhancing the fitness and reproductive value of an organism was skillfully portrayed by Charles Darwin (Darwin, 1872). His work promoted the view that emotion and expressional behaviour associated with emotion is phylogenetically ancient, a set of mechanisms evolved by natural selection that humans share with a multitude of other animals. Importantly, Darwin argued that emotional expression may have largely evolved and survived for its benefit in animal communication (between or within species), communicating the organism's state and behavioral intentions. Note that this expressional feature of emotion may be not of eminent use in an isolated organism, but becomes highly relevant if a species is socially organized and members of the species interact in a coordinated fashion (K. R. Scherer, 1981), promoting social bonding, group cohesion, and consequently group activities such as hunting and food sharing. Darwin famously illustrated his accumulated evidence for similar emotional expression behaviour in humans and other animals (Darwin, 1872), describing it in anthropomorphic metaphor⁶.



Figure 1. An example taken from Darwin's book "The expression of the emotions in man and animals", illustrating similarities in emotional expression between

⁶ "Historically, anthropomorphisms have been used to attempt to (...) get traction in a domain unknown and perhaps unknowable such as the subjective experience of an animal. In the domain of human-animal interactions, anthropomorphism might be best thought of as attributions of human qualities to nonhumans not proven to bear these qualities" (Horowitz, 2007).

different mammals. The illustrations show teeth display during anger in a dog and a human (Darwin, 1872).

From comparing these common features he deduced that what we humans experience as emotion reaches far back in our phylogenetic history and was presumably shared by the common ancestors between us and the respective species he considered for comparison. He inferred that such an evolutionary origin would predict emotions to be cross-culturally universal.

His evolutionary scenario has contributed importantly to the concept of “basic emotions”, which is in detail described below in *Chapter 1.1.3*. In basic emotion theory a subset of emotions are regarded to be distinct and quite stereotypical patterns of bodily expression and physiological activation that are expressed by an organism to signal an attitude towards another agent in an immediate manner and to facilitate an appropriate (in terms of survival and reproductive value) action in relation to this agent. As such, each basic emotion would correspond to different functions, for example fear motivates flight from danger⁷, anger motivates fighting for survival, etc.

Emotions as a set of evolutionary optimized mediation processes between an organism and its environment thus constantly map external stimuli onto appropriate responses. In addition to the communicatory, expressive purpose outlined above, they therefore have to fulfill the function of evaluating the relevance and significance of particular stimuli or stimulus configurations⁸ in constantly changing situations, and facilitating a response involving complex physiological changes (e.g. for action preparation or memory retrieval/storage

⁷ Note however that Gray considered fear and anxiety to be mediated by a behavioral inhibition system (corresponds better with the freezing response) rather than by a fight-flight system (Gray, 1991) that may mediate terror which would instead motivate a flight response in a dangerous situation (Ortony & Turner, 1990).

⁸ Rolls argues that stimuli and stimulus configurations that provoke an emotional response can always be considered positive or negative reinforcers, corresponding to rewards and punishers (Rolls, 2000). A termination of reward or punishment may also work as a reinforcer. He distinguishes between unlearned (primary, e.g. food) and learned (secondary) reinforcers.

(Rolls, 2000)) matching the organisms' needs, plans and preferences. This suggests that emotions are heavily involved in learning processes (K. R. Scherer, 1981).

Emotions engage several specialized neural mechanisms for memory and motor control in order to deal with such complex tasks and enhance fast and precise coordination of physiological responses and actions.

An anecdote of the discovery of the memory system specialized for the storage of 'emotional' information illustrates its working: At the beginning of the 20th century, the French physician Edouard Claparede described the case of a patient who seemingly had lost all ability to create new memories. The case was so severe that the patient would forget about knowing Claparede if he left the room for a few minutes, so that he would have to reintroduce himself each time he re-entered the room. In a typical fashion they would then shake hands. This procedure would repeat each time they met until during one session Claparede fixed a tack at the palm of his hand and pricked her pretending that he wanted to shake hands. After this occasion the patient hesitated to shake hands with the doctor, but could not tell why. Claparede thus observed evidence for the existence of (at least) two dissociated memory systems. One that was engaged in creating memory from experiences that could be consciously recollected at a later occasion and another that operated outside awareness, unapproachable by introspection (LeDoux, 1996)⁹.

⁹ The former one, the so-called explicit or declarative memory (the terms are often used interchangeably, although they originate in different topics of research: the term explicit memory was formed due to research on the psychology of memory while the term declarative memory came out of research on the function of the temporal lobe), was not veritably approached until the past mid-century due to the famous case of H.M. who was operated in order to gain control over his severe and intractable epilepsy. Indeed, the initial medical goal was achieved and the seizures became controllable by anticonvulsant medication. Postoperatively however, the patient suffered from severe anterograde amnesia (so that he could not convey information from short-term-memory to long-term-memory) and a mild retrograde amnesia. The findings thus suggested that explicit long-term memory involves at least two stages: an initial one requiring the regions that were removed and another one at a later stage where supposedly areas of the neocortex are involved (McClelland, McNaughton, & O'Reilly, 1995; Squire, Knowlton, & Musen, 1993). Large regions of the temporal lobes had been

LeDoux suggested that information about stimuli associated with unpleasant or painful experiences is stored in the amygdala and related brain regions (LeDoux, 1996). This system seems to mediate emotional reactions which are elicited when such stimuli are reencountered (LeDoux, 1996, 2000a).

Emotions also enhance the precision and duration of explicit memories. Christianson provided evidence that memories with emotional content have a higher vividness and are longer lasting (Christianson, 1992). McGaugh et al. suggest that stories with emotional content are remembered better than similar stories lacking emotional implications, and that lesions of the amygdala could prevent this effect (McGaugh, Cahill, & Roozental, 1996). Emotional content is suggested to gain mnemonic advantage through an enhancement of encoding and consolidation in memory that has suggested to be at least partly mediated at the neural level by the modulatory influence of the amygdala (Dolan, Lane, Chua, & Fletcher, 2000; Hamann, Ely, Grafton, & Kilts, 1999; Morris & Dolan, 2001; Phelps et al., 1998; Richardson, Strange, & Dolan, 2004).

The existence of specialized emotional mechanisms of motor control is substantiated by evidence demonstrating that emotionally influenced motor activity might engage muscular patterns that cannot be involved in voluntary movements (Bandler & Keay, 1996; Damasio, 1995; Nieuwenhuys, 1996). Already Darwin and Duchenne de Boulogne realized that smiling due to real amusement involves musculature which cannot be activated when smiling voluntarily (Figure 2) (Ekman & Davidson, 1993) and lesion-case data suggest

removed bilaterally including the amygdala and major portions of the hippocampus, as well as surrounding transitional areas. Thus, a distinct area of the brain was realized to be of special importance concerning long-term (but not short-term) memory and from the temporal regions involved in the ablation, the hippocampal circuits were the regions traced to be particularly important to the creation of declarative longterm-memory. It was the first time that the concept of the limbic system to be the executive organ of emotion was challenged, showing that areas ascribed to the limbic system were crucial to higher functions of conscious processing. For a detailed critical argument on the concept of the limbic system see (Brodal, 1982; Kotter & Meyer, 1992; LeDoux, 1996).

that there are partly differing neural circuits underlying this effect (Figure 3) (Holstege et al., 1996).

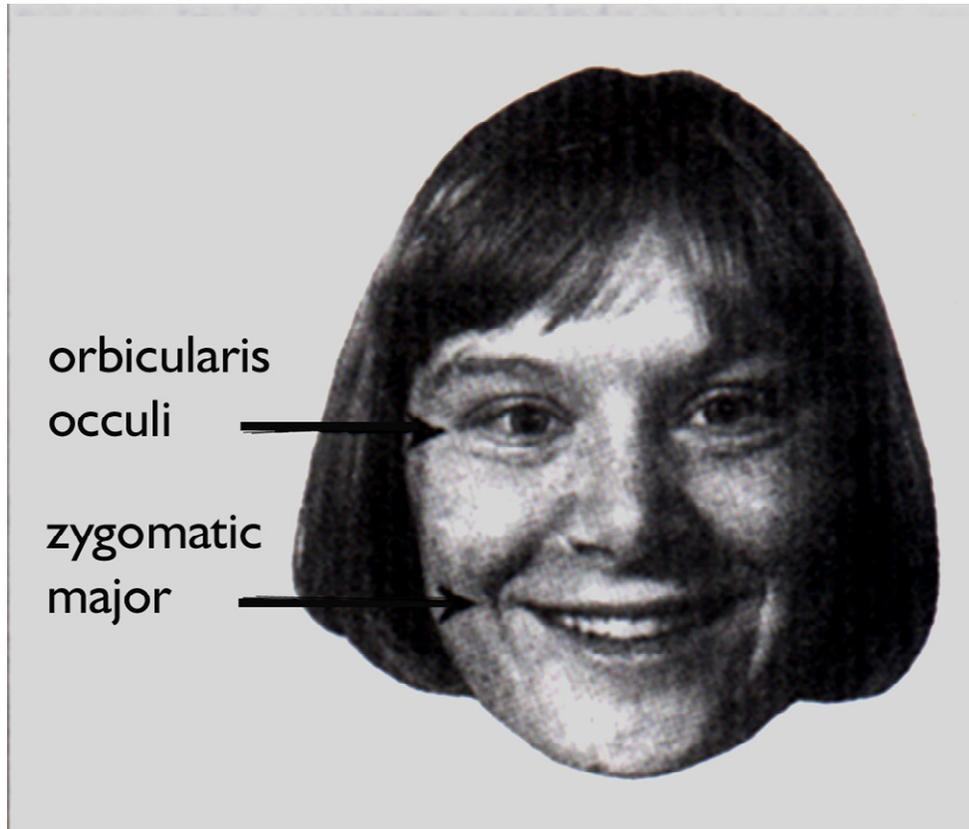


Figure 2. “The emotion of frank joy is expressed on the face by the combined contraction of the zygomatic major muscle, and the orbicularis oculi. The first obeys the will but the second is only put in play by the sweet emotions of the soul.” (Duchenne de Boulogne cited in Ekman & Davidson, 1993). More recent studies have provided evidence that it is more specifically the pars lateralis, the outer part of the orbicularis oculi that can rarely be accessed by voluntary action (Ekman & Davidson, 1993). Picture taken from Damasio, 1995; labelling changed.

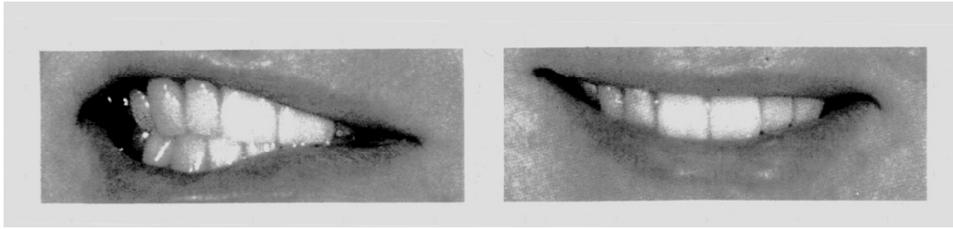


Figure 3. The mouth of a patient that had a small infarction in the white matter, interrupting the corticobulbar fibers that originate in the face part of the right-hemisphere motor cortex. While patients displaying this kind of disorder are unable to voluntarily use muscles that are located left from their mouth (see left picture), they will still be able to innervate these muscles when reacting to a funny situation. “Apparently, the motoneurons in the facial nucleus innervating the oral muscles, are controlled by two different motor systems, one voluntary and one emotional” (picture and citation taken from Holstege et al., 1996).

It has become evident that the function of emotion by far exceeds simple reflex-like mechanisms. As Antonio Damasio has laid out, so-called higher order mental processes such as rational decision making largely draw on social emotional capabilities and their intact underlying brain networks (Damasio, 1995). He put forward the concept that afferent feedback is crucial to the process of how emotions guide and modulate higher order mental processes such as decision making (Damasio, Tranel, & Damasio, 1991), and laid out a theory that emphasized the ventromedial prefrontal cortex to be an important relay station mediating such functionality.

He points out that the mechanisms by which emotion supports rational decision making are likely acquired through socialization and that such emotions which are acquired through learning should be differentiated from basic emotions and regarded as secondary¹⁰ emotions. From a developmental cognitive neuroscience perspective, emotion and cognition have been proposed to be dynamically linked and work together to process information and execute action

¹⁰ The term “secondary emotions” he mentioned is not similar to the secondary emotions that have been hypothesized to arise from a combination of basic/primary emotions.

(Bell & Wolfe, 2004). The authors proposed that especially during the first year of life an integration of emotion regulation and cognitive processing is of major importance.

1.3 Elements

A popular approach to the understanding of emotion is that the large spectrum of human emotional experience is achieved by the combination and blending of distinct (basic) emotion states. According to this concept, basic (or primary) emotions are the building blocks of other, non-basic emotions (secondary emotions), similar to how primary colors can be combined to create the whole color spectrum (W. James, 1890/1950; Mc Dougall, 1908/1960; Plutchik, 1962), or how tones may merge to create new sensations (Wundt, 1896) e.g. contempt = anger + disgust. The assumption that basic emotions have evolved as hardwired psychological mechanisms corresponding to biological functions enhancing the fitness of organisms implies that the basic emotions cannot be reduced to even more fundamental emotions, but are the smallest possible building blocks. This operational discreteness can be regarded a prerequisite for simultaneous and independent activation of several emotions during mixing, fusing, blending or compounding of basic emotions into secondary emotions (Ortony & Turner, 1990; Reisenzein, 2000). It may also correspond to an anatomical organization allowing a high degree of automaticity and related to this the high speed of basic emotion response (Griffith, 1990, 1997).

René Descartes can be regarded the founder of the idea of primary and secondary emotions (or passions, as he termed them) in the sense outlined above. He characterized six primary emotions: admiration, love, hatred, desire, joy, and sadness, and he suggested that "all the others are composed of some out of these six and derived from them" (Descartes, 1649/1984; Mc Dougall, 1926; Reisenzein, 2000).

Also the work of Darwin¹¹ (Darwin, 1872) and James (W. James, 1884) may qualify as precursors of basic emotion theory, because their emotion concepts include the assumption that a subset of the human emotions is psychologically and/or biologically fundamental (Reisenzein, 2000).

However, a well framed theory of basic emotions in psychological terms has first been put down by William Mc Dougall (Mc Dougall, 1908/1960), which was then variously adapted by other basic emotion theorists (Buck, 1985; Drever, 1917; Ekman, 1977; Izard, 1977; Johnson-Laird & Oatley, 1989; Lazarus, 1991; Panksepp, 1982; Plutchik, 1962, 1980; Shand, 1914/1920; Tomkins, 1962, 1980).

As outline above, basic emotion theory is based on the assumption that human emotional experience is achieved by a combination and blending of distinct (basic) emotion states. It has been theorized about the nature of this blending mechanism, especially with respect to whether a novel emotional quality arises through the blending of emotions and whether the blending emotions are still distinguishable and maintain an identity. The following table comprises three possibilities of how secondary emotions may arise from basic emotions that have been mainly considered (Hupka, 1984; Reisenzein, 2000):

	novel emotional quality	basic emotions lose their identity in the process of combination
1. theory	yes	yes, basic emotions no more perceivable
2. theory	yes	no, although fusion of basic emotions, these are still perceivable as part of an emotion compound
3. theory	no	no, only mixing of the basic emotions

Table 1. Blending mechanisms of how secondary emotions may arise from basic emotions.

¹¹ Darwin considered beforehand Paul Ekman's approach to examine primary emotions by investigating an intercultural recognition of emotional expressions (Darwin, 1872).

There are several reasons to doubt basic emotion theory as depicted above, and it has been argued that it is “an article of faith rather than an empirically or theoretically defensible basis for the conduct of emotion research” (Ortony & Turner, 1990). The different models that attempt to classify emotions in terms of basic emotion building blocks contain little agreement about the identity of the “basic” building blocks and how many emotions are basic. For example, the number of suggested basic emotions includes two (pleasure and pain (Mowrer, 1960)), three (fear, love, rage (J. B. Watson, 1930)), four (expectancy, fear, rage, panic (Panksepp, 1982); fear, anger, depression, satisfaction (Kemper, 1987)), five (happiness, sadness, anxiety, anger, disgust (Oatley & Johnson-Laird, 1987)), etc. with eighteen at the end of the scale (Frijda, 1986).

Two particularly popular basic emotion systems were proposed by Robert Plutchik (includes eight basic emotions: anger, fear, sadness, joy, disgust, curiosity/interest, surprise, acceptance (Plutchik, 1962)), and Paul Ekman (classifies six basic emotions, the “big six”: sadness, happiness, anger, fear, disgust, surprise (Ekman, 1977)), but takes into consideration up to 17 (Ekman, 1992, 1994a).

Plutchik adopted the color metaphor as lined out above, suggesting that basic emotions adjacent or close to each other on his model of a “circle of emotions” fuse easily, whereas emotions further apart tend to lead to conflict when combined (Plutchik, 1962, 2003). For example, joy and acceptance, which are adjacent to each other can fuse to love, whereas joy mixed with fear in his model creates guilt.

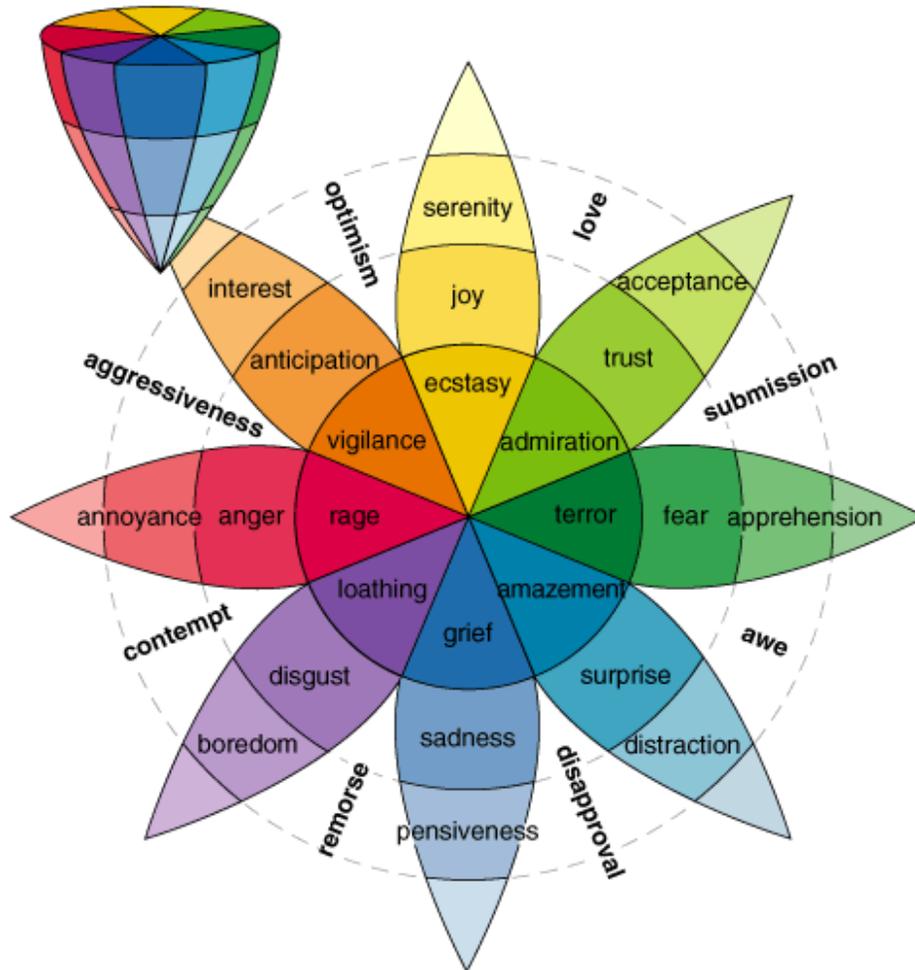


Figure 4. Plutchik's three-dimensional model depicts how basic emotions should mix analogous to the colors on a color wheel (Plutchik, 2003). The cone's vertical dimension represents intensity, and the circle represents degrees of similarity among the emotions with related emotions arranged adjacent to each other. The eight sectors indicate that his theory comprises eight primary emotion dimensions arranged as four pairs of opposites. In the exploded model the emotions in the blank spaces are mixtures of two primary emotions.

Based on the assumption that hardwired biologically fundamental basic emotions are more likely to be found across cultures (and possibly across species) than non-basic emotions, Paul Ekman devised his system of basic

emotions from cross-cultural research on the South Fore of Papua New Guinea and later validated it in cross-cultural research with a large variety of other cultures (e.g. the Dani of Irian Jaya in Indonesia) (Ekman, 1973). This indicates that at least some emotional expressions are universally decoded in all human beings¹². However, his work based chiefly on the intercultural production and recognition of distinct emotional facial expressions, which has been methodologically criticized (Ortony & Turner, 1990) because (only the major arguments):

- facial expressions can arise independently of emotions (e.g. lifting something heavy seems to universally produce a distinct facial expression)
- facial expressions of extremely positive emotions such as intense relief or pride (may include weeping) are often indistinguishable from such of extreme distress
- embarrassment is usually not classified as a basic emotion, although it is accompanied by a characteristic facial expression pattern including blushing which appears to be hardwired and thus meets his criteria defining a basic emotion.¹³

In his basic emotion system, Ekman considerably reduced the number of non-basic emotions, arguing that many emotion categories do not define emotions, but instead moods (e.g. euphoria), emotional attitudes (e.g. love), character traits (e.g. hostile, fearful), or emotional disorders (e.g. mania). Furthermore he reasoned that some non-basic emotions could be fast sequences of basic emotions rather than actual mixtures or fusions (Ekman, 1994b). Note that, like several authors who have promoted the basic emotions theory, he is reluctant to

¹² However, recognition rates of emotional expressions are usually lower in cultures more unfamiliar with the stimulus material, and Russel and Ekman have had an intense dispute on how the evidence provided by Ekman really demonstrates universals of emotion expression recognition (Ekman, 1994c; Russell, 1994).

¹³ It has been argued that despite the qualifying characteristics, embarrassment was not considered a basic emotion because in Western society, other than for example in Balinese society, it is not among the emotions most frequently in discourse (Ortony & Turner, 1990).

clearly address the issue of how secondary emotions may be reduced to primary ones (Ekman, 1977; W. James, 1884; Ortony & Turner, 1990; Panksepp, 1982).

Some languages do not distinguish clearly between some of the basic emotion categories proposed above, which all refer to English (Russell, 1991). For example, in some African languages the same word covers the concepts *anger* and *sadness* (Leff, 1973), or anger and sorrow (Orley, 1970).

As mentioned above, there is no general agreement about which emotions are to be considered basic and the total number of such basic emotions. As several emotion researchers have stated, there are likely hundreds of emotions (Kemper argued that the number of possible emotions is limitless corresponding to her specific social constructivist view that secondary emotions are acquired socially and that new emotions will emerge as long as society differentiates new social situations (Kemper, 1987)) and it is arguable which are primary (Averill, 1992)). A sample of the 100 words most strongly rated to be emotions (out of a list of 213 emotion names) from Shaver et al. illustrates this point (Shaver, Schwartz, Kirson, & O'Connor, 1987): Love, anger, hate, depression, fear, jealousy, happiness, passion, affection, sadness, grief, rage, aggravation, ecstasy, sorrow, joy, compassion, envy, fright, terror, elation, guilt, excitement, anguish, embarrassment, worry, panic, unhappiness, anxiety, desire, horror, sympathy, shame, lust, disgust, hostility, jubilation, loneliness, delight, pleasure, tenderness, pity, bitterness, disappointment, humiliation, dejection, despair, frustration, hurt, adoration, agony, thrill, fury, remorse, agitation, outrage, resentment, dislike, glee, alienation, distress, enjoyment, relief, gloom, misery, euphoria, bliss, gladness, regret, rejection, pride, gaiety, homesickness, jolliness, nervousness, woe, longing, loathing, satisfaction, hope, abhorrence, insecurity, defeat, dread, fondness, enthusiasm, sentimentality, hopelessness, annoyance, cheerfulness, displeasure, melancholy, glumness, shock, spite, suffering, dismay, exasperation, infatuation, apprehension.

However, not all variation in the basic emotion systems that have been proposed seems to be substantial, because in several cases just about the same emotions have been labeled differently by different researchers. For example, the following terms may largely be used interchangeably: anger and rage, fear and anxiety, happiness and joy. Yet, most differences between the basic emotion models are not due to the latter reason, but because of a large variety of criteria by which emotions have been categorized as basic: for example

- in terms of the emotion eliciting conditions that must be simple or “elementary” (Arnold, 1960)
- as processes that produce a change in action readiness and that are not composites of other emotions (Frijda, 1986)
- processes where the connection between a valenced appraisal and “some other response” is hardwired (Ortony & Turner, 1990)
- as distinct emotions you can experience without being able to attribute a reason for the experience (Johnson-Laird & Oatley, 1989; Oatley & Johnson-Laird, 1987)
- in terms of ontogenetic primacy (occurring early in life history) (Bridges, 1930; Sroufe, 1984; Weiner & Graham, 1984)
- in terms of universal similarity in emotional facial expression production and recognition (Ekman, 1973).

A particularly strong argument against basic emotion theory as laid out above arises from the notion that emotions held to be basic may yield more general emotion subsets. For example it has been put forward that anger minus the attribution of responsibility should result in frustration, fear minus the inclination to flee result in worry, etc. (Ortony & Turner, 1990). For a more detailed outline of this argument, see the “dimensional emotion model” described in *Chapter 1.4*.

Aside from basic emotion theory, other combinatorial models of emotion-assembly by elements which do not necessarily need to be emotions have been proposed, including elements such as specific appraisals (see also Cognitive Perspective in *Chapter 1.1*), action tendencies, physiological responses, desires, and feelings (Ortony & Turner, 1990). These raise the question whether some of the components should be regarded as prerequisite and characteristic features of emotions, or whether all subcomponents of emotions are capable of being decoupled and of also variably occurring in combination with other elements (Averill, 1982; Fehr & Russell, 1984; Ortony & Turner, 1990; Shaver et al., 1987).

1.4 Dimensions

Several authors promote the view that the number of basic emotions is smaller and of a different kind than proposed by basic emotion theorists. In their opinion, the “discrete” basic emotions are not really the fundamental building blocks of emotions because they can be reduced to still more fundamental components¹⁴: The emotional dimensions.

Both, the classification of the emotional stimulus property, and the emotional experience of the perceiver can be addressed with the ‘dimensional approach’. This is based on the assumption that the emotional impact of a sensual stimulus can be qualitatively characterized on various continuous dimensions and that each dimension can be investigated discretely.

Since Wilhelm Wundt first put forward a multi-dimensional model of emotional experience in 1896 (Wundt, 1896), emotion researchers have repeatedly attempted to classify both emotional experiences and emotional expressions in terms of dimensional models.

¹⁴ For example, an essential component of anger (often described to be a basic emotion) likely corresponds to another emotion that may be labeled unhappiness/distress/displeasure about an undesirable event (Ortony & Turner, 1990). This implies that the described component is more

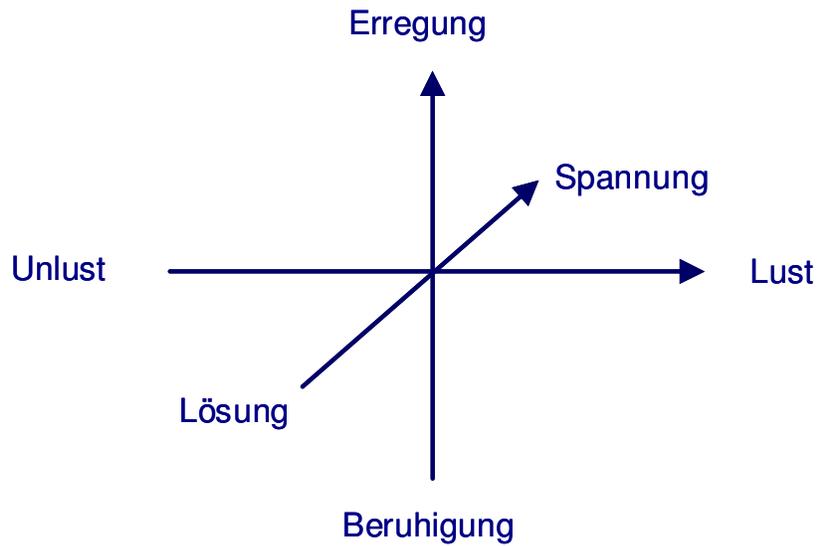


Figure 5. Figure of the 3-dimensional model proposed by Wilhelm Wundt, 1896 (the original version is in german). Lust / Unlust ~ pleasure / displeasure, Erregung / Beruhigung ~ excitement / sedation, Spannung / Lösung ~ tension / relaxation.

Adjectives potentially appropriate to describe emotions are manifold, and to date no consensus has been achieved about the exact nature and number of dimensions of emotional experience. However, most authors propose 3-dimensional models of emotion, with two dimensions that are quite similar between models and which will be described in detail below, and another dimension that differs heavily between the models. The following table gives an overview of a variety of dimensional models that have been developed to characterize emotional experience and expression.

Developed for the characterization of	Reference	1. dimension	2. dimension	3. dimension	4. dimension
Emotional experience	(Wundt, 1896)	Lust/Unlust (pleasure/displeasure)	Erregung/Beruhigung (excitement/sedation)	Spannung/Lösung (tension/relaxation)	
Facial emotional expressions on photographs	(Schlosberg, 1954)	Valence (pleasant/unpleasant)	Activation	Attention/rejection	
Facial expressions	(Osgood, 1952, 1966, 1969; Osgood & Tannenbaum, 1957) ¹⁵	Evaluation	Activity	Potency	
Emotion inducing pictures	(Lang, Bradley, & Cuthbert, 1998)	Valence	Arousal		
Categorization of emotional experiences	(Davitz, 1969)	Hedonic Tone	Activation	Relatedness	Competence
Verbal texts ¹⁶	(Mehrabian & Russell, 1974)	Valence (labeled 'pleasure')	Arousal	Dominance	
Emotion words	(Russell, 1980)	Valence	Arousal		
Voice perception	(Green & Cliff, 1975)	Valence	Excitement		
Emotional expression of music	(Madsen, 1997; Rickard & Ritossa, 2004; Schubert, 1999, 2001, 2004; Witvliet & Vrana, 1995)	Valence	Arousal		

Table 2. Dimensional models to characterize emotional experience and expression.

In Table 2, the dimensions listed in columns 1 and 2 are largely consistent between models, and differences between the dimension labels can be explained

¹⁵ Whereas most dimensional models have to be interpreted as introspectively inspired creations, Osgood and colleagues addressed a more systematic approach, rating verbal stimuli on 50 bipolar scales (e.g., hot-cold, white-black, fast-slow) and then performing a factor analyses on these data. The calculation indicated that 50% of the variance in the judgments was accounted for by three factors, denoted as evaluation, activity and potency.

¹⁶ Mehrabian & Russel constructed a set of verbal texts (in first-person narrative) and applied a semantic differential scale for their assessment. They obtained three factors that corresponded to the ones Osgood had suggested. Other authors, Bradley & Lang, argued that their account for variance among very different stimuli types suggests that these dimensions should be regarded „primary in organizing human experience“, and applicable for both semantic and affective

by differences in the emphasis of the models on either a characterization of emotional experience of the perceiver or on a characterization of emotional stimulus qualities (see column 1 in the table above). These dimensions largely correspond to the concepts of “valence” (column 1) and “arousal” (column 2). There is no agreement about the third dimension, and none has been described to be replicable across studies or cultures (Russell, 1978, 1980; D. Watson & Tellegen, 1985).

The term “valence” (lat. *valere*, to be worth) was first introduced in psychology by Kurt Lewin (1890-1947) in his theory of motivation, in which positive and negative valence resembled the attraction or repulsion that a region in the psychological environment has for someone (Lewin, 1935). This concept was inherent to his theory of vector psychology in which psychological situations could be described topologically (Lewin, 1936). Accordingly to Lewin’s original concept, in emotion research it defines a dimension ranging from displeasure (negative valence) to pleasure (positive valence) associated with an aversiveness or attractiveness of an event, object, or situation (Frijda, 1986). Researchers using dimensional emotion models share a broad general accord that valence is a reliable dimension of emotion that can successfully be addressed in experimental paradigms, which is largely due to the circumstance that participants find it easy to assess their percept of pleasure/displeasure and indicate it on a scale. However, the origin of the idea that valence is central to emotion goes back beyond Lewin and Wundt and has already been elaborated by philosophers, as for example Immanuel Kant:

“Daß Geschmacksurteile synthetische sind, ist leicht einzusehen, weil sie über den Begriff, und selbst die Anschauung des Objekts, hinausgehen, und etwas, das gar nicht einmal Erkenntnis ist, nämlich Gefühl der Lust (oder Unlust) zu jener als Prädikat hinzutun.“

“§ 9 Untersuchung der Frage: ob im Geschmacksurteile das Gefühl der Lust vor

der Beurteilung des Gegenstandes, oder diese vor jener vorhergehe“

Immanuel Kant, Kritik der Urteilskraft (Kant, 1790/1995)

In „Kritik der Urteilskraft“, Kant already introduced the concept that ‘the feeling of pleasure and displeasure’ imbue our aesthetic judgements, and discussed whether the percept of pleasure/displeasure (valence) arises as a consequence of an assessment of a stimulus, or if the assessment of the stimulus was to be interpreted as a consequence of (or at least modulated by) a percept of pleasure/displeasure.

„(...) hinter den Gefühlen stehen Urtheile und Werthschätzungen, welche in der Form von Gefühlen (Neigungen, Abneigungen) uns vererbt sind.“

Friedrich Nietzsche, Morgenröthe: Gedanken über die moralischen Vorurtheile (Nietzsche, 1887)

In Friedrich Nietzsches „Morgenröthe: Gedanken über die moralischen Vorurtheile“, he argued that innate experiences of attraction and aversion were modulating our feelings.

In recent times a multitude of authors have regarded valence as a basic dimension of emotion (see table above), furthermore, pleasure has been discussed as a basic emotion (Mowrer, 1960), and an imbuelement with valence has been regarded a crucial property of emotion in the discourse on basic emotion theory (Ortony & Turner, 1990)¹⁷. Some evidence from language development in historical perspective has emphasized historical changes in the meaning of emotion words, in that in earlier stages rather basic valence states would be denoted instead of more differentiated distinct emotions: Leff argued

¹⁷ On the basis of this assumption it has been argued that surprise is not an emotion, but is better viewed as a cognitive state (Ortony, Clore, & Foss, 1987), because the valence of surprise can be neutral: E.g. “being surprised by some highly improbable but personally irrelevant fact such as that all the members of some committee by chance share the same birthday” (Ortony & Turner, 1990).

that such a root word referring to valence would in a course of language development split into a number of more differentiated variants¹⁸ (Leff, 1973, 1977, 1981). He proposed that as a result, "we find that emotions we consider as distinct, namely, anger, fear (anxiety) and sadness, at one stage in the development of English were all represented by words which derived from the same hypothetical Indo-Germanic root Angh" (Leff, 1973). However, this is a single observation, and it is unclear whether such developments for emotion words have analogues in other language developments, especially because language development corresponds to both language complexification processes and language simplification processes.

It has been challenged, however, whether displeasure and pleasure may only be regarded as poles of a binary opposition on a continuous scale, or whether they might better be regarded as two distinguished emotions corresponding to two separate neural systems (Lewis, Critchley, Rotshtein, & Dolan, 2007).

How the valence percept relates to music processing is reviewed in detail in *Chapter 2 From music perception to valence percept*.

Although the term arousal strongly implies physiological response in the listener, involving an activation of the autonomic nervous system, the term is often used synonymously with the concepts *Erregung/Beruhigung* (excitement/sedation), and activation, which more strongly connote a subjective experience of the perceiver. This has to be regarded as a concession to the circumstance that arousal states, especially in response to rather short stimuli, cannot yet unambiguously be quantified physiologically. Although subjects often report difficulties in the subjective assessment of their personal arousal state, this remains a method deficient but inevitable, until more appropriate technologies making possible a quantification of physiological arousal have been developed.

¹⁸ Leff suggested that consequently languages differ with respect to how many or few distinctions among emotional states they include.

Arousal mediated by music has been suggested to largely correspond to the dynamic (Bigand, Vieillard, Madurell, Marozeau, & Dacquet, 2005), loudness (Schubert, 2004), and the tempo (Husain, Thompson, & Schellenberg, 2002; Schubert, 2004) of the musical piece.

The valence-arousal-model derived from these two dimensions has become widely accepted in emotion research (Bigand et al., 2005). It is often referred to as a circumplex model, corresponding to a concept introduced by Schlosberg (Schlosberg, 1941) in which he argued that emotional experience could be characterized as a system of ordering of emotional states on the circumference of a circle. However, most emotion researchers agree that this model can only be an interim solution, because a localization of emotions in a thereby defined two-dimensional space is not specific enough¹⁹. Hence, different emotions may not differ significantly with respect to their position in the two-dimensional space defined by the model (Larsen & Diener, 1992; Lazarus, 1991). This insufficiency of the valence-arousal model is plainly exemplified by its failure to differentiate the two different emotions fear and anger in valence-arousal space: Both share the same location characterized by a low valence and high arousal. Despite this critique, the model provides the theoretical framework for a multitude of studies, and evidence suggests that both the valence and the arousal dimension may correspond to specific neural substrates, as outlined in detail in *Chapter 1.5.3*. Therefore, a systematic investigation of either valence or arousal requires that the set of stimuli used to elicit responses in the perceiver is matched for arousal when examining valence and matched for valence, when examining arousal. However, although the dimensions valence and arousal theoretically constitute an orthogonality in the model, the two factors valence are often correlated and not completely independent, because higher intensity tends to amplify valence (Lewis et al., 2007).

¹⁹ Along these lines, Russell regarded these as general ‘core affects’ (Russell, 2003) that may only partially account for complex emotions.

Challenging the valence-arousal-model, Juslin & Vjöstfall (in press) have proposed a different model that emphasizes the occurrence of several emotions simultaneously, arguing that these may be induced by different mechanisms via the same music stimulus. For example, a piece that encodes a happy mood, but is associated with a sad memory may elicit a happy and sad emotion at the same time. The authors suggest that this may be true for the perception of most musical pieces, and that a dimensional model would be inadequate for the assessment of the whole variety of such ‘mixed emotions’ (Juslin & Västfjäll, in press).

Interestingly to the present study, Bradley & Lang introduced a methodology by which emotional states could be categorized visually on several emotional dimensions (valence, arousal, dominance) (Bradley & Lang, 1994). The dimensions were depicted in terms of abstracted figures representing body gestures (valence), physiological (arousal) and mental (dominance) experiences: The Self-Assessment Manikings (SAMs).

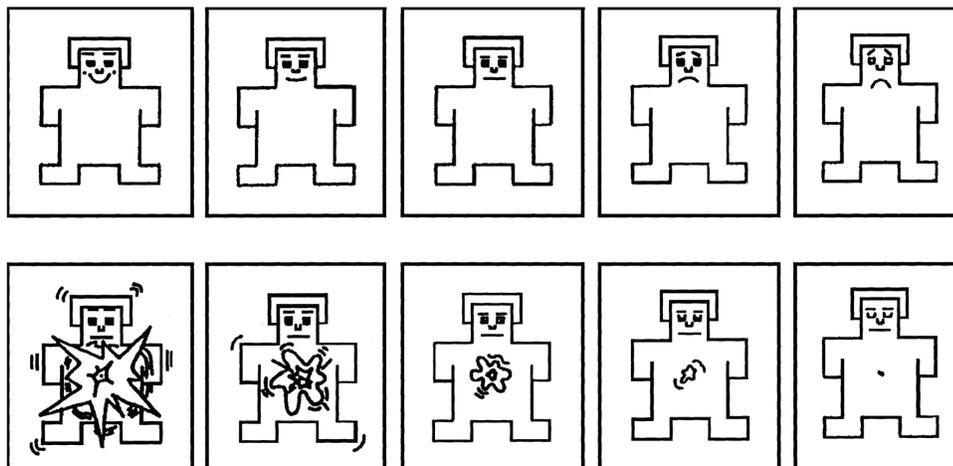


Figure 6. The figure depicts the Self-Assessment manikins for valence (above) and arousal (below) as suggested by Bradley and Lang (1994).

1.5 Substrate

Inferences about the substrate of emotion can be made from lesion studies in non-human animals, patient studies in humans, and from functional imaging techniques. There is no clear picture yet of what the substrate of emotion is, neither for certain distinct emotions, nor for emotional dimensions (but see also *Chapter 1.5.4.1 Music as a tool to investigate the neural circuitry of the valence dimension*). However, there has been some reasonable progress in this field of research, some of which will be outlined in this chapter.

In the early times of functional imaging, the use of static images dominated emotion research. In recent years, dynamic stimuli such as music are increasingly used as stimulus material and have proven even more effective in eliciting emotional responses in the perceiver. Research on the substrates of emotion has repeatedly revealed the engagement of a number of so-called limbic and para-limbic brain areas, most of which are also engaged in music processing (more detailed descriptions on the investigation of emotional substrates with music in *Chapter 1.5.4 Music as a tool to investigate the substrate of emotion*). The following table gives an overview of these brain areas, their putative function, and the functional imaging studies that reported their engagement during music processing (Koelsch, Siebel, & Fritz, in press).

Structure	Functions	Studies
inferior colliculus and thalamus	Detection of auditory signals of danger.	(Blood & Zatorre, 2001; Fritz, Ott, Mueller, & Koelsch, submitted.)
orbitofrontal cortex (BA 47, 11)	Control of emotional behaviour, imbueing of stimuli with emotional valence, generation of "moral emotions" such as guilt, regret, shame, bad consciousness. The OFC appears to contain knowledge about social norms and roles. Activation of the OFC in functional imaging experiments (in which subjects are	(Blood & Zatorre, 2001; Blood, Zatorre, Bermudez, & Evans, 1999; Fritz et al., submitted.; Koelsch, Fritz, Schulze, & Schlaug, 2005; Tillmann et al., 2006)

	required to lie still during the presentation of musical stimuli) might reflect that participants wanted to move (e.g., dance, tap) during the presentation of the music, but that they had to control this impulse to fulfil the requirements of the experimental setting.	
amygdala	Initiation of emotional, autonomic, and hormonal responses. Termination of positive emotions in the face of danger.	(Ball et al., 2007; Baumgartner T, 2006; Blood & Zatorre, 2001; Eldar, Ganor, Admon, Bleich, & Hendler, ; Fritz et al., submitted.; Koelsch, Fritz, von Cramon, Müller, & Friederici, 2006)
hippocampus	Memory formation, mediation of stress response.	(Baumgartner T, 2006; Blood & Zatorre, 2001; Brown, Martinez, & Parsons, 2004; Fritz et al., submitted.; Koelsch et al., 2006)
parahippocampal gyrus	Consonance/dissonance processing.	(Baumgartner T, 2006; Blood et al., 1999; Fritz et al., submitted.; Koelsch et al., 2006)
temporal poles	Emotional memory retrieval, perhaps also multisensory integration.	(Baumgartner T, 2006; Fritz et al., submitted.; Koelsch et al., 2006)
anterior cingulate cortex	Synchronization of biological subsystems (cognitive appraisal, vegetative modulation, motor activity, motivation, and monitoring), regulation of autonomic and emotional responses, modulation of motivation and attention, interface between emotion and cognition	(Blood & Zatorre, 2001)
hypothalamus	Hormonal regulation with autonomic effects.	
Insula	Autonomic regulation and integration of visceral and somatosensory information with autonomic activity	(Baumgartner T, 2006; Blood & Zatorre, 2001; Fritz et al., submitted.; Koelsch et al., 2006)

ventral striatum (NAc)	Invigoration, selection and direction of behaviour in response to incentive stimuli, attribution of reward value.	(Baumgartner T, 2006; Blood & Zatorre, 2001; Brown et al., 2004; Fritz et al., submitted.; Koelsch et al., 2006; Menon & Levitin, 2005)
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Table 3. Overview of limbic and paralimbic structures, as well as their putative music-processing related function, and previous functional neuroimaging studies on music and emotion that reported an engagement of a respective structure during music processing (adapted from Koelsch, Siebel, & Fritz, in press).

Although studies on the neural substrate of emotion repeatedly describe an involvement of the structures mentioned above, the functional significance of each of these structures is still not well understood. It is likely that the brain physiology of emotions is organized in specific functional networks, but there is no consent about the architecture of such networks. Discrete emotion theories (which include basic emotion theories) usually imply an existence of discrete functional networks corresponding to specific behavioral adaptations of an individual or of a group that enhance individual and group survival. However, the list of unique emotions is long (see *Chapter 1.3 Elements* for a top 100 excerpt) and it is unlikely that each corresponds to a separate functional network. How is such a variability structurally achieved? Basic emotion theory originally implies (Mc Dougall, 1926) that our diversity of emotions arises by mixture and blending (see *Chapter 1.3 Elements* for detailed description). Accordingly, on a structural level one might assume that distinct networks are engaged simultaneously. However, emotional processes usually correspond to a highly precise physiological pattern of temporally coordinated procedures. Whatever the neurophysiological mechanism underlying such an elaborate synchronization, it needs to be fast, and it needs to be connected to the various emotion mediating networks. As will be described in detail in *Chapter 8 Summary and General Discussion*, my proposition is that this is likely a structure or a small network of structures in a position to exert an immediate influence on the hormonal system, most likely with subcortical components

including the amygdala. As described in detail below, the amygdala anatomically well qualifies to be involved in such a mechanism.

The common structural denominator between the various emotions may well correspond at least partly to the functional network underlying the valence dimension, because as has been elucidated above (see *Chapter 1.3 Elements*) valence has been suggested to be a fundamental component to all distinct emotions (Ortony & Turner, 1990) (see also *Chapter 1.4 Dimensions*).

1.5.1 The dual circuit model of information processing

During the past 20 years, the majority of imaging studies on emotion has focused on the examination of emotions with negative valence, which have been demonstrated to be quite reliably elicited in experimental settings. In the course of this research a circuit for the processing of aversive stimuli has been described in which the amygdala plays a crucial role. It is most popularly regarded to address the ‘basic emotion’ fear, and its neural substrate is commonly considered the “fear circuit”. However, fear of an electric shock and fear of having cancer produce very different expressive behaviors and physiological states and may be regarded quite different processes (Ortony & Turner, 1990). Rather than being a system that conveys subjective states of experience, LeDoux regarded the fear circuits to be defined by a set of mechanisms that detect and respond to danger²⁰, and on this basis made inferences from the neural architecture of fear from rats to humans²¹. Accordingly he considered whether a more precise term for the response he addressed through investigation may be “defensive behavior” (LeDoux, 1996,

²⁰ According to this definition, fear can be provoked consistently and is easily identifiable throughout many organisms of the phyla.

²¹ The ‘fear’ behaviour of a rat is easy to recognize because of its characteristic freezing response accompanied by an increase in arterial pressure and heart rate. However, evidence showed that only the arterial pressure and freezing responses reflect the formation of an association between the tone and shock (Iwata, LeDoux, Meeley, Arneric, & Reis, 1986). It should be noted that other fear-typical responses are also observed like endocrine (hormone release) responses, alterations in pain sensitivity (analgesia) and reflex expression (fear-

2000a).

However, the dual circuit model of information processing put forward by Joseph LeDoux (LeDoux, 1996), can be regarded a basic framework that well illustrates the workings of a specific neural substrate of emotion, a more or less integral piece in the puzzle of aversive emotional processing which has likely been largely responsible for the renaissance of interest in emotion within neuroscience (LeDoux, 2000a). To set out why he investigated amygdala function only with respect to defensive behaviour, the dual circuit model of information processing and the methodology accounting for its development are outlined below.

In order to trace pathways that process acoustic stimuli of emotional relevance he used the fear conditioning method, where an unconditioned stimulus (typically a brief, mild footshock) is delivered at the end of a conditioned stimulus (usually a tone or light). After a few pairings, the conditioned stimulus acquires the capacity to elicit bodily reactions that usually occur in the presence of natural dangers. In this manner emotional processing can be dissociated from the perceptual content of the eliciting stimulus.

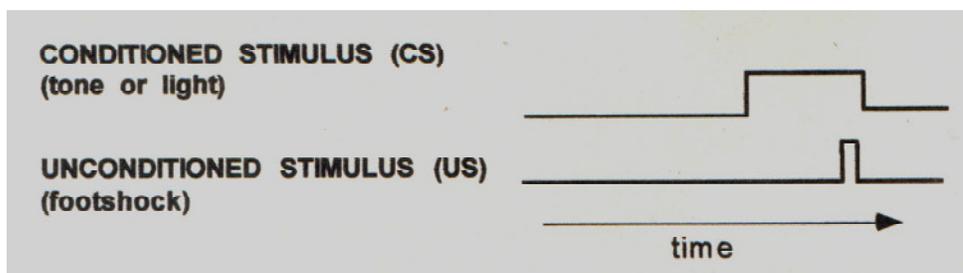


Figure 7. The figure depicts the pairing of a conditioned and an unconditioned stimulus in fear conditioning (from LeDoux, 1996).

Focussing on which neural structures are essential to the auditory fear conditioning, LeDoux found that lesioning the auditory cortex would have no effect on either the freezing or the blood pressure responses, whereas lesioning

potentiated startle and eyeblink responses) (LeDoux, 2000a).

the next lower level, the auditory thalamus (or a next lower auditory station in the midbrain) would completely prevent the conditioning of auditory stimuli²².

When further projections were traced by means of injecting an anterograde tracer²³ into the auditory thalamus, several subcortical structures could be shown to be connected directly to it, namely the amygdala (lateral and central nuclei), the hypothalamus (ventromedial nucleus), the caudate-putamen and the subparafascicular region of the thalamus (LeDoux, Sakaguchi, & Reis, 1983). The amygdala was identified to be the dominant subcortical structure involved in fear conditioning by the evidence that it was specifically the lesioning of the interconnections between the thalamus and the amygdala that would prevent fear conditioning (Iwata et al., 1986).

The lateral amygdala receives input from both the auditory thalamus and the auditory cortex (LeDoux, Cicchetti, Xagoraris, & Romanski, 1990) and fear conditioning can be mediated by either of these pathways (Romanski & LeDoux, 1992). As passing the cortical pathway will take the signal approximately twice as long (about 24ms) to reach the amygdala as passing the thalamus-pathway (in about 12ms) the latter pathway is supposed to play an essential role during the fast reaction to dangerous situations (LeDoux, 1996)²⁴ and pre-attentive emotional processing (Armony & LeDoux, 2000; Armony, Servan-Schreiber, Cohen, & LeDoux, 1996, 1997), whereas the projection to the lateral amygdala via the auditory cortex plays a substantial role when rather complex auditory stimuli are involved²⁵.

²² Indeed, it has long been recognized that even complete bilateral removal of the neocortex will not stop a multitude of autonomic responses that are known to relate to emotional behaviors (especially signs of anger that have been labelled "sham rage") provoked by sensory stimulation (Bard, 1929; Cannon, 1929; Kaada, 1960), or by aversive classical conditioning to relatively simple stimuli (Bloch-Rojas, Toro, & Pinto-Hamuy, 1964; DiCara, Braun, & Pappas, 1970; Pinto-Hamuy, Santibanez, & Rojas, 1963).

²³ Horseradish peroxidase (HRP)

²⁴ Note that reactions to dangerous situations already take place earlier, at brainstem level (e.g. startle reaction).

²⁵ Rabbits in a conditioned stimulus experiment where two distinct but very similar tones are presented but only one of them is coupled with an electric shock learn to distinguish the two sorts of stimuli so that increased heart rate response will only be evoked by the true conditioned tone. Subsequent ablation of the auditory cortex will result in a loss of this ability to distinguish

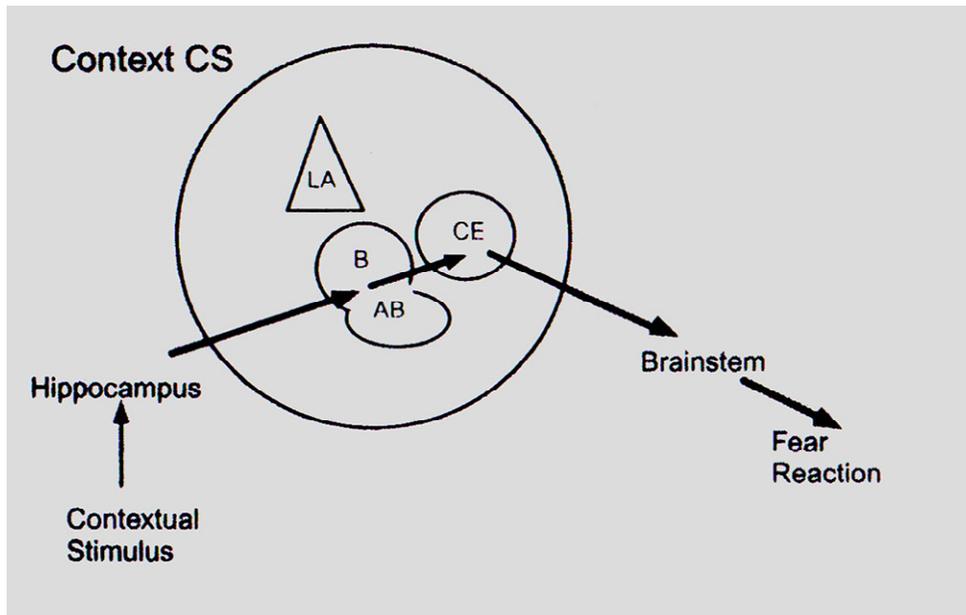


Figure 8. Amygdala pathway in contextual fear conditioning. Conditioned stimulus (CS), basal nucleus of the amygdala (B), accessory basal nucleus of the amygdala (AB), central nucleus of the amygdala (CE), lateral nucleus of the amygdala (LA) (LeDoux, 2000a).

Rats not only exhibit fear responses as a reaction to conditioned stimuli, but also when they return to the chamber where tone and shock were paired, or to a chamber where shocks alone occur. This phenomenon is called contextual fear conditioning and involves the amygdala as well as the hippocampus. Ablations of the hippocampus will impair contextual conditioning (Phillips & LeDoux, 1992) but not the conditioning to a tone (LeDoux, 1996). Particularly ventral areas of the hippocampus (CA1, subiculum) are proposed to project to the basal and accessory basal nuclei of the amygdala (Canteras & Swanson, 1992) and are meant to play an essential role during contextual conditioning. Damage to these areas will interfere with this mechanism (Maren & Fanselow, 1995; Majidishad et al., 1996).

and instead the animals will react to both stimuli with an increase in heart rate response (Jarrel, Gentile, Romanski, McCabe, & Schneiderman, 1987).

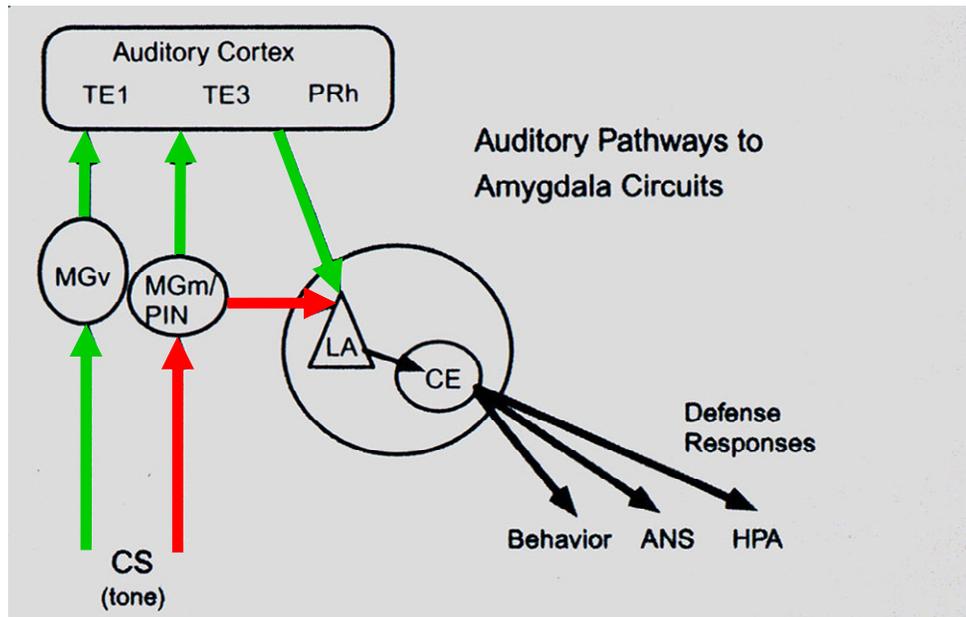


Figure 9. This illustration incorporates the dual circuit model of information processing, depicting the 'low road' in red, and the 'high road' in green. Conditioned stimulus (CS), ventral division of the medial geniculate body (MGv), medial division of the medial geniculate body (MGm/PIN), primary auditory cortex (TE1), auditory association cortex (TE3), perirhinal cortex (PRh), lateral nucleus of the amygdala (LA), central amygdala (CE), autonomic nervous system (ANS), hypo-thalamic-pituitary axis (HPA) (adapted from LeDoux, 2000a).

The central²⁶ nucleus of the amygdala (CE) is regarded to be the major output pathway of the amygdala during 'fear' responses (LeDoux, Iwata, Cicchetti, & Reis, 1988). In accordance with this, an impairment of the CE will interfere with the expression of conditioned fear responses (Iwata et al., 1986). The amygdala seems to delegate different aspects of the fear response to different neural areas: there is evidence that damage to the lateral hypothalamus affects blood pressure but not freezing responses, while damage to the periaqueductal grey disrupts freezing but not blood pressure responses (LeDoux et al., 1988). Impairment of

²⁶ Note that in humans the CE is not centrally, but superiorly located in the amygdala.

the bed nucleus of the stria terminalis shows no effect on either the freezing or the blood pressure responses, and instead interferes with the conditioned release of pituitary-adrenal stress hormones (Van de Kar, Piechowski, Rittenhouse, & Gray, 1991).

The coupling between the amygdala and the cortex is such that it mainly receives input from the late stages of cortical processing, but projects towards even the earliest stages. Thus it appears likely that the amygdala influences the sensory processing occurring in cortical areas (Amaral, Price, Pitkanen, & Carmichael, 1992; Gloor, 1992; LeDoux, 2000a; Turner, Mishkin, & Knapp, 1980): *“Thus, once the amygdala is activated by a sensory event from the thalamus or cortex, it can begin to regulate the cortical areas that project to it, controlling the kinds of inputs it receives from the cortex”* (LeDoux, 2000a).

Apart from modulating other brain areas by direct interconnection, the amygdala is meant to indirectly influence cortical processing by innervating ‘arousal’-modulating networks such as the basal forebrain cholinergic system, the brainstem cholinergic system and the locus ceruleus noradrenergic system, which again project to cortical areas (Aston-Jones, Rajkowski, Kubiak, Valentino, & Shipley, 1996; Holland & Gallagher, 1999). Furthermore, the amygdala contributes to hormonal, proprioceptive and visceral changes. It has been suggested that the representation of these processes in somatosensory-related cortices might have a modulating influence on other cortical activity, and that these areas are closely linked to emotional experience, probably resembling an affective convergence zone (Anderson & Phelps, 2000; Damasio, 1995).

Brain regions within the medial prefrontal cortex, while not required for conditioning, seem to play a crucial role in modulating the amygdala, contributing to the extinction of conditioned fear responses (for a review see Quirk, Garcia, & Gonzalez-Lima, 2006). Extinction usually takes place when the conditioned stimulus appears several times without being followed by the unconditioned stimulus. Certain categories of conditioned stimuli take longer for

extinction than others, which may correspond to their resemblance of predisposed patterns of events of potential danger (LeDoux, 1996). Rats with a lesioned medial prefrontal cortex, however, prolong the maintenance of any conditioned aversive responses, whether triggered in a predisposed fashion or not (Morgan, Romanski, & LeDoux, 1993). Between the amygdala and the prefrontal cortex there are extensive reciprocal connections, particularly to the medial and orbital zones of the prefrontal cortex. The glutamatergic efferents coming from the prefrontal cortex likely synapse on GABA neurons and thus provide an inhibitory input to the amygdala (Amaral et al., 1992). Supporting this idea it has been demonstrated that glucose metabolism in the lateral and medial prefrontal cortex including the orbitofrontal cortex is reciprocally associated with glucose metabolic rate in the amygdala (Davidson, 2000; Davidson, Putnam, & Larson, 2000).

1.5.2 The role of the amygdala in emotional processing in humans

Evidence suggests that brain mechanisms analogous to the ones investigated in animal experiments as outlined above are involved in defensive response or in the detection of defensive expression such as ‘fear’ in humans across modalities. Patients with lesions of the temporal lobe that include the amygdala showed deficits in fear conditioning (Bechara et al., 1995; LaBar, LeDoux, Spencer, & Phelps, 1995) and in the detection of fear in facial expressions (Adolphs, Tranel, & Damasio, 1998; Adolphs, Tranel, Damasio, & Damasio, 1994)²⁷ and voices (Scott et al., 1997).

The role of the amygdala in fear conditioning in humans is further substantiated

²⁷ Note however that it has been shown that the inability to detect fear in facial expression which had been discovered with SM, a patient with bilateral amygdala damage, could be attributed to her impairment to allocate attention to the most important feature for identifying a facial fear expression: the eyes. Her recognition of fearful faces became normal when she was instructed explicitly to look at the eyes (Adolphs et al., 2005).

by functional imaging studies (Büchel & Dolan, 2000; Critchley, Mathias, & Dolan, 2002; LaBar, Gatenby, Gore, LeDoux, & Phelps, 1998; Morris & Dolan, 2004; Morris, Ohman, & Dolan, 1999).

The perception of facial emotional expression of 'fear' seems to engage largely unconscious decoding mechanisms in humans that involve the amygdala (Morris, Öhman, & Dolan, 1998; Whalen et al., 1998). Case studies on patients with damage to the amygdala suggest that the amygdala supports the appraisal of auditory signals of danger (Anderson & Phelps, 2001; Scott et al., 1997). Furthermore, a study investigating music perception in participants with amygdala resections reported an impaired recognition of the emotional expression 'fear'/'scary' in the music (Gosselin et al., 2005).

Importantly, Breiter et al. found a rapid habituation of the amygdala response to facial expressions of emotion using fMRI and suggest that the amygdala might preferentially signal the detection of novel affective signals and in the initial stages of learning when the emotional meaning of signals is actively encoded (Breiter et al., 1996). Further, it has been suggested that the role of human amygdala activity comprises an influence in initial perceptual encoding, enhancing the likelihood that verbal stimuli of aversive content (compared with stimuli of neutral content) are given attention (Anderson & Phelps, 2001).

There is some evidence that the amygdala and the auditory thalamus are themselves sites of plasticity during fear conditioning (LeDoux, 2000a; Quirk, Reppas, & LeDoux, 1995) and it has been suggested that the plasticity in the auditory thalamus during fear conditioning crucially depends on amygdala activity (Maren, Yap, & Goosens, 2001; Poremba & Gabriel, 2001).

Although LeDoux argued that one should be careful not to replace the generally outdated limbic system theory of emotions and its overambitious explanation of all emotions as functions of one big system, by an amygdala theory of emotion

(LeDoux, 2000b), he suggested that the amygdala might be essential for generally differentiating pleasant from unpleasant stimuli (LeDoux, 2000a).

Indeed, there is accumulating evidence that the amygdala may not be confined to fear processing, but bears a much broader function in emotion processing than originally assumed by LeDoux. Evidence has been provided, which suggests that it responds in general to aversive stimuli (Taylor et al., 1998; Zald, 2003; Zald & Pardo, 1997, 2002), including unpleasantly manipulated music (Koelsch et al., 2006).

Furthermore, the amygdala has been shown to be involved in the response to appetitive stimuli such as words and photographs with positive connotation (Aharon et al., 2001; Garavan, Pendergrass, Ross, Stein, & Risinger, 2001; Hamann et al., 1999; Hamann, Ely, Hoffman, & Kilts, 2002; Liberzon, Phan, Decker, & Taylor, 2003; Zald, 2003), and learning about positively valenced stimuli (Davis & Whalen, 2001).

Accordingly, the amygdala may be sensitive to either direction of the valence dimension (Garavan et al., 2001; Hamann et al., 2002). However, until now the role of amygdala subregions in possibly valence-specific emotion processing has remained elusive.

Although there has been progress in the research of circuits underlying the experience of emotions with negative valence, brain imaging studies investigating the neural correlates of an experience of emotions with a positive valence are still sparse (see Nitschke et al., for an overview (Nitschke et al., 2004)). The investigation of the neural correlates of emotions with positive valence is challenging, because in an experimental setting these emotions are more difficult to evoke than negative emotions (especially in experimental settings like those required when applying functional imaging techniques such as PET or fMRI).

1.5.3 Emotional expression vs. emotional experience

Evidence about the neuroanatomy of emotional processing is highly inconsistent. This may relate to the complexity of emotional processing, in that emotion can be investigated at different levels that involve different mechanisms and processes (Juslin & Västfjäll, in press). In accord with this idea Nico Frijda states „*investigating the relationships between appraisals and emotion labels is research into emotion word meanings or into the structures of experience [...] distinct from research that qualifies as investigation of emotion antecedents*“ (Frijda, 1993). Along these lines, Scherer argued that the emphasis of appraisal research by mapping emotion words onto emotional experiences focuses on the way experiences are verbally labelled, rather than on the underlying processes that give rise to appraisals (K. R. Scherer, 1993).

Juslin & Västfjäll emphasized that perception of emotional expressions is primarily a sensory or cognitive process that does not necessarily relate anything about an emotional experience of a listener (Juslin & Västfjäll, in press), and it has been shown that a perception of representational features of music that mediate emotional expressions may be independent from an emotional involvement of the perceiver (Gabrielsson, 2002; Harré, 1997).

Accordingly, Davidson, Leventhal and Tomarken have proposed that the failure to distinguish between the perception or decoding of emotional information, and the experience or expression of emotion might be a major reason for disagreements and inconsistencies in the field of emotion research (Davidson, 1984; Leventhal & Tomarken, 1986).

Damasio reports cases of patients with lesions in the prefrontal cortex who are no longer capable of having any emotional arousal to pictures with cruel content, but are still capable of judging the emotional valence conveyed by these (Damasio, 1995). A case study conducted with an individual with bilateral

amygdala damage showed impaired ability to interpret facial expressions of emotion (especially fear), but showed intact ability to pose the emotion (Damasio, 1995). The authors suggested that this might be in support for the hypothesis that evaluation and production of emotion involve differing brain regions²⁸.

Taking into account that there might be dissociations between mere recognition and experience of emotion, it might thus be important to distinguish experiments that address an elicitation of an emotion from experiments where participants have to assess a stimulus quality.

1.5.4 Music as a tool to investigate the substrate of emotion

There is anecdotal evidence that music listeners regard emotional responses to be the strongest motivation for listening to music (Panksepp, 1995), and that music listening entails a level of intensity of emotional response they rarely experience in everyday life (Panksepp, 1995; Sloboda, 1991). Music has been reported to be capable of inducing strong emotions with both positive and negative emotional valence in experimental conditions consistently across subjects (Krumhansl, 1997). Carol Krumhansl recorded psychophysiological measures while listeners heard excerpts of music which were meant to represent distinct emotions such as sadness, happiness and fear. The emphasis was on dynamic changes in physiological response occurring during listening to the excerpts. One group of listeners gave dynamic self-report ratings (adjusting the position of a slider) of the degree of sadness, happiness, fear and tension which they experienced while in another group of subjects physiological responses were determined. Physiological measures covered a fairly wide spectrum of

²⁸ Although it can be argued that voluntary posing is not adequate to draw conclusions on the production of emotion, given the fact that emotionally controlled movements might engage partly different brain regions compared to voluntarily controlled movements (see *Chapter 1.2 Functions*).

parameters that are known to relate to emotional reactions (Schmidt & Thews, 1997), including cardiac, vascular, electrodermal, and respiratory function.

Both physiological measurement and emotion judgements were taken at one-second intervals during the three-minute excerpts. It showed that inter-subject consistency of judgment was strong and that patterns of physiological response proved to correspond to certain (musical²⁹) emotions. For example the dynamic ratings of sad correlated strongest with the factors of blood pressure, skin conductance, skin temperature measures, and cardiac inter-cycle interval. The dynamic ratings of happy correlated strongest with respiration measures while the dynamic ratings of fear correlated strongest with the factors pulse transmission time and amplitude³⁰. Krumhansl thus argued that musical emotions correspond to patterns of physiological measures, emphasizing that these physiological changes indicate that listeners indeed experienced emotions when listening to music³¹.

Several threads of research have taken advantage of a physiological indicator, the chills/thrills-response, for an investigation of so-called “strong emotions” elicited by music.

The term “chill” as an indicator for strong emotions in response to music was originally coined by Avram Goldstein in 1980 (A. Goldstein, 1980), and has since then been a topic of investigation in the cognitive sciences. Goldstein originally used this term to specify the somatosensory sensation during so-called “thrills” induced by music listening, but since then the terms “chills” and “thrills” are often being used synonymously. In a questionnaire based

²⁹ A comparison of the measured physiological changes with such occurring in “non-musical” emotions indicates that some patterns of physiological activation diverge between “musical” and “non-musical” emotion (Krumhansl, 1997).

³⁰ In greater detail: Sad music would produce slower heart rate, increased blood pressure, decreased skin conductance level, and decreased finger temperature; happy produced a faster breathing rate and a decreased respiration depth; fear produced increased pulse transmission time, decreased pulse amplitude, faster breathing rate, and decreased finger temperature.

³¹ She argued in favor of an ‘emotivist position’ which holds that music elicits emotions that are really experienced and qualitatively comparable to non-musical emotions. The ‘cognitivist position’ in contrast holds that emotion is an expressive property of music but that the listeners only recognize it without experiencing emotion themselves.

investigation he characterized thrills/chills as “a subtle nervous tremor caused by intense emotion”, which corresponded to a usually positive emotional peak experience and often (but not always) a “goosepimples” response. Interestingly not all subjects seem to be susceptible to thrills. Goldstein reported that the proportion of individuals perceiving “chills” events differed between occupational groups (e.g. between medical students and music students) ranging between 53 and 90% (in total $n = 249$). He tested the hypothesis that “chills” are mediated by endorphins by intravenously administering the opiate antagonist naloxone hydrochloride to block their effect. Goldstein argued that the drug may attenuate the occurrence of thrills/chills, showing that the null hypothesis (that naloxone has no effect) could be rejected at $p < 0.01$.

Blood and Zatorre used positron emission tomography (PET) to investigate the cerebral structures involved in the chills response when listening to music (Blood & Zatorre, 2001). Although “chills” are often experienced as distinct physiological events (especially when accompanied by a “goosepimples” response), they asked the participants to categorize their chills experiences on a continuous scale. They reported that for increasing chill intensity the cerebral blood flow increased in areas that have previously been suggested to be involved in the processing of euphoria and positively valenced emotions, such as the ventral striatum, dorsolateral midbrain, bilateral insula, OfC, thalamus, anterior cingulate cortex, SMA, and cerebellum. They observed decreases of rCBF with increasing chills intensity in the amygdala, hippocampus/amygdala, ventromedial prefrontal cortex, and in cuneus and precuneus. That several cerebral structures related to the processing of positive valence seem to be involved in the processing of the chills experience may be interpreted as neurophysiological evidence for the claim that the chills experience is most often perceived as pleasant (A. Goldstein, 1980). Another possibility is that participants may confuse chills and valence when asked to rate their chills experience on a continuous scale.

Although the chills response is predominantly described as a physiological marker, the detection of “chills” responses has so far been largely dependent on introspective observations and subjective reports. However, recently considerable effort has been made to identify the chills experience with physiological measures (Craig, 2005; Grewe, Nagel, Kopiez, & Altenmüller, 2007b; Kaernbach, Lukas-Wolfbauer, & Wilfling, 2006). This is an ambitious venture, because no single physiological measure except pilo erection has proven to reliably and objectively indicate a chills experience (Kaernbach et al., 2006). Measurement of the pilo erection, however, seems to be a reliable measure only in the proportion of the participants who generally show strong pilo erection responses.

Because the present work puts an emphasis on the investigation of pleasantness and unpleasantness as conveyed by music, studies investigating the substrates of discrete emotions such as happiness and sadness with music (Baumgartner, Esslen, & Jäncke, 2006; Gosselin et al., 2005; A. C. Green et al., 2008; Khalfa, Schön, Anton, & Liégeois-Chauvel, 2005; Kreutz, Russ, Bongard, & Lanfermann, 2003; Mitterschiffthaler, Fu, Dalton, Andrew, & Williams, 2007) will not be discussed here.

1.5.4.1 Music as a tool to investigate the neural circuitry of the valence dimension

It appears that listeners very rapidly (already during the first second) appreciate or dislike music excerpts (Bigand et al., 2005). This finding suggests that music, even music pieces with short stimulus duration, can effectively be employed for an investigation of the valence dimension.

Several experiments have addressed the investigation of the valence dimension with music³²:

³² Note that music as reward (Menon & Levitin, 2005) will not be elaborated here, but see also

Using PET, Blood et al. (1999) investigated the valence dimension ranging from neutral to unpleasant with sequences of harmonized melodies. The stimuli varied in their degree of (permanent) dissonance, and were accordingly perceived as less or more unpleasant (stimuli with highest permanent dissonance were rated as most unpleasant). They used computerized stimuli without dynamic expression. This paradigm was, thus, not intended to induce the percept of pleasantness, yet it allowed the examination of emotional processing with music while mostly excluding effects of musical preference.

Increasing unpleasantness of the stimuli correlated with activations of the right parahippocampal gyrus and the precuneus³³, while decreasing unpleasantness of the stimuli correlated with activations of frontopolar, orbitofrontal, and subcallosal cingulate cortex. Using regional covariation analyses, the authors suggested that reciprocal functional interactions might exist between parahippocampal and orbitofrontal (Talairach coordinates: 8, 20, -17; -7, 20, -17), as well as frontopolar (Talairach coordinates: 23, 61, -3; -28, 56, -5) regions.

A PET study by Brown et al. addressed the neural response elicited by unfamiliar pleasant music. Contrasted to rest, pleasant music activated a network including several so-called limbic and paralimbic structures, comprising the ventral striatum, subcallosal cingulate cortex, anterior cingulate gyrus, retrosplenial cortex, hippocampus, the anterior insula, and the superior temporal poles (Brown et al., 2004).

Koelsch et al. (2006) investigated the temporal dynamics of neural correlates of both intense positive and negative valence. They presented naturalistic music excerpts and unpleasantly manipulated counterparts of the same pieces that were

Chapter 2.4 From structure building to valence percept for a description of how temporal distortion of a musical signal as applied by Menon & Levitin (2005) can be used to alter the valence percept in a listener.

³³ The precuneus region is known to be engaged in the processing of a large variety of stimuli, presumably due to an important role in memory-related and selective attention processes (Berthoz, 1997; Le, Pardo, & Hu, 1998).

comparable in dynamic outline, rhythmic structure, contour and were matched for arousal (Koelsch et al., 2006), see also (Sammler, Grigutsch, Fritz, & Koelsch, 2007). The manipulated music, consistently considered to be unpleasant by all participants, evoked activity changes in the amygdala, the parahippocampal gyrus, the hippocampus and the temporal poles in both hemispheres. The original music, consistently rated pleasant by all participants, evoked activity changes in the left anterior insula, and the ventral striatum in both hemispheres. Their study was not designed to investigate the initial response to music and was therefore perhaps not optimally suited to investigate amygdala behavior, which likely is particularly sensitive to novel stimuli (Breiter et al., 1996).

1.5.5 Putative components of a neural circuitry of the valence dimension

As outlined above, the amygdala seems to be involved in mediating the response to both pleasant and unpleasant stimuli. The amygdala is not a functional unity, but instead is functionally segregated. Whether valence-specific engagement of the amygdala corresponds to the workings of discrete subnuclei, however, is yet unknown. It has been shown that the amygdala is responsive to the processing of music with negative (see above), but also positive valence: Koelsch et al. (2006) and Blood & Zatorre (2001) both provide evidence for deactivations in the amygdala in response to pleasant music stimuli, which corroborates the evidence reported above which suggests that the amygdala is not only engaged in the mediation of a response to unpleasantness, but also in a response to pleasantness (see also (Davis & Whalen, 2001; Zald, 2003).

Other putative areas responsive to valence seem to be more specifically involved either in positive or negative valence. Olds and Milner first identified a brain site (septal area of the rat) where direct electrical stimulation functions as a

reinforcer (Olds & Milner, 1954). The laboratory animals would press the triggering lever at high rates (> 6,000 times per hour) to obtain the stimulation pulses. The reinforcement from such direct electrical activation seems to be more potent than rewards such as food or water. Its reinforcing power is most dramatically illustrated in a classic experiment where the animals suffered self-imposed starvation when presented with the choice between obtaining food and water or electrical septal and hypothalamic stimulation (Routtenberg & Lindy, 1965).

Many of the seemingly diverse stimulation sites were linked by a common neural pathway: the medial forebrain bundle (Olds, 1977), which is a (descending) bundle of axons connecting the ventral tegmentum and the nucleus accumbens in the ventral striatum and which is linked to the (ascending) mesolimbic dopamine system. Stimulation of the medial forebrain bundle seems to produce the most robust rewarding effects, also engaging the mesolimbic dopamine system (Bozarth, 1994). Dopamine appears to be the essential neurotransmitter essential for the reinforcing effect of a medial forebrain bundle electrical stimulation³⁴.

The mesolimbic dopamine system (also known as ventral tegmental dopamine system) is widely accepted to play an important role in the processing of incentive/rewarding stimuli and in the mediation of a percept of pleasure, and craving may be related to its hypoactivation and decrease of dopamine in the system (Bozarth, 1994; Posner, Russell, & Peterson, 2005). It includes the ventral tegmental area, the nucleus accumbens, the amygdala, the hippocampus, the dorsomedial thalamus, and the prefrontal cortex (Nestler, 2001). The nucleus accumbens of the ventral striatum has been shown to be involved in the invigoration, selection and direction of behaviour in response to incentive stimuli and is commonly regarded to be related to euphoria and the percept of

³⁴ However, a number of neurotransmitters may be involved in the rewarding effects mediated by electrical stimulation from different electrode locations (Bozarth, 1994).

pleasure (see also Table 3 in *Chapter 1.5 Substrate*). Repetitive electrical self-stimulation of both the ventral striatum and the orbitofrontal cortex (which has been suggested to be involved in an imbuelement of stimuli with emotional valence (see also Table 3 in *Chapter 1.5 Substrate*)) is observed in non-human animals, even at the consequence of dehydration and starvation (Mora, Avrith, & Rolls, 1980; Rolls, Burton, & Mora, 1980). This underlines the possible role of both structures in the mediation of hedonic value. In humans, an engagement of the orbitofrontal cortex for example has been shown to vary with the valence of odors (Anderson et al., 2003; J. Gottfried, 2007; J. A. Gottfried, O'Doherty, & Dolan, 2002) and gustatory stimuli (Small et al., 2003).

Hemispheric preponderance of EEG activity during the processing of emotions with positive and negative valence has been related to lateralized frontal and prefrontal engagement, with higher left lateralized activity for positively valenced emotions (Davidson, 1984, 2000; Heilman, 1997). The idea of a hemispheric preponderance for the processing of positive and negative emotions is supported by data from lesion studies that report right-hemispheric lesions to be more likely associated with (seemingly inappropriate) euphoric mood change (Sackheim et al., 1982) and left hemisphere lesions to be more often accompanied by anxious, agitated, and sad mood (K. Goldstein, 1948)³⁵. Additionally, research on emotional states of patients recovering from selective hemispheric barbiturate-induced anaesthesia (Wada test) suggested that right carotid injections were more likely associated with euphoria, while the contralateral injections were more likely associated with so-called catastrophic reactions (Rossi & Rosadini, 1967; Terzian, 1964). However, the correlation between valence and hemispheric lateralization of activity is still a matter of debate because it does not consistently occur in experiments addressing the valence dimension, and its possible functional significance cannot easily be

³⁵ It might be argued, though, whether this so called 'catastrophic reaction' of the left hemisphere patients is due to the often severe impairments such as aphasia. Furthermore, it has been argued that the right-hemisphere patients' indifference or enhanced mood may be related to the denial or unawareness of illness (anosognosia) which is more likely to be an effect of right-

assigned.

Note that the valence dimension is not exclusive to emotion as will be described in more detail in section 1.7 *What is special about musically induced emotions?*. Patrick Haggard has addressed the neural correlates of the valence dimension through aesthetic assessment of dance movements (Calvo-Merino, Jola, Glaser, & Haggard, in press). In this study he addressed the underlying correlate of five key aesthetic dimensions³⁶ identified by Berlyne in his seminal book “Experimental Aesthetics” (Berlyne, 1974). Haggard reported robust neural correlates only for the valence dimension but not for the other aesthetic dimensions he examined, with increasing valence corresponding to an increased engagement of occipital and right premotor areas. He argued that the valence percept of the perceivers may be mediated by these occipital and premotor regions. However, he applied an extremely high threshold of 10 voxels as a criterion for significance, so that the regions he reported may not have been the only brain regions mediating the valence percept in the viewers, and small brain areas (for example many subcortical areas) were not considered in the analysis. It is thus possible that such subcortical mediators of the valence percept slipped through the mesh, while for example the reported premotor engagement may reflect a secondary process as a consequence of the valence percept in the listener, similar to the valence dependent engagement of so-called mirror neuron networks during passive perceptual processes (Koelsch et al., 2006) (see also *Chapter 2.2 Emotion modulates the perceptual process*)³⁷.

hemisphere lesions.

³⁶ (1) simple–complex, (2) dull–interesting, (3) tense–relaxed, (4) weak–powerful, and (5) like–dislike.

³⁷ Furthermore, the premotor engagement observed for increasing valence may be biased by a corresponding higher motor skill and virtuosity display of the dancers during the dance moves assessed to be more pleasant to watch. More difficult and motorically engaging actions included for example jumping, which was supposedly more pleasant to watch than (possibly rather boring) slow movements. Accordingly, the higher involvement of premotor areas may reflect a higher engagement of mirror-neuron function due to an observation of greater movement, rather than the neural correlate of the valence dimension.

1.6 Emotion related terminology

To exclude misunderstandings caused by incorrect or ill-defined use of emotion terms carried over from every day speech, it is necessary to more precisely define the terminology related with emotional processes. Note though that such characterizations are sometimes not unambiguous, but are working definitions that do not always meet consensus across the field of emotion research.

- Affect: often used as a synonym for emotion, but sometimes as a term comprising all other terms that describe valenced states, including emotion, mood and preference (Juslin & Västfjäll, in press). The term is sometimes applied to emotional experience that has been qualified (in psychiatry e.g. intense, labile, appropriate affect) or quantified on a scale.

- Mood: Refers to an emotional state of duration intermediate between an emotion and a disposition (e.g., depressed, euphoric, neutral, or irritable mood)³⁸. Duration may not be the only distinguishing parameter between emotions and moods, indeed a multitude of criteria have been suggested, which vary considerably (Ekman & Davidson, 1994) and include physiological, neurological, behavioral and social criteria (Beedie, 2005). However, these claims largely lack reliable evidence (Beedie, 2005). Ekman suggested that emotions always have specific causes, whereas moods do not (Ekman, 1999). In order to deduce from this criterion whether the response provoked by music is an emotion or a mood³⁹, one would first have to clarify whether music is a specific cause or not, or whether it is a specific cause only occasionally.

- Feeling: Refers to the subjective experience of emotion, sometimes also to the subjective experience of mood. LeDoux argued that working memory⁴⁰, a

³⁸ Lazarus disagrees with the notion that moods always endure longer than emotions (Lazarus, 1994).

³⁹ Thayer argued that moods are susceptible to music perception (Thayer, 1996), when self-regulating 'bad moods', tensions, and 'feelings of energy'.

⁴⁰ A variety of studies with humans and non-human primates attempted to locate this system and

“*mental workspace where things can be compared and contrasted and mentally manipulated*” (Armony&LeDoux, 2000, see also Baddeley, 1992) is likely to be the system where conscious aspects of emotion, the so-called ‘feelings’ arise (Damasio, 1995; LeDoux, 1996). He argued that working memory routines should be similar for emotional and non-emotional subjective states, differing only in the information integrated, not in the processes that lead to consciousness. However, he argues that “*the core of an emotion*” that is the processes involved in the assembly of an emotion may remain unapproachable by conscious introspection. Furthermore he argued that when we register ‘automatic’ emotional arousal, where the triggering stimuli remain unconscious, we tend to ascribe the arousal to be elicited by the contents of working memory and interpret it in this context⁴¹.

- Temperamental predisposition: Psychological profile of affective tendencies which is supposed to be relatively stable throughout life history. The term tendency relates to the frequencies with which positive or negative emotions are experienced. The structure of the profile has been supposed to depend on an individual’s inclination to imbue certain classes of situations and experiences either more with positively or negatively valenced emotions (Posner et al., 2005).

suggested the dorsolateral prefrontal areas, as well as the orbital cortical areas and the anterior cingulate to be involved (Fuster, 1998; Goldman-Rakic, 1996). Stored representations and actually present stimuli are correspondingly meant to be integrated by way of interaction between the long term explicit memory system (involving hippocampal circuits including areas of the temporal lobe), sensory processing systems (that are meant to serve as perceptual processors, as well as short-term memory buffers) and dorsolateral prefrontal regions.

⁴¹ Evidence for this idea comes from a case study, where electrical stimulation in the anterior part of the left supplementary motor area (SMA) consistently elicited laughter (Fried, Wilson, MacDonald, & Behnke, 1998). Duration and intensity of laughter increased with the level of the stimulation current and since at low currents a smile was induced while at high currents laughter, the authors suggested that smiling and laughter might be related phenomena organized along a single continuum. The laughter was accompanied by a sensation of merriment or mirth and although it was evoked by stimulation several times, the patient each time offered a different explanation for his behaviour. The laughter was attributed to whatever external stimuli were present - e.g. to viewed objects (“*the horse is funny*”), to the content of a paragraph while reading, or to people present in the room during a finger apposition task (“*you guys are just so funny....standing around*”).

1.7 What is special about musically induced emotions?

Usually genuine sadness is perceived as negatively valenced. When it comes to an aesthetically (e.g. musically) induced emotion, this is somewhat different: a perceiver may feel sad when for example listening to a music piece, but at the same time may assess his experience as positively valenced. This nicely illustrates the special case of musically induced (as a subcategory of aesthetically induced) emotions. According to Ortony et al. (Ortony & Turner, 1990), who proposed that a prerequisite for a biologically basic emotion must be that the connection between a valenced appraisal and other responses associated with the emotion is hardwired, it is thus arguable how far musical emotions (and aesthetically induced emotions in general) can be considered congruent with basic emotions (if the basic emotions concept is valid at all, see *Chapter 1.1.3*).

Scherer suggested that accordingly, it should prove useful to differentiate between utilitarian and aesthetic emotions when addressing the investigation of emotion induced with music (K. Scherer, 2004). The term utilitarian emotion refers to the concept of emotions as immediate reflex-like response patterns to events in our environment to enhance an organism's fitness in terms of survival and reproductive value (Darwin, 1872), whereas the term aesthetic emotion refers to processes of abstracted appreciation or dislike elicited by the perception of stimuli with hedonic qualities.

Two classical perspectives are differentiated in aesthetics: Objectivist and subjectivist theories (Calvo-Merino, Jola, Glaser, & Haggard, in press). Objectivist theories treat aesthetic properties such as valence as attributes of stimuli such as symmetry, balance, complexity, and order that correspond to a compositional arrangement between parts of the stimulus, and between individual parts and the whole (Leder, Belke, Oeberst, & Augustin, 2004). They often claim a generality of effect across individuals based on a proposed

similarity of perceptual systems among humans (Calvo-Merino et al., in press). Subjectivist theories on the other hand, maintain the view that 'beauty is in the eye of the beholder'. Accordingly, aesthetic values such as valence are supposed to be dependent on individual taste and preference. This is probably closely related to Zajonc's findings that familiarity has an influence on aesthetic judgement (Zajonc, 1968). The subjectivist view thus stands for the idea that individual differences in aesthetic judgement may be due to individual differences in prior experience, and thus to cultural environment (Calvo-Merino et al., in press). Both objectivist and subjectivist theories are probably partly correct.

According to the emotion definition of Paul Ekman, an emotion is characterized by a short duration, an immediate onset and its automatic and relatively stereotyped physiological pattern. Musically induced emotions may constitute a special case with respect to their time course, because they may differ to a great degree from these stereotypical time courses, in that either the decay of the emotional responses may be decreased or not present at all during a musical stimulation (Grewe, Nagel, Kopiez, & Altenmüller, 2007a; Schubert, 1999), or that the emotional responses are induced repetitively and as such are present over remarkably long durations. Thus it may be argued that musically evoked emotions rather correspond to the concept of mood outlined above (*Chapter 1.1.7*), perhaps with occasional emotional responses embedded in the experiential process. Note however that the criteria by which mood is distinguished from emotion are manifold, and that according to some of these musical emotions are rather emotions than moods.

As the valence dimension is integral to both emotion and mood (D. Watson & Tellegen, 1985), one is at the safe side to utilize music to investigate emotion through valence, instead of investigating ostensibly basic emotions (see above, *Chapter 1.1.3*) such as for example happiness and sadness.

1.8 Summary

The present chapter outlined distinguishing characteristics of emotion, with an emphasis on valence as a fundamental component of utilitarian and aesthetic emotions, as well as mood.

Emotional processes recruit additional and partially discrete processes of perception, memory, and motor processes, which explains why a better understanding of emotion is beneficial for cognitive science, especially when taking into account that a disregard of emotional processes is likely to be a source of confound in the design of experimental paradigms.

Taking into consideration the ambiguous nature of emotion definitions, it has been proposed that emotion research strategies are required that try to circumvent vaguely defined aspects of emotion (LeDoux, 2000). Evidence has been accumulated, suggesting that a dissonance paradigm addressing the investigation of the valence dimension is likely to be more adequate to approach emotional aspects of musical processing in listeners than paradigms based on distinct emotion concepts. The work of Bigand et al. indicates that even music pieces with short stimulus duration can effectively be employed for an investigation of the valence dimension (Bigand et al., 2005).

Emotional processes correspond to highly precise physiological patterns of temporally coordinated procedures, depending on mechanisms of fast synchronization that are closely linked to the hormonal system, and thus most likely to a network of subcortical components including the amygdala.

Evidence suggests that the amygdala is involved both in mediating the response to pleasant and unpleasant stimuli, but a putative valence specific engagement of amygdala subregions has not yet been thoroughly investigated.

Chapter 2

From music perception to valence percept

“[W]e must immediately insist that aesthetic emotion, pure and simple, the pleasure given us by certain lines and masses, and combinations of colours and sounds, is an absolutely sensational experience, an optical or auricular feeling that is primary, and not due to the repercussion backwards of other sensations elsewhere consecutively aroused. To this simple primary and immediate pleasure in certain pure sensations and harmonious combinations of them, there may, it is true, be added secondary pleasures; and in the practical enjoyment of works of art by the masses of mankind these secondary pleasures play a great part.”

From William James, Principles of Psychology (W. James, 1890/1950)

The neurophysiology of music processing is as complex as the neurophysiology of speech perception. In order to subject it to purposeful investigation, it is essential to differentiate it into various component mechanisms. In the following the modularity of music processing will be briefly portrayed by means of two influential models for the neurocognition of music, stressing processes that are likely to be involved in the attribution of valence (pleasantness/unpleasantness) to a music signal.

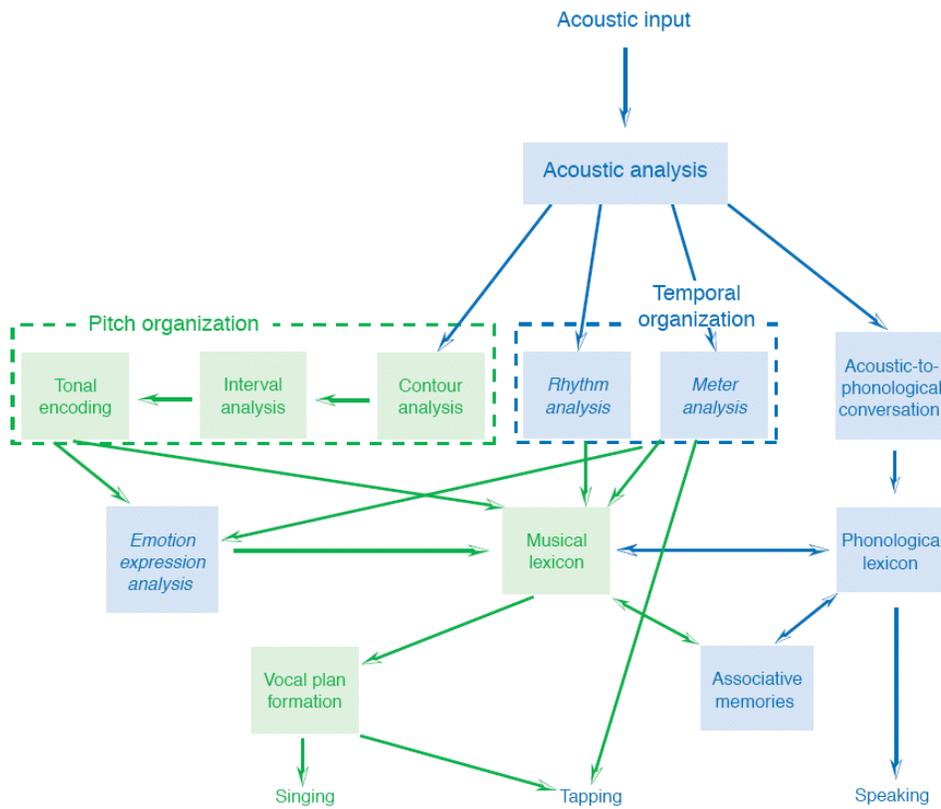


Figure 10. Model A: Modular model of music processing, Peretz & Coltheart, 2003.

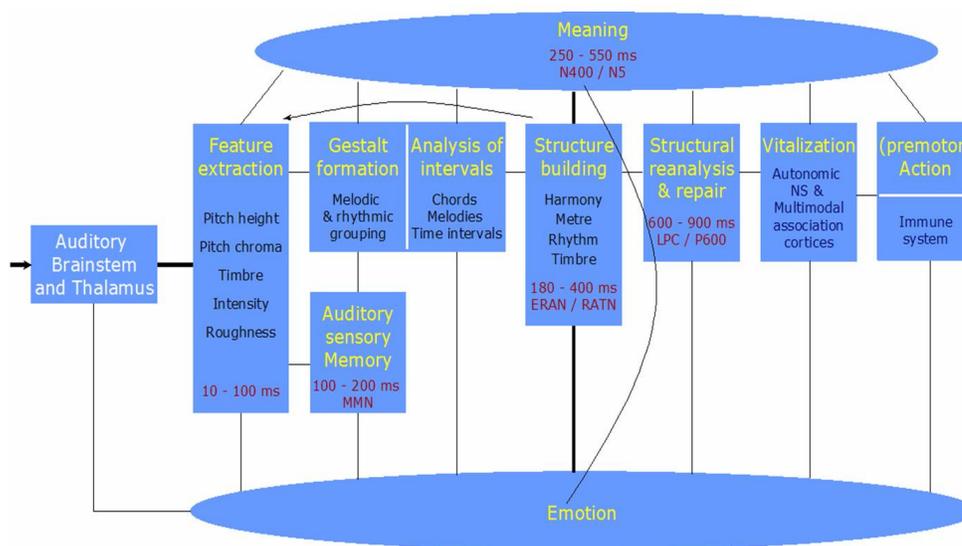


Figure 11. Model B: Neurocognitive model of music perception, Koelsch & Siebel, 2005. This model nicely illustrates the relevance of the current thesis: Emotion likely modulates all modules to which different aspects of music perception can be assigned.

Each box in the above models represents a mental module thought to be involved in music processing (in the model by Koelsch et al. the modules are labelled in yellow characters). Both models propose that music processing is not one homogeneous mechanism, something that a person can either do or not do. Instead they underline that musical abilities are likely correspondent to various neural circuits dedicated to separate functions.

In model A, the authors try to differentiate between components that are music specific (in green) and such that apply also to speech processing (in blue⁴²). Such a distinction can be derived from case studies demonstrating that the neural networks underlying the processing of speech and music to some degree exhibit a double dissociation. In other terms, it is possible to lose or never develop certain modules for music or speech processing without displaying an impairment in the respective other domain⁴³. On the other hand, certain modules seem to be essential to both domains, and an injury in the neural network supporting such modules will result in impairments in both the speech and the music domain. Model B relates the operation of several modules to ERP components (in red characters), thus providing information about the timecourse of their activity in the music perception process. Whereas in model A the authors emphasize shared and distinct processing modules for speech and music, this is not the case for Model B. However, the modules in the Model B are not

⁴² Components unclear whether specific to music are indicated in italics (rhythm analysis, meter analysis and emotion expression analysis).

⁴³ Some examples: individuals who are normal at recognizing lyrics of songs, but not their corresponding melodies (congenital (innate) amusia (Peretz et al., 2002), and acquired amusia (Griffiths et al., 1997; Peretz et al., 1994) in patients with neurological disorders), individuals that lose the ability to recognize spoken words (verbal agnosia) while remaining able to recognize melodies (Godefroy et al., 1995; Mendez, 2001), aphasic patients that preserve an ability to sing (Hebert, 2003).

meant to be domain-specific (as in Fodor's originally proposed model, see below), because for example the module of music-syntactic processing has been shown to interact with language-syntactic processing (Steinbeis & Koelsch, 2008).

2.1 Modular theory

The idea of mental modules derives from the concept of modularity of cognitive functions as in an early version formulated by Fodor (Fodor, 1983). He referred to a module as a reflex-like, hardwired device which processes narrow types of information in a stereotypical fashion (Barrett & Kurzban, 2006), but a functional rather than anatomical entity with neural correlates that may correspond to networks of widely distributed brain areas. According to his theory, a module's main characteristic property is 'information encapsulation', which is a process by which information is retained and processed in a fairly autonomous neural circuit. Other characteristic properties of modules he suggested are rapidity of operation, automaticity, domain-specificity, neural specificity and innateness. However, according to Fodor, none of these are obligatory (Fodor, 1983). His original view was that modularity applies only to "peripheral" sensory processing and that these systems should, in accordance with Chomsky's nativist view (Chomsky, 1965), be innate. The modularity concept he proposed for "peripheral" systems in his original theory was later extended by other authors to apply to a multitude of information processing systems in the brain, including "higher order" processes underlying for example reasoning, judgement and decision making (Cosmides & Tooby, 1994; Pinker, 1997; Sperber, 1994; Symons, 1987; Tooby & Cosmides, 1992). These extensions of Fodor's original modularity concept largely correspond to their view that modules should be defined by the specific operations they perform on the information they receive, rather than by a feature list of necessary and sufficient properties (Pinker, 1997). Note that modularity theory is not generally

accepted (Tomasello, 1999), and that it has especially been opposed for Fodors' originally strong claim for innateness (Karmiloff-Smith, 1992), which cannot easily explain putatively novel modular systems for e.g. playing chess, driving, or reading. In recent writings, Fodor takes a more moderate stand towards this issue, recognizing that the reading system can be defined as a module (Fodor, 2001), although it is obviously not innate.

Similarly in the music domain, some of these modules are clearly shaped by cultural imprinting. This becomes obvious, for example, when comparing the neural correlate of music perception between musicians and non-musicians. Corresponding to the high degree of motor-auditory pairing that musicians experience through practice and music performance, they show an increased recruitment of areas involved in motor planning and execution when only passively listening to music (Bangert et al., 2006). However, how susceptible modules of music perception are to cultural shaping, and how much they are defined by hardwiring, is only poorly understood.

2.2 Emotion modulates the perceptual process

The differences in the models depicted above largely derive from the different purposes for which the models were developed. While the Peretz & Coltheart model was largely developed to interpret clinical evidence, and correspondingly strongly emphasized commonalities and differences between music and speech perception, the model of Koelsch & Siebel was mainly developed in the effort to describe neurophysiological processes of music perception, and to integrate knowledge about the processing of musical syntax (Koelsch & Friederici, 2003; Maess, Koelsch, Gunter, & Friederici, 2001; Patel, 2003) and musical semantics (Koelsch, 2005; Koelsch et al., 2004) in a common scheme.

A prominent difference between both models is that the more recent one by Koelsch & Siebel considers that an emotional state of the listener may modulate the music perceptual process on several levels (Koelsch & Siebel, 2005). Such a

modulatory influence of emotion on perceptual processes may not necessarily only exist for music perception, but is likely a more general perceptual mechanism (Fredrickson, Mancuso, Branigan, & Tugade, 2000; Warren et al., 2006). However, neither the physiology of emotion, nor its modulatory role on perceptual processes is yet sufficiently understood.

The neurology of music perception appears to be an ideal system to investigate the physiology of emotion and the modulatory influence of emotion on auditory perceptual processes. Music above all other means of perceptual stimulation is exceptional for its capacity to evoke emotional responses in the perceiver. Indeed, many seventeenth and eighteenth-century writers - including Johann Mattheson, Charles Batteux, Johann Joachim Quantz, Jean Jacques Rousseau, Johann Nikolaus Forkel, Johann Georg Sulzer, and Heinrich Christoph Koch – have already sought to explain the emotional power of instrumental music designating it as “the language of the heart” or “the language of the emotions” (Bonds, 2006).

2.3 From feature extraction to valence percept

The module ‘feature extraction’ depicted in the ‘Neurocognitive model of music perception’ above is certainly not exclusive to music processing, but generally engaged in auditory processing. It likely comprises the whole auditory pathway from the cochlea to the auditory cortex, which has been extensively studied. However, although we know about top-down modulating projections to early stages of processing, it is still unresolved how much this module is influenced by cultural shaping and how much it is defined by hardwiring. Below, it is briefly sketched out how sound is encoded into neural signals travelling along the auditory pathway and how some of these early perceptual processes are thought to relate to the valence percept.

Kant discerned aesthetic perception into the categories experience of “free” and “dependent beauty”, with instrumental music (along with wallpaper) belonging into the category “free beauty” (Bonds, 2006). He argued that “free beauty” was an inferior category of art, causing a distraction of the mind and mere contemplation on form. According to this view, it would largely engage innate perceptual mechanisms, speaking “only through sentiments and without concepts, and thus [leaving] nothing to be contemplated”, and is to be regarded as pleasure rather than culture (as cited in Bonds, 2006).

From the perspective defined by our present-day knowledge about culturally determined emotional responses to music (even for purely instrumental music), we cannot share this view, because enculturation has been shown to hold an important role in the perception of emotions when listening to music (Adachi & Trehub, 2000; Gerardi & Gerken, 1995; Terwogt & Grinsven, 1991).

In most cultures, a fundamental feature of music is harmony, which is defined by simultaneous note combinations, a so-called “vertical” musical structure. Around 600 BC Pythagoras had already described that different chords vary in their pleasantness (Apel, 1972). Chords combined of tones with simple frequency ratios (e.g. octave: 2/1, perfect fifth: 3/2) are usually judged to be more harmonious, smooth, and consonant, than chords combined of tones with complex frequency ratios (e.g. minor second: 256/243, major seventh: 243/128) (Fishman et al., 2001), which are considered inharmonious, rough, and dissonant. Within Western musical tradition, auditory roughness is intimately linked to the concept of consonance/dissonance. Consonance/dissonance has in music history further been distinguished in musical consonance/dissonance, which relates to an aesthetical evaluation of a sound within a musical context (Apel, 1972; Burns & Ward, 1982; Kameoka & Kuriyagawa, 1969) and psychoacoustic or sensory consonance/dissonance, which relates to more objective sound properties (Braun, 1999; Greenwood, 1991; Helmholtz, 1885/1954; Kameoka & Kuriyagawa, 1969; Plomp & Levelt, 1965; Sethares,

1993; Terhardt, 1974). The concept of musical consonance/dissonance emphasizes a “resolving, static” effect of consonant sounds, and a “dynamic, driving” effect of dissonant sounds that “require resolution by an ensuing consonant sound” (Apel, 1972; Burns & Ward, 1982; Cazden, 1945; Lundin, 1947; Terhardt, 1983, 1984). From the medieval designation of the tritone as “diabolus in musica”⁴⁴ until today, the degree of dissonance in music has increased at an overall level, possibly corresponding to a process of cultural habituation to dissonance in music listeners, and indicating that the valence percept mediated by consonance and dissonance is likely to be culturally influenced.

On the other hand, sensory consonance/dissonance cannot be regarded as music-specific, but applies to both music and non-musical sounds, and has been reported to chiefly depend on three auditory sensations: roughness (which is described in more detail below), as well as sharpness and tonalness that can be regarded to be components of timbre (Terhardt, 1983).

Roughness is the most prominent theory that has been proposed to explain why intervals with simple frequency ratios sound more consonant, than intervals characterized by complex frequency ratios⁴⁵ (Helmholtz, 1885/1954). It was introduced by Helmholtz to define the aural sensation of harsh, raspy, hoarse sounds (Vassilakis, 2005). The physical phenomenon underlying roughness is acoustic interference of frequencies, which has an effect in amplitude fluctuations. These fluctuations occur when the difference between the frequencies is within a so-called “critical bandwidth”, that is, less than 10-20% of the center frequency⁴⁶ (Zwicker, Flottorp, & Stevens, 1957), and the frequency of amplitude modulation corresponds to the difference between the lower and upper frequency. The percept of sound roughness is strongest for

⁴⁴ This example was chosen for eidetic reasons – an accustoming to dissonance began even earlier in Western music history.

⁴⁵ For an overview of major consonance/dissonance theories see (Lundin, 1947; Plomp & Levelt, 1965).

⁴⁶ This is the arithmetic mean of the lower and the upper frequency.

amplitude fluctuation rates between $\sim 20\text{--}150\text{ Hz}$ ⁴⁷ (depending on the pitch register⁴⁸). Each natural tone (other than sinus tones) has a spectrum of harmonics with frequencies related to its fundamental frequency with integer ratios. Roughness theory explains the phenomenon that intervals with simple frequency ratios sound more consonant than intervals characterized by complex frequency ratios, arguing that intervals with complex frequency ratios have fewer harmonics in common and instead more harmonics laying within the same critical bands. The summation of roughness that is contributed by each of these unresolved pairs of harmonics is supposed to determine the overall perceived roughness, which has been reported to closely correlate with the perceived dissonance of musical intervals (Fishman et al., 2001).

It has been shown that for Western listeners, the valence dimension of a musical signal can be systematically and purposefully altered while increasing the roughness of a signal by a distortion of the spectral (Ball et al., 2007; Blood et al., 1999; Koelsch et al., 2006; Sammler et al., 2007) order that is intimately associated with the perceived harmonic of a polyphonic sound.

By monitoring orienting reactions to musical stimuli varying in their consonance/dissonance, several researchers have accumulated evidence that may suggest a preference for consonance over dissonance in Western infants (Crowder, Reznick, & Rosenkrantz, 1991; Trainor & Heinmiller, 1998; Trainor, Tsang, & Cheung, 2002; Zentner & Kagan, 1996, 1998). However, these studies have the methodological constraint that the fetus is sensitive to music stimulation (James, Spence, & Stepsis, 2002) and preference in infants could thus have been influenced by mere exposure (McDermott & Hauser, 2006; Zajonc, 1968) or a form of evaluative conditioning in the womb where the infant associates its auditory perception with bodily states of the mother (Parncutt, in press).

⁴⁷ The disappearance of roughness for higher amplitude fluctuations is thought to be related to a low pass characteristic of the auditory nervous system (Terhardt, 1974).

⁴⁸ At low registers, even harmonics with wider intervals such as minor thirds may sound rough, which is why in traditional Western music orchestration these were usually avoided (Vassilakis,

Insights about music universals can also arise from comparative animal research (Fitch, 2005), but evidence is yet sparse because methodological constraints are a great challenge, and it remains elusive how these results are applicable to humans (McDermott & Hauser, 2006).

Josh Mc Dermott and Marc Hauser (2006) examined the musical preferences of Tamarin monkeys (McDermott & Hauser, 2006). They built a maze with two branches, where in each one, a specific type of musical sound was presented. The animal could thus control what it was exposed to by selecting its whereabouts. If it had a preference for one type of sound over another, the researchers expected it to spend more time on the respective side. Whereas the animals e.g. did show a preference for low volume over high volume noise (indicating that the paradigm really works), the consonance and dissonance of the presented musical sound had no influence on the Tamarin behaviour.

Although above we criticized Kant's notion that perceptual processes stimulated by instrumental music are rather independent of culture on the basis of reasonable evidence, we cannot exclude that his theory may nevertheless be at least partially valid. The reason for this is that the possibility of a universally similar perceptual mechanism mediating the valence percepts in response to physical features of the music has never been addressed experimentally with groups of individuals that were naïve towards the respective other music culture (but only with individuals that shared music cultural imprinting by mass media, but were additionally exposed to regional musical specifics (Butler & Daston, 1968)⁴⁹).

2005).

⁴⁹ Butler & Daston demonstrated that Japanese psychology students who were familiar with Western music ranked a selection of dyads (harmonies, where only two tones are audible) with respect to their valence rather similar to American students. However, because the participants shared a common cultural imprinting by mass media, no clear conclusion can be drawn from this approach.

In order to subject the module ‘feature extraction’ to experimental functional neuro-imaging investigation, it is indispensable to understand the anatomy underlying the workings of this module, and how the respective stages of processing may contribute to the decoding of the feature acoustic roughness and as a consequence to the experience of the closely associated valence percept:

Sound reaches the pinna⁵⁰, which directs it to the auditory meatus (ear canal), a tube running from the outer ear to the middle ear where it hits the tympanic membrane (eardrum). This vibrates corresponding to the alternating compression and rarefaction of the air. Coupled to the ear drum are the three smallest bones of the body (malleus, incus, and stapes), which vibrate in sympathy with the ear drum and amplify the vibration of the tympanic membrane, transmitting it onto the fenestra ovalis (oval window) on the outside of the cochlea, which vibrates the perilymph in the scala vestibuli (upper chamber of the cochlea). The function of the cochlea is to convert the vibration impulses into nerve impulses that are interpreted in the course of auditory processing. The mechanism underlying this process is largely brought about by the architecture of the cochlea. It has the form of a tapered tube wrapped in the form of a snail (lat.: cochlea) shell, with the effect that different frequencies of sound produce different travelling waves with peak amplitudes at different locations of the basilar membrane. Higher frequencies result in peak amplitudes closer to the base of the cochlea, lower frequencies in peaks near the apex of the cochlea (for a more detailed description see e.g. Schmidt & Thews, 1997).

The cochlea consists of three fluid-filled compartments, the scala tympani, scala media, and the scala vestibuli. The basilar membrane separates the scala media and the scala tympani, and carries the organ of Corti, which is the sensory transduction apparatus. It contains the sensory receptor cells of the inner ear. The organ of Corti contains two types of receptor cells, inner and outer hair cells. Above the hair cells is the tectorial membrane that touches the longest

⁵⁰ While reflecting from the pinna, a filtering process is applied to the sound by the ear shape, which adds directional information about vertical or horizontal origin to it.

stereocilia (receptors) of the outer hair cells. The movement of the scalae induced by the travelling waves results in a deflection of the stereocilia in both inner and outer hair cells. The outer hair cells specifically augment the response to the peak of a travelling wave. Interestingly, this is a dynamic feature modulated by an active change of outer hair cell body morphology. These cells, which are innervated by efferent nerve fibers can change their body length, which is likely to at least partly relate to top-down processing and thus possibly also to cultural shaping.

An excitation of inner hair cells spreads via chemical transmitters to bipolar neurons whose cell bodies are located in the spiral ganglion and whose central axons constitute the auditory nerve. Each nerve fiber is frequency selective in that it responds most strongly to a particular frequency, its so-called characteristic frequency (however, it also responds to a lesser degree to neighbouring frequencies), corresponding to the inner hair cells by which it is innervated. The sound pressure level (SPL) is encoded by the firing rate of the respective afferent nerve fiber, also engaging adjacent fibers when the SPL is high. At this early stage of the auditory pathway, sounds are thus already roughly coded by frequency and intensity.

Natural tones such as a piano tone or the sound of a guitar string never consist of solely one frequency, but of a fundamental frequency that corresponds to the tone played plus a number of background frequencies that relate to the fundamental frequency with integer ratios, called harmonics or overtones (see above). Correspondingly, already a single natural tone excites a resonance pattern in the cochlea.

The arrangement of the harmonics in a sound largely determines whether we perceive it as pleasant or unpleasant. This may relate to constraints of our hearing physiology (Parncutt, 2005b) (possibly as early as the cochlea) to resolve distinct frequency bands with high integer ratios in the acoustic input (see also above). However, it is still unclear how much the valence percept of a

sound is defined by the physiology of the hearing mechanism and how much it is influenced by cultural influence. For example, a close interval like the major second which is regarded to be unpleasant in most western music cultures is appreciated in Bulgarian music culture.

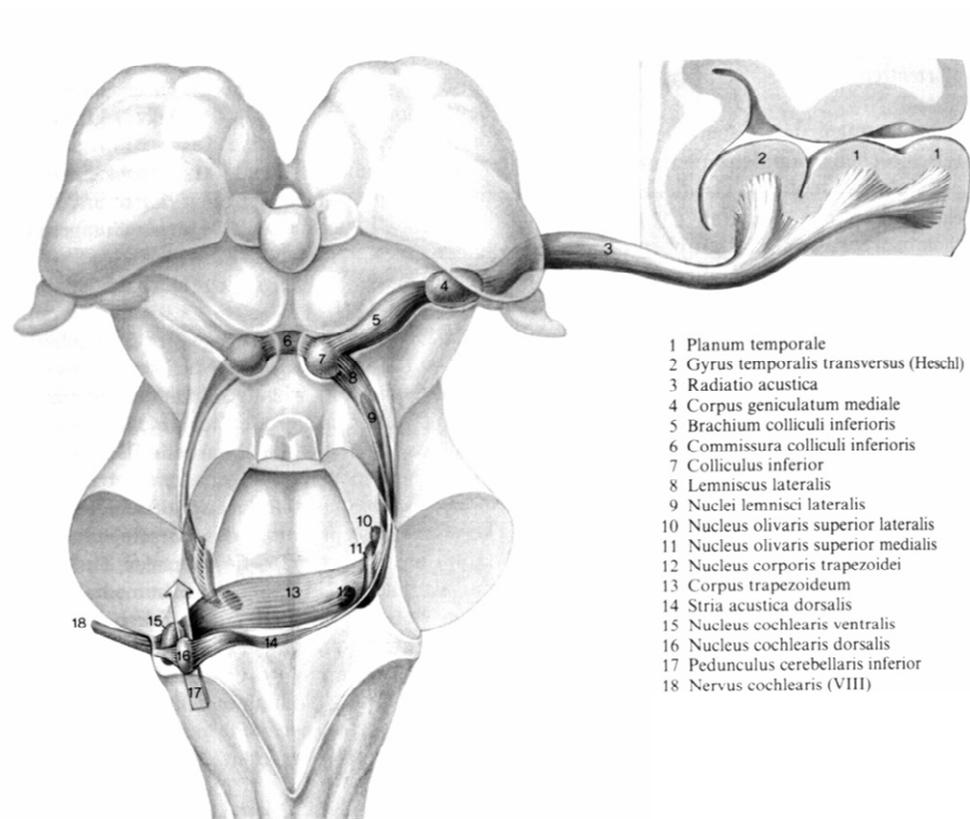


Figure 12. Depiction of the auditory pathway (Nieuwenhuis et al., 1995).

Coming from the cochlea, the information about the sound signal reaches the central nervous system via the cranial nerve VIII (cochlear nerve). It projects to the cochlear nuclei in the brain stem, from where it travels both via ipsi- and contralateral connections (see Figure 12) to the olivary nuclei, where the integration of ipsi- and contralateral information (reflecting interaural differences in phase and intensity) becomes crucial for a localization of sound source (Nieuwenhuys, Voogd, & Huijzen, 1995).

The subsequent stage of the auditory pathway, the inferior colliculus in the midbrain, receives both the ascending auditory pathway input from the ipsilateral and contralateral cochlear nucleus (partly via the ipsilateral olivary nucleus, and with an emphasised contralateral projection), as well as descending inputs from the auditory cortex and the medial geniculate body. The inferior colliculus can be divided into three parts, the Central Nucleus of IC (ICC), pericentral nucleus and external nucleus; however, the Central Nucleus is the principal station for ascending auditory information.

The inferior colliculus is involved in the integration and coordination of fast responses, such as startle reflex and ocular reflex, and also seems to be involved in spatial localization by binaural hearing. However, most interestingly to the present investigations, the ICC has representations of pitch and amplitude modulation (Schreiner & Langner, 1997), where the isofrequency and isoperiodicity contours of these representations are oriented roughly orthogonal to each other (Langner, Schreiner, & Albert, 1992).

Thus the ICC is putatively organized in a tonotopic and periodotopic manner, featuring mechanisms capable of spectral integration, that is, an analysis of frequencies and temporal structures early in the auditory pathway at the level of the midbrain (Schreiner & Langner, 1988; Schulze & Langner, 1997). This occurs likely in close coordination with the auditory cortex, putatively projecting from different aspects of the ICC through the thalamo-cortical pathway to different cortical units (Schulze & Langner, 1997), which may engage contrast enhancing mechanisms on the output of the IC by processes of lateral inhibition.

This work suggests that the percept of roughness is coded in the inferior colliculus by the temporally structured neural activity, whereas pitch by the spatial representation (Schulze & Langner, 1997).

The inferior colliculus projects through the brachium to the ipsilateral medial geniculate body of the thalamus, which represents the thalamic relay between the inferior colliculus and the auditory cortex. It is made up of a number of sub-nuclei that are distinguished by their neuronal morphology and density, by their afferent and efferent connections, and by the coding properties of their neurons. The medial geniculate gyrus can be divided into ventral, dorsal, and medial divisions. The complex signal output from the inferior colliculus is in accord with evidence for multiple parallel auditory pathways through the thalamus (Calford & Aitkin, 1983).

The ventral division of the medial geniculate body receives a topographical projection from the central nucleus of the inferior colliculus, preserving tonotopicity. The medial part of the ICC has been reported to project to the deep dorsal nucleus, which contains only units tuned to high frequencies. The major inputs to the caudodorsal nucleus of the medial geniculate body stem from the nucleus sagulum and the pericentral nucleus of the inferior colliculus. This widespread input is reflected in a wide range of auditory responses found in the medial geniculate body (Calford & Aitkin, 1983) that must be regarded a more powerful system than merely a relay station for passing frequency, intensity and binaural information to the cortex.

As such, the interconnection between the medial geniculate body and the amygdala is important for classical conditioning and the coupling of emotional significance to acoustic stimuli seems to crucially involve the relay of sensory input from the medial geniculate body to the amygdala (Iwata et al., 1986).

Note that importantly for the investigation in *Chapter 4.2 (Opening up to consonance – an amplification mechanism in the auditory pathway dependent on harmonic roughness)* both inferior colliculus and medial geniculate body are macroscopically discernable from surrounding structures and easy to localize in MRI images.

The cells of the medial geniculate body mainly project to the ipsilateral primary auditory cortex via the radiatio acustica (see Nieuwenhuis et al. (1995) for a detailed description). The primary auditory cortex (comprising Brodman's area 41 (Koniocortex)) has a well developed layer IV, which corresponds to its strong input from the thalamus. It corresponds to the medial aspect of the transverse gyrus of Heschl located in the superior temporal gyrus (STG).

There is good evidence that the auditory cortex and its surrounding auditory association cortex is involved in the discrimination, detailed analysis, and conceptualization of sounds and sound patterns (Pandya, 1995; Pickles, 1982), as well as in auditory memory.

Lesions of auditory cortex cause a variety of music perception impairments, including a deviated consonance/dissonance perception (Peretz, Blood, Penhune, & Zatorre, 2001; Tramo, Bharucha, & Musiek, 1990). It has been suggested that roughness may be represented in monkey primary auditory cortex (A1) by neuronal response phase-locked to the roughness related amplitude modulations of the auditory signal (Bieser & Muller-Preuss, 1996; Schulze & Langner, 1997; Steinschneider, Reser, Fishman, & Arezzo, 1998), and it has been shown that the magnitude of phase-locked activity in A1 correlates with the degree of dissonance of musical chords (Fishman et al., 2001).

A recent study by the author showed that the primary auditory cortex is engaged more strongly during the processing of pleasant consonant than during the processing of unpleasant continuously dissonant music (Koelsch et al., 2006). We had attributed these findings to hypothesized top-down attentional processes previously shown to be able to modulate an engagement of the auditory cortex (Jäncke, Mirzazade, & Shah, 1999), according to the hypothesis that the original and pleasant music may have caused greater attention, leading to a greater activation of Heschl's gyri. However, we had no conclusive evidence for the true mechanism underlying this phenomenon.

One might infer from the theoretical background outlined in this chapter that music composers would rather avoid dissonance, and only write music with consonant and thus pleasant sounds. However, this would probably sound rather bland or like a children's nursery rhyme. Instead, Western musical tradition largely exploits tensions created by dissonance to shape musical compositions.

2.4 From structure building to valence percept

In his classical book on music and emotion, Meyer theorized that listeners often have (implicit) expectations of what will happen in the music and, depending on whether these expectations are fulfilled or not, experience relaxation, or tension and suspense (Meyer, 1956) (see also Juslin & Vjästfall, in press). Thus, according to Meyer (1956), music-syntactically unexpected chords may lead to a sensation of surprise, or suspense. It may also modulate the valence percept of the listener, but this has not yet been experimentally addressed.

The idea that violations of musical expectation are closely related to emotional responses was supported by a study from Sloboda, which showed that specific musical structures lead to specific psychophysiological reactions (Sloboda, 1991) (in that study, new or unexpected harmonies evoked shivers). The perception of irregular (i.e., unexpected) chords has also been shown to lead to an increase of perceived tension (Bigand, Parncutt, & Lerdahl, 1996), and the perception of tension has been linked to emotional experience during music listening (Krumhansl, 1997). Moreover, a recent study (Steinbeis, Koelsch, & Sloboda, 2006) provided a direct test of Meyer's theory (Meyer, 1956), investigating the role of music-specific expectations in the generation of emotional responses in the listener. In that study, unexpected chords elicited an increased skin conductance response (SCR), and behavioural measures indicated that musical stimuli containing unexpected chords were generally perceived as more emotional. In corroboration, two previous fMRI studies on the processing of regular vs. irregular chords reported activations of orbito-frontal (Tillmann et

al., 2006) as well as orbitofronto-lateral cortex (Koelsch et al., 2005), taken to reflect emotive processing elicited by the unexpected chords.

A parameter that can be purposefully manipulated to address the investigation of valence by distortion of musical structure is temporal order. This can for example be achieved by presenting scrambled music where the temporal structure is lost, which is perceived as more unpleasant than the original (Menon & Levitin, 2005). However, it is yet unclear how universal a distortion of the temporal order influences the valence percept of music (especially when assessing completely unknown music from another music culture), particularly if the temporal coherence (Deutsch, 1999) and temporally driven expectations (Levitin & Menon, 2003) of the musical signal are preserved in the manipulated counterparts.

2.5 From a-referential meaning to valence percept

Music has frequently been considered a non-verbal means of communication (Koelsch, 2005; Koelsch & Siebel, 2005; Meyer, 1956; Patel, 2003; Sloboda, 1986; Swain, 1997), a system that in Western music culture usually comprises a composer who creates a score, musicians who interpret the score⁵¹, and perceivers who decode the composers' intentions and musically phrased emotional expressions from the sound. Koelsch et al. showed that music, like words, can prime the processing of semantic meaning, indicating that music is indeed a means of communication (Koelsch et al., 2004). Musical priming was also successful for semantic meaning corresponding to emotional expressions like "happy" and "sad", corroborating that emotional expressions in music can be regarded a form of semantic information (Koelsch et al., 2004; Patel, 2007).

⁵¹ Some forms of music do not require a composer because the musicians spontaneously compose while performing, sometimes in an interactive manner (e.g. Free Jazz). Other forms of music do not need a musician, only a composer (e.g. 'Tape Music').

Meyer (Meyer, 1956) differentiated “referentialists” who claim that musical emotions are elicited through associations with extra-musical experiences⁵², and “absolutists”, who believe that the structure of the music itself induces the emotion by a supposedly “purely musical” (Parncutt, 2005a) and universal perceptual process. The latter, putatively universal a-referentially expressive gesture (Fitch, 2006) of music may comprise the mediation of emotional expressions such as happiness, sadness, and fear. However, it is not clear cut how much the decoding of such emotional expressions actually depends on referential information such as culturally learned musical clichés.

Only few studies have addressed the attribution of emotional expressions to music of other cultures (Balkwill & Thompson, 1999; Balkwill, Thompson, & Matsunaga, 2004; Gregory & Varney, 1996). Unfortunately none of these can give a clear answer to whether the decoding of emotional expressions is an a-referential process, because they were not conducted with listeners isolated from the respective foreign music, but with participants from cultures that were extensively exposed to modern media. Whilst these approaches thus cannot be called on to draw clear conclusions about music universals, some provide evidence in favor of cultural specifics in music perception, e.g. showing that music listeners perform better on same-culture, than on other-culture materials (Balkwill & Thompson, 1999; Balkwill et al., 2004).

To my knowledge it has never been investigated how the capacity to decode putatively a-referential semantic information like emotional expressions from music modulates the degree of pleasure (the valence percept) we derive from the music.

⁵² Note that other authors have defined referential meaning in music both in terms of reference to an extra-musical event, as well as in terms of reference to a part or theme within one musical piece (Sloboda, 1986).

2.6 Summary

Although our knowledge about functional modules of music processing has increased substantially during the last years, it is still largely incomplete. One major issue unresolved is the question how susceptible modules of music perception are to cultural shaping, and how much they are defined by hardwiring. It appears that the neurology of music perception is an appropriate system to investigate the physiology of emotion and the modulatory influence of emotion on auditory perceptual processes. In order to investigate the influence of culture on emotional responses to music it has been shown that cross-cultural comparison of individuals who are naïve of the respective other music culture is most suitable.

The difference between musical and sensory consonance/dissonance has been elaborated, and the roughness-phenomenon, one of the components of sensory consonance/dissonance which is intimately linked to the valence percept has been described in detail.

It was sketched out how sound is encoded into neural signals travelling the auditory pathway and it has become evident how complex some of these 'early' perceptual processes are already organized, featuring spectral integration, that is, an analysis of frequencies and temporal structures (including roughness) early in the auditory pathway at the level of the midbrain. The stages of the auditory pathway have been examined with respect to their putative involvement in roughness analysis and consequently a possible role in the mediation of a valence percept.

Methods have been described by which a manipulation of musical structure building can be applied to systematically vary the valence percept. Mediation of meaning through music has been differentiated in referential and a-referential musical perceptual processes, suggesting that emotional expressions can probably be regarded a universal a-referential process.

Chapter 3

General methodologies

3.1 Ethnomusicological cross-cultural comparison

Ethnomusicology has been defined as a study of the modes of music making as a means of cultural expression and as sources of meaning (Becker, 2001). The present study pushes the understanding of ethnomusicological investigation further. It is largely concerned with music processing in the listener, a psycho-ethnomusicological approach.

Each of us imposes a series of abstractions on what we perceive, transforming complex information into more abstract and meaningful representations that can be stored in memory (Harwood, 1976). This is largely compatible with the view that we understand and analyse our world by synthesizing it from our culturally learned expectations (Neisser, 1967). Accordingly, it has often been proposed that perceptual processes are influenced by culture, largely attributing differences in perceptual processes to cultural differences in social structure and social practice (Nisbett & Miyamoto, 2005). The term 'culture' is commonly used to sum up the physical and intellectual products of human society, including commonly held ideas, the generation and development of such ideas, and their sharing and communication (Parncutt, 2005a). Harwood claims that these perceptual workings are as indicative of language and vision, as they are of music perception. Accordingly she suggests that more than the music itself

the process of understanding and engaging in musical behaviour may be universal (Harwood, 1976).

Musical form and the contexts where music is involved differ to a great extent between cultures (Cook, 1998), often rendering it challenging to listen to music of a different music cultural background. Musical field recordings for example may sometimes rather be perceived as strange noises than music, and yet members of another culture perceive them to be music⁵³ (rather in support of a referentialist view, see above in *Chapter 2.5 From meaning to valence percept*). Note also that other cultures may not even have a term for “music” at all (which is true for the Mafa, see also below *Chapter 6 Universal preference for consonance over dissonance and forward over backward in music*).

In order to address similarities and cultural specifics of music appreciation in an ethnomusicological cross-cultural comparison it thus necessitates an objective understanding of design features of music.

List of key design features of music as proposed by Fitch, 2005:

- Complexity: Music is often regarded a complex signal, although it is unclear what threshold of “complexity” may be required for a signal to qualify as complex. Furthermore, there are constraints hindering a reliable quantification of the complexity of all musics (Pressing, 1998).
- Generative: Music consists of rule-governed combinations and permutations of a limited number of items (“notes”). These can be composed to produce an unlimited number of hierarchically structured signals (Merker, 2002).
- Culturally transmitted: Although musical behaviour such as dance may to some extent be innate, certain musical features, such as musical styles, like individual languages, are learned by experience.
- Discrete pitches: Melodies are usually created from notes belonging to a

⁵³ Or alternatively try going to a concert at the International Conference for Computer Music.

scale. In some percussive African music, discrete pitches may be largely absent, as well in some singing styles (e.g. lament, rap).

- Isochronic: Music often has a relatively regular periodic pulse (also termed ‘beat’, or ‘tactus’) that represents a reference framework for other temporal features of the music (Arom, 2000; Merker, 2002). Discrete time and pitch render music acoustically more predictable, and thus can enhance acoustic integration between multiple individuals in an ensemble. However, there are also exceptions to this feature, non-isochronic musical genres (e.g. sung lament).
- Transposability: A melody is considered identical when it is performed in different keys, because (in human music) a melody is defined by the relationships between notes, and not the absolute frequencies of the notes.
- Performative context: Particular songs or styles recur in specific social contexts, especially in religious ritualistic contexts (Arom, 2000; Cross, 2003; Nettl, 2000).
- Repeatable: Songs or performances are often repeated (often with great frequency), usually without any obvious decrement (and sometimes an increment) of dedication in the listener.
- A-referentially expressive: Music is *not* meaningless. Music can for example express emotions such as happiness, sadness, and fear. However, musical meaning is not limited to emotional expression. Koelsch et al. showed that music like words can prime the processing of semantic meaning (Koelsch et al., 2004). Ian Cross argues that music has a capacity to imbue any situation with meaningfulness, a so-called “floating intentionality” that may however be quite different for different participants (Cross, 1999; Cross, 2005). Fitch also considered this design feature a “gestural form” that can above its expressiveness relate to both mood and movement (Fitch, 2006).

3.2 Functional magnetic resonance imaging

The present chapter outlines basic principles of the fMRI method. Specific scanning paradigms and fMRI data analyses as used in the different experiments will be described in the chapters addressing the respective experiments.

fMRI is a non-invasive method that exploits the fact that nerve cell metabolism is not uniform throughout the brain, but is instead increased in specific brain areas during specific tasks and perceptual conditions. In fMRI, time series of Magnetic Resonance (MR) images are recorded. The image intensity therein is a representation of the density and chemical environment of hydrogen nuclei (protons) in the brain (particularly in water and fat).

Protons have a quantum mechanical property called spin. Particles such as ^1H (proton) or ^{31}P , with an odd atomic number, have a so-called non-zero spin and therefore a magnetic moment.

In MRI, the protons are subjected to a strong magnetic field, where due to their magnetic moment they align in parallel (low energy) or anti-parallel (high energy). Under standard conditions, the proportion of anti-parallel to parallel alignment is around 1 to 100000. A transition between these two states can be induced by a radio frequency (RF) field which corresponds to the energy difference between the parallel and anti-parallel states.

Note that this description corresponds to quantum mechanic theory. When considering ensembles of spins it is valid, and in the scope of the present description more easy graspable, to address the principles of MRI with a description in terms of classical physics.

If the applied RF-field fulfils the resonant condition at the so-called Larmor frequency, the spin ensemble switches from the longitudinal axis which is

parallel to the main magnetic field into the so-called transversal plane (transverse magnetisation).

In this plane the spins⁵⁴ precess (rotate) with their Larmor frequency, producing a small, but detectable electromagnetic field as they do so.

The spins then return back to equilibrium state (longitudinal axis), a process which is called spin relaxation.

Three time constants are essential in the description of spin relaxation: (1) T1 or “Time 1”: Recovery of the longitudinal component of net magnetization (corresponds to the realignment of a defined percentage of the tissue's nuclei with the external magnetic field), (2) T2: Decay of the transverse component of net magnetization due to accumulated phase differences caused by spin-spin interactions (local dephasing), (3) T2*: Decay of the transverse component of net magnetization due to both accumulated phase differences and local magnetic field inhomogeneities (provides additional sensitivity to relaxation processes that cause incoherence of transverse magnetization).

Since protons in different molecules realign with different characteristics, different tissues can be distinguished, and ratios of oxygenated and deoxygenated blood can be determined in the images. MR images mainly reflect brain structure, but also contain small contributions from blood flow (on the order of 2% of maximum intensity). The changes in the contributions of blood flow are delayed with respect to a corresponding brain cell electrical activity. If neurons are active, they release increased amounts of messenger molecules such as NO, which cause an increase of arteriolar diameter and in turn increased blood flow. At the same time, their metabolic rate, including the consumption of oxygen, will increase. The blood flow increase over-compensates for increased

⁵⁴ Note that it is possible to describe quantum mechanical properties like the spin in terms of classical physics.

oxygen extraction, resulting in a local hyperoxygenation of blood. The peak of this hemodynamic response usually has a latency of around 4-5 seconds. Oxygenated blood has a higher ratio of oxyhemoglobin (i.e., hemoglobin carrying oxygen) to deoxyhemoglobin (i.e., hemoglobin that has dispensed its oxygen), than deoxygenated blood. Importantly, oxyhemoglobin and deoxyhemoglobin have different magnetic properties - oxyhemoglobin is diamagnetic and exerts little influence on the local magnetic field, whereas deoxyhemoglobin is paramagnetic and causes greater inhomogeneities in the local magnetic field that can be determined with $T2^*$. Blood-oxygen-level dependent (BOLD) image contrast measured with functional MRI thus relies on $T2^*$ and provides an indirect measure of preceding neural activity.

The encoding of spin with spatial information is realized by applying three gradient magnetic fields, corresponding to the three dimensions, the so-called (1) slice selective gradient, (2) phase encoding gradient, and (3) frequency encoding gradient. These gradient magnetic fields can be switched on and off, and their durations and strengths can be controlled. Because there is a linear interrelation between field strength and Larmor frequency, the location for the resonant condition (at the Larmor frequency) can be defined by the gradient fields. By applying the magnetic gradients at defined timepoints in relation to the radio frequency pulse and the readout of the signal, the spins can be encoded (and later decoded with a Fourier-transformation of the signal readout) by slice, phasing, and frequency. The timing and characteristics of signal readout and the switching of the gradient magnetic fields defines different so-called pulse sequences.

The minute vibrations of the coil materials during scanning propagates into the surrounding air, in which they are audible as loud noise. The sound intensity can reach up to 130 dB, which can damage the hair cells in the inner ear. Hence, the appropriate use of ear protection is mandatory during fMRI. Both the loud scanner and the requirement for ear protection make it challenging to perform

experiments with auditory stimulation in the fMRI scanner.

Unlike PET (or Computer Tomography, a method commonly employed for structural imaging), fMRI does not employ radioactive substances or ionizing radiation and is therefore regarded as a very safe procedure, if safety precautions are strictly followed. These include that individuals with ferromagnetic metal implants, large scale tattoos, and cardiac pacemakers are prevented from having (f)MRI scans (due to the high magnetic field), and that no ferromagnetic metals are brought into the scanner room, especially not while an individual is scanned (the magnetic forces of the scanner can easily turn ferromagnetic objects into projectiles).

II

Empirical part

Chapter 4

Experiment 1

4.1 The neurology of the valence dimension as investigated with pleasant and unpleasant music

4.1.1 Introduction

The literature demonstrates that the amygdala is a key structure in defensive response in a wide variety of species, including humans and other primates (LaBar et al., 1998). Nevertheless, as outlined in *Chapter 1.5 Substrate*, the amygdala's role in emotion is much more multifaceted: it may be involved in the complex orchestration of both positive and negative emotions. It has been proposed in the *Chapter 1.8 Summary* that a better understanding of amygdala-subnuclei functionality will help to clarify the amygdala's workings, and the above theoretical outline suggests that its sensitivity to valence renders it susceptible to such detailed investigation.

Music has the capacity effectively to induce the experience of both negative and positive emotions in laboratory experimental settings, even in the MRI scanner.

Therefore, the investigation of music perception has been able to contribute substantially to the understanding of neural correlates of emotion (Blood & Zatorre, 2001; Blood et al., 1999; Brown et al., 2004; Koelsch et al., 2006; Menon & Levitin, 2005; Peretz, Gagnon, & Bouchard, 1998).

The amygdala is known to respond rapidly to information with emotional quality; during perceptual processing it even receives direct “low road” input from a subcortical pathway independent of cortical processing. The evolutionary importance of this is evident regarding the rapid recognition of potential threats; the amygdala exerts an important influence on the current focus of attention and can thus direct the necessary cognitive resources to the stimulus in question. The work of Bigand et al. shows that the listener very rapidly (already during the first second) appreciates or dislikes music excerpts (Bigand et al., 2005). It is conceivable that the amygdala plays an important role in the underlying neuronal network.

For these reasons, the paradigm of the present study was optimized to show cerebral BOLD-signal changes in a very early stage of music perception, with a special focus on the amygdala. It contributes to the investigation of the valence dimension with a paradigm that was especially designed to examine amygdala behavior related to both increasing and decreasing stimulus pleasantness. In contrast to the study by Koelsch et al. (2006), the present experiment examined the immediate, initial response to music with short stimulus durations (3.6-10 seconds) (Koelsch et al., 2006). In this paradigm, a sparse temporal sampling design was used allowing the presentation of the auditory stimuli in the absence of scanner noise (Figure 13), whilst acquiring 24 axial slices that covered the whole brain volume.

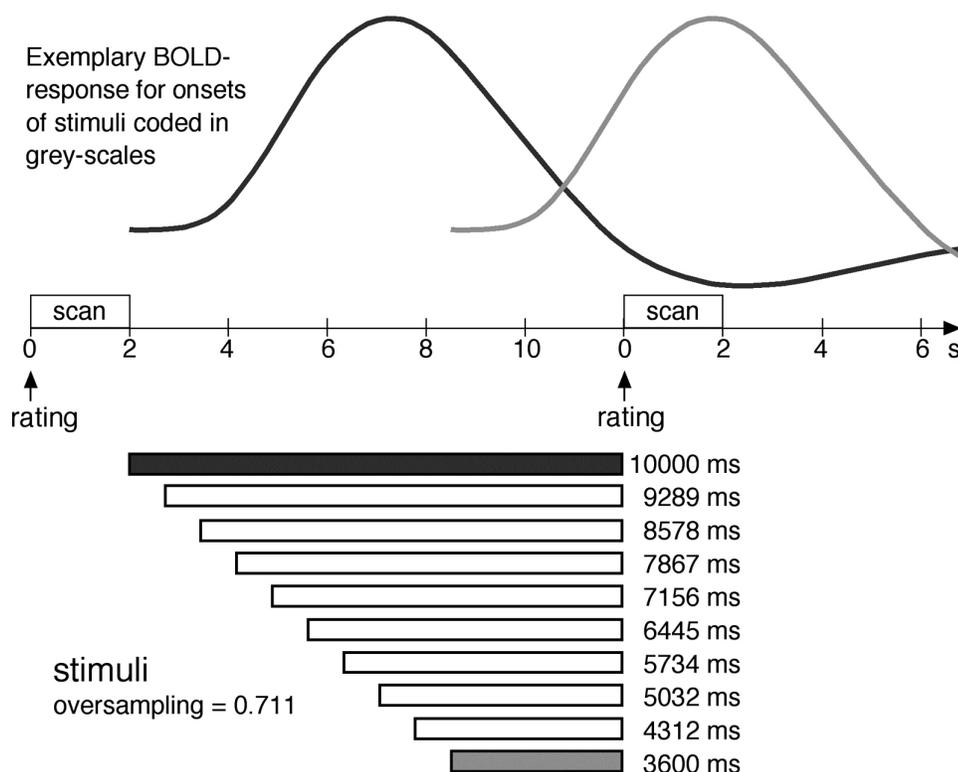


Figure 13. Trial design: The participants had to rate the perceived valence of each musical excerpt during the scanning periods. The diagram illustrates that due to the high TR of 12 seconds, BOLD response related to this task could not spill over into the next scan.

4.1.2 Methods

4.1.2.1 Participants

16 right-handed (Oldfield, 1971) non-musicians (8 females; age range 23-33 years, mean: 26.5 years) with normal hearing participated.

4.1.2.2 Stimuli

Joyful instrumental tunes from the last four centuries (all major-minor tonal

music, covering a wide variety of different styles) and their manipulated counterparts (reversed, cacophonous, reversed cacophonous; matched for arousal) were used (Koelsch et al., 2006; Sammler et al., 2007).

Two pairs of stimulus categories were thus comparable with respect to their spectral information and two pairs were comparable with respect to their temporal structure.

The original music pieces comprised excerpts from the following tunes (artist/band/composer – name of piece):

Anonymous – Entre Courante, Dvorak – Slavonic Dance No. 8 (Op. 46), J. S. Bach – Badinerie, J. S. Bach - Rejouissance, Benny Goodman – I got Rhythm, F. Canaro – La Punalada, P. F. Caroubel - Volte, Dvorak – Slavonic Dance No. 9, Flairck – Odd Waltz, Flook – Calico, Flook - Happy Jigs, Friend N Fellow – Blue in You, Gene Urupa – Drummin Man, Gene Urupa - Jeepers Creepers, Glenn Gould – Das Wohltemperierte Klavier Nr. 5 (by J. S. Bach), Herb Alpert & The Tijuana Brass – Zorba the Greek, Liquid Soul – Yankee Girl, J. Pastorius – Soul Intro “The Chicken”, Riluiruairc - Leaba, Santiago - Amarru, Shantel - Bucovina, The Ventures – Kicking Around, P. Xanten – In Advance (re-edit; Music for dancefloors, KPM Music); for more information see also Koelsch et al., 2006, and Sammler et al., 2007.

The stimuli were presented in a pseudo-randomized manner at ten different time points relative to the trial onset (TR = 12 sec) in the absence of scanner noise (Figure 13). Each stimulus was presented twice at two different time points and the total duration of each stimulus was matched (the sum of the durations of the two presented versions of each stimulus was 13600 ms). Five scans were measured for each sampling point in each condition.

4.1.2.3 Procedure

Participants had to listen carefully to the music and indicate how it had influenced their emotional state in terms of valence on a 6 point scale, using a four button response box suitable for use inside MRI scanners. In order to attain

a 6-point scale, the participants were asked to indicate the extremes in the valence scale by double-clicking with the index- or little finger.

4.1.2.4 Image acquisition

Scanning was performed on a 3-T Siemens Magnetom Trio. 24 axial slices were acquired parallel to the AC-PC plane. A gradient-echo EPI sequence was used with a TE 30ms, flip angle 90 degrees, TR 12s, acquisition bandwidth 100kHz. Acquisition of the slices within the TR was arranged so that the slices were all rapidly acquired in less than 2 s, followed by a period of no acquisition to complete the TR, so that the stimuli were presented in the absence of scanner noise (sparse temporal sampling). The matrix acquired was 64x64 with a FOV of 19.2cm, resulting in an in-plane resolution of 3mmx3mm. The slice thickness was 4 mm with an interslice gap of 1 mm.

Prior to the functional sessions, anatomical data sets were acquired. T1-weighted MDEFT (Ugurbil et al., 1993) images (data matrix 256x256, TR 1.3 s, TE 7.4 ms) were obtained with a non slice-selective inversion pulse followed by a single excitation of each slice (Norris, 2000). For registration purposes, a set of T1-weighted spin-echo EPI images (TE 14 ms, TR 3000 ms) were taken with the same geometrical parameters (slices, resolution) and the same bandwidth as used for the fMRI data. A slice-selective inversion pulse was applied with an inversion time of 1200ms.

4.1.2.5 Data-Analysis

The data processing was performed using the software package LIPSIA (Lohmann et al., 2001). This software package contains tools for preprocessing, co-registration, statistical evaluation, and visualization of fMRI data. Functional data were motion-corrected offline with the Siemens motion correction protocol (Siemens, Erlangen, Germany). To correct for the temporal offset between the slices acquired in one scan, a cubic-spline-interpolation was applied. A temporal high pass filter with a cutoff frequency of 1/264 Hz was used for baseline

correction of the signal and a spatial gaussian filter with 7.06 mm FWHM was applied. To align the functional data slices with a 3D stereotactic coordinate reference system, a rigid linear registration with six degrees of freedom (3 rotational, 3 translational) was performed. The rotational and translational parameters were acquired on the basis of the MDEFT image (Norris, 2000; Ugurbil et al., 1993) and EPI-T1 slices to achieve an optimal match between these slices and the individual 3D reference data set.

This 3D reference data set was acquired for each subject during a previous scanning session. The MDEFT volume data set with 160 slices and 1mm slice thickness was standardized to the Talairach stereotactic space (Talairach & Tournoux, 1988). The rotational and translational parameters were subsequently transformed by linear scaling to a standard size. The resulting parameters were then used to transform the functional slices using trilinear interpolation, so that the resulting functional slices were aligned with the stereotactic coordinate system. The resulting voxel size was 3x3x3 mm.

The statistical evaluation was based on a least-squares estimation using the general linear model for serially autocorrelated observations (Friston, 1994; Friston, Holmes, Poline et al., 1995; Friston, Holmes, Worsley et al., 1995; Worsley & Friston, 1995).

The design matrix was generated with a synthetic hemodynamic response function (Friston et al., 1998; Josephs, Turner, & Friston, 1997). The model equation, including the observation data, the design matrix and the error term, was convolved with a Gaussian kernel of dispersion of 4 s FWHM to deal with the temporal autocorrelation (Worsley & Friston, 1995). In the following, contrast-images, i.e. estimates of the raw-score differences between specified conditions, were generated for each subject.

As noted before, each individual functional dataset was aligned with the

standard stereotactic reference space, so that a group analysis based on the contrast-images could be performed.

The single-participant contrast-images were then entered into a second-level random effects analysis for each of the contrasts. The group analysis consisted of a one-sample t-test across the contrast images of all subjects that indicated whether observed differences between conditions were significantly distinct from zero (Holmes & Friston, 1998).

Subsequently, t-values were transformed into Z-scores. Only regions with z-scores greater than 3.1 ($p < 0.001$; uncorrected) and with a volume greater than 81 mm³ (3 voxels) were considered.

4.1.2.6 Functional connectivity analysis

In our investigations, we applied the definition of “functional connectivity” in terms of correlations between neurophysiological events. Friston et al (1993) showed that this definition is operational and provides a simple characterization of functional interactions (Friston, Frith, Fletcher, Liddle, & Frackowiak, 1996). Although this concept of functional connectivity does not allow conclusions about the direct influence of one brain region over another, it does provide a very useful phenomenological characterization of cortical interactions (Friston et al., 1996). Using correlations between fMRI time series, these cortical interactions can be discussed at the physiological level of hemodynamics.

4.1.3 Results

4.1.3.1 Behavioral data

All participants rated the original stimulus category as pleasant and the manipulated stimulus categories as significantly more unpleasant ($p < 0.001$). No category showed an interaction with experiment duration, showing that the

pleasant music was still perceived as pleasant towards the end of the experiment (see *Appendix A Supplementary Figures*, Figure 33).

4.1.3.2 Functional imaging data, parametric analysis for a valence continuum from unpleasant to pleasant

An fMRI parametric analysis investigating a bipolar valence continuum from unpleasant to pleasant revealed that two distinct anatomical regions in the amygdala were involved in the response to pleasant and unpleasant music stimuli. Moreover, a positive correlation of BOLD signal with increasing valence could be observed in the right orbitofrontal cortex, the left SMA, the right BA44, the left putamen, the superior temporal gyrus (STG) bilaterally, and the right cerebellum. A positive correlation of BOLD signal with decreasing valence was observed in the premotor cortex bilaterally, the right motor cortex, the paracentral lobule bilaterally (predominant to the right), and the right superior parietal lobe (Figure 14, see also table in *Appendix B Supplementary Tables*, Table 6).

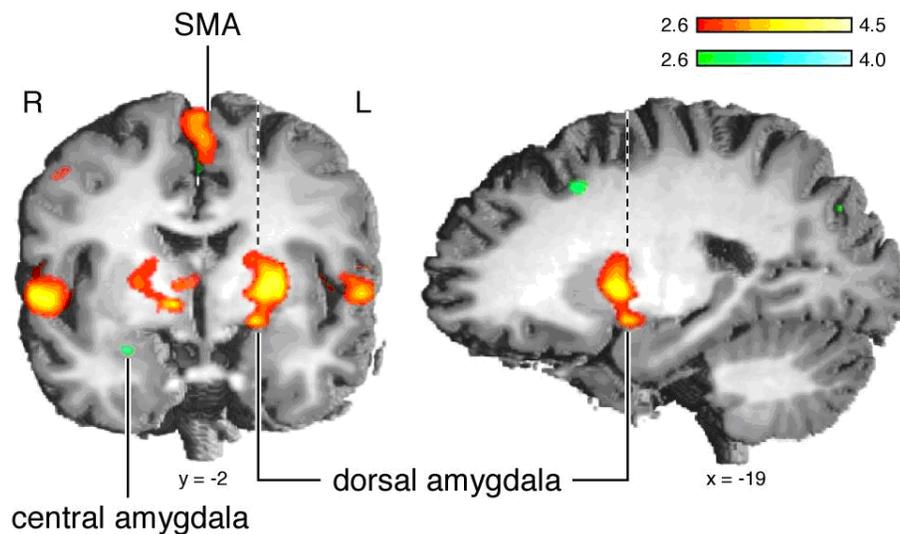


Figure 14. Depiction of parametric analysis with BOLD response correlating with increasing pleasantness in red and BOLD response correlating with increasing unpleasantness in green, threshold for depicted z-values is $p < 0.005$.

Functional imaging data, functional connectivity analysis: A functional connectivity analysis with seed voxels in the dorsal and central aspects of the amygdala revealed two networks displaying BOLD synchronies with the respective amygdala regions (Figures 15, 16; see also Table in *Appendix B Supplementary Tables, Table 7*).

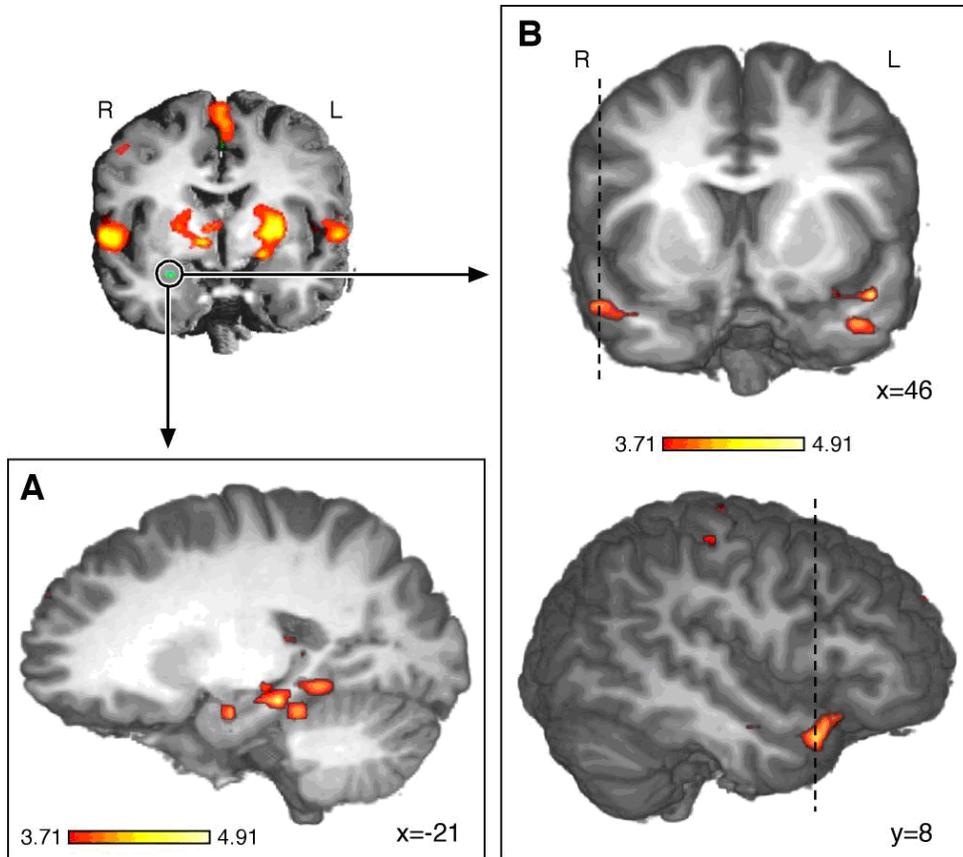


Figure 15. Network synchronous with BOLD response in central amygdala (see also corresponding table in Appendix B Supplementary Tables, Table 7).

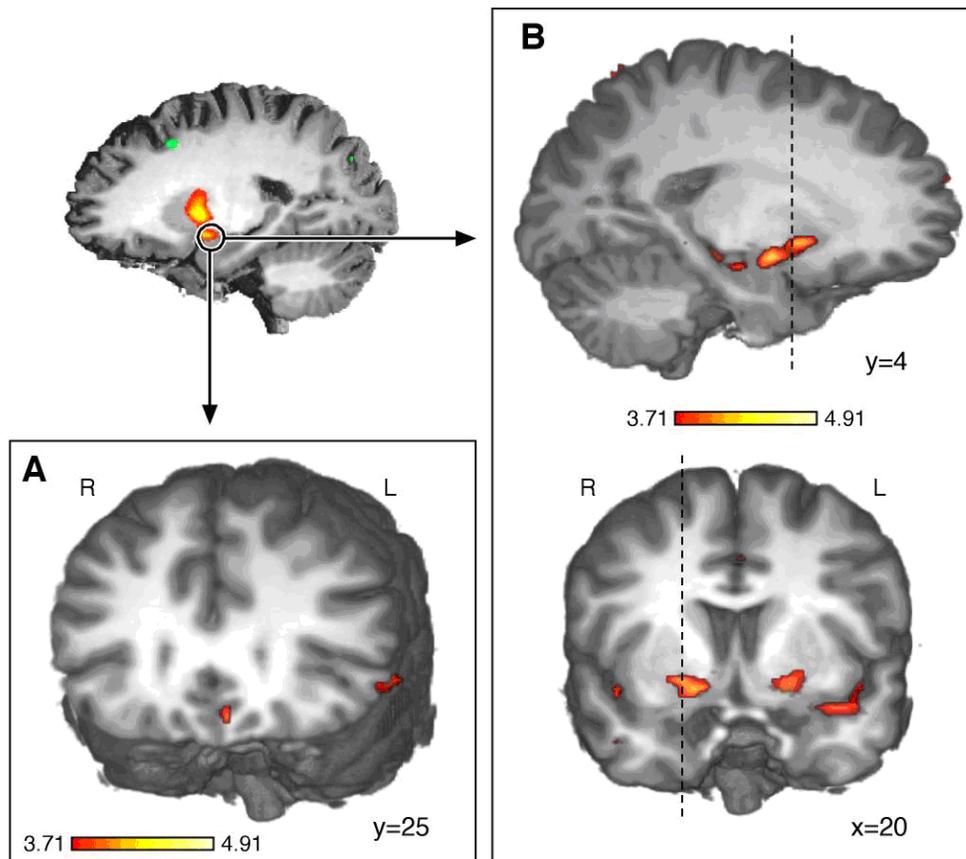


Figure 16. Network synchronous with BOLD response in dorsal amygdala / substantia innominata (see also corresponding table in Appendix B Supplementary Tables, Table 7).

4.1.3.3 Functional imaging data, separate parametric analyses for independent positive and negative valence dimensions

These analyses were conducted to include the possibility that separate brain regions may be relevant to the processing of either only pleasantness or only unpleasantness (Lewis et al., 2007). Note that an involvement of some of these areas may not have become evident in the parametric analysis in *Chapter 4.1.3.1* where a bipolar valence continuum from unpleasantness to pleasantness was assumed (see discussion).

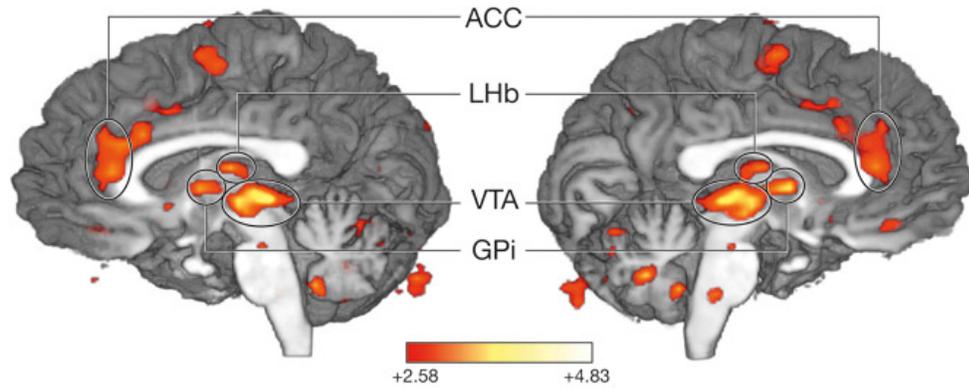


Figure 17. The figure shows results from a separate parametric analyses for an independent positive valence dimension for increasing pleasantness (depicted for $p < 0.005$), indicating that well-known components of the dopaminergic system were involved.

Tables showing brain regions responding to increasing and decreasing valence for independent positive and negative valence dimensions are depicted in *Appendix B, Supplementary Tables, Tables 11 and 12.*

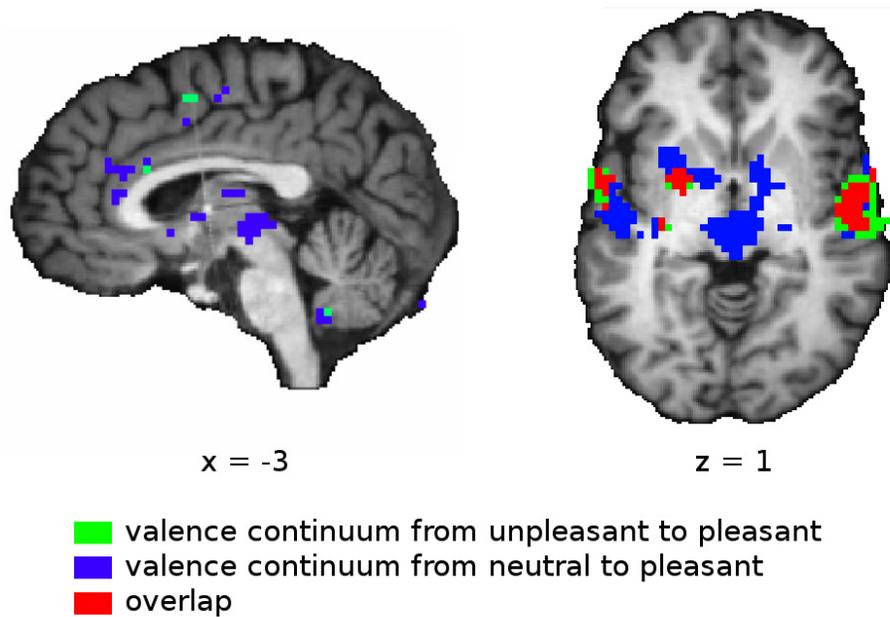


Figure 18. This figure shows the depiction of a conjunction analysis comprising the results for increasing pleasantness across the whole valence spectrum from unpleasantness to pleasantness (in green), from neutral to pleasantness (in blue), and overlapping activations (in red), illustrating that the dopaminergic system is only observed when an independent positive valence dimension is analyzed separately.

4.1.4 Discussion

The interpretation of fMRI-activations within the amygdala is challenging due to a number of difficulties and pitfalls: first, the amygdala complex appears as a mostly homogenous mass with ill-defined borders on anatomical MR images, leaving its microscopic divisions indiscernible. The same holds true for functional data, with the consequence that a single voxel is often too large to be assigned to a specific amygdaloid subregion.

Furthermore, it is still a matter of intense research to disentangle the projections

to and from discrete amygdaloid nuclei and their subdivisions and integrate these into a functional framework.

Bearing these caveats in mind, the exploration of amygdala subregions and their functional significance in humans nonetheless is a highly relevant issue indispensable for a comprehensive understanding of brain function, emotion in particular.

The present data demonstrate for the first time distinct roles for dorsal and central aspects of the amygdala in governing the response to music stimuli with positive and negative valence. This indicates that the amygdala's role in emotion processing is not confined to negative emotions, as still widely believed. Instead, different subregions of the amygdala respond to opposites in the valence dimension.

Valence specific amygdala subregions and their functional connectivities.

The parametric analysis yields an activation in a central to lateral aspect of the right amygdala (22 -3 -15) for increasing unpleasantness, a region mainly comprised by the lateral and basal nuclei (Mai, Assheuer, & Paxinos, 2004). The lateral nucleus is the amygdaloid nucleus known to have the most widespread connections with sensory related cortical areas, while the basal nucleus is the main amygdaloid relay for frontomedian structures (McDonald, 1998).

Functional connectivity analysis with the supposed basolateral complex revealed BOLD-synchrony in a number of regions previously implicated in the processing of negative valence, including the parahippocampal gyrus (Blood et al., 1999; Koelsch et al., 2006), the hippocampus (Campeau et al., 1997; Koelsch et al., 2006; Lopez, Akil, & Watson, 1999), and the temporal poles (Koelsch et al., 2006; Zald & Pardo, 2002), and additionally subcortical structures including the bilateral posterodorsal thalamus (supposedly pulvinar), the contralateral medial geniculate body and the inferior colliculus. These regions have been shown to monosynaptically connect with the basolateral

complex in different mammal species (Amaral & Price, 1984; Pitkänen, 2000) .

Interestingly, the correlation analysis revealed a coupling with activation in the ipsilateral central sulcus adjacent to the omega-shaped knob. This region corresponds to sensory motor hand representations. Because the participants' contralateral (left) hand remained still during the experiment but held the panic alarm button, it might show a certain readiness to abort the experiment during unpleasant passages.

In the parametric analysis, increasing stimulus pleasantness revealed a quite distinct pattern of amygdala activation and functional connectivity. The peak of the amygdaloid BOLD-signal lies dorsally in the left amygdala complex (-20 -3 -6), and spreads to lateral basal forebrain regions referred to as the *substantia innominata*. Both are commonly embraced in the concept of the extended amygdala and brought into close functional and structural relationship with the ventral striatum which is thought to play a major role in reward appraisal (Heimer, 2003). The central and medial nuclei are most prominent in this amygdala subregion.

The functional connectivity analysis shows strong co-activation in the right-hemisphere equivalent (dorsal/extended amygdala). Pronounced coupling with the ventral striatum, which has previously been implicated in positive emotion processing (Blood & Zatorre, 2001; Brown et al., 2004; Delgado, Nystrom, Fissell, Noll, & Fiez, 2000; Koelsch et al., 2006), as well as discrete pre-commissural activation that could be assigned to the nuclei of the *stria terminalis* or the *septum* are in line with the concept of the extended amygdala anatomy and function (Heimer, 2003).

Furthermore, BOLD-synchrony can be observed in other regions previously implicated in the processing of positive valence, as the prefrontal ventral and orbitofrontal cortex (BA10, BA11/12) (Blood & Zatorre, 2001; Nitschke et al., 2004; Rolls, 2004), and additionally subcortical structures including the

ipsilateral anteromedial (“limbic”) thalamus and medial geniculate body and the contralateral substantia nigra. All these regions have been shown to receive projections from the centromedial nuclei in a variety of mammal species (Amaral & Price, 1984; Pitkänen, 2000).

Other valence specific network components. The parametric analysis revealed a network that comprised several other components besides the amygdala regions described. The correlation of BOLD-response with increasing stimulus pleasantness underpins a previously postulated role for the orbitofrontal cortex in emotional processing. BOLD-data of orbitofrontal areas are difficult to acquire due to susceptibility artifacts from the frontal and ethmoidal sinuses, and the present finding is the first to report orbitofrontal activity in response to music in an fMRI study. The orbitofrontal cortex is known to be involved in emotional processing in all modalities (Rolls, 2004), and its lesion can result in impaired recognition of emotions from the face and voice (Hornak, Rolls, & Wade, 1996). It has previously been shown to be involved in the processing of stimuli with positive valence, such as pleasant music (Blood & Zatorre, 2001), and mothers viewing pictures of their newborn infants (Nitschke et al., 2004).

Interestingly, the present data demonstrate a correlation of activity in the supplementary motor area (SMA) with increasing pleasantness of the music. Previous evidence indicates that music listening engages processes in premotor areas that mediate between sound perception and movement production (Koelsch et al., 2006). Note that premotor (including supplementary motor) areas could not be fully investigated in the experiment previously conducted by Koelsch et al. (2006), as this study mainly focused on obtaining data from subcortical regions, measuring only 9 slices. The supplementary motor cortex has been suggested to participate both in movement generation and perception of similar movements (Iwase et al., 2002), and its electrical stimulation can produce laughter accompanied by a feeling of mirth (Fried et al., 1998). Accordingly, the present finding suggests that the SMA may be involved either

in decoding the pleasant music in terms of ones own movement repertoire, or mediating an inclination to move along to the pleasant music, or both.

Conclusions on the role of the amygdala in valence processing. The amygdala's highly complex anatomy has so far hampered a differentiated research on amygdaloid subdivisions, so that for a long time it was treated as a functional unit. Only recently methodological advances permitted a more detailed analysis of its segregation, regarding both anatomy and function. Our data underline an involvement of the amygdala in the processing of both positive and negative valence. In contrast to previous results (Liberzon et al., 2003), however, the present data demonstrate distinct roles for dorsal and central aspects of the amygdala in the response to music stimuli with positive and negative valence. The current design, which was optimized for the examination of amygdala behavior with music, has proven effective for the investigation of a neural correlate of an initial emotional response, and is a good example of how music research can be integrated in medical science. We hope that the approach taken in the present study may help to resolve the multifaceted role that the amygdala plays in emotional processing. In future research it could be applied to investigate disturbed amygdala functionality in psychiatric disorders involving emotional dysregulation including major depression and schizophrenia.

Investigation of the dopamine system with music. It has been debated whether displeasure and pleasure should be regarded only as the poles of a continuous scale, or whether they should rather be understood as two distinctive emotional dimensions corresponding to two separate neural systems (Lewis et al., 2007) (see *Chapter 1.1.4 Dimensions*). To explore the possibility that at least some brain regions may be exclusively relevant for the processing of either pleasantness or unpleasantness, two further parametric analyses were conducted separating positive and negative valence. In this analysis the individual valence ratings were separated into positive and negative appraisals, which were then included as covariates in the two analyses. Importantly, for an independent

Dopamine is produced almost exclusively in the ventral tegmental area (VTA) and the pars compacta of the substantia nigra (SN). As seen in Figure 19, the dopaminergic network can be understood as an open loop in which the VTA projects strongly to the lateral habenula nucleus of the epithalamus (LHb). The lateral habenular nucleus sends inhibitory projections to the VTA, thereby providing an inhibitory feedback mechanism controlling dopamine release. Additional excitatory input to the LHb is provided by the prefrontal cortex, especially the anterior cingulate cortex (areas 32, 24) (Chiba, Kayahara, & Nakano, 2001; Parent, Gravel, & Boucher, 1981). In our parametric analysis from neutral to pleasant, we can observe all of these components engaged for increasing pleasantness underlining their pivotal role in the processing of pleasure.

Other projections originating in the VTA, and in a much higher degree in the SN, have an excitatory effect on the nucleus accumbens (NAcc), which itself send inhibitory GABAergic fibers to the internal globus pallidus (GPi). Our results suggest that increasing pleasantness does not engage the SN in our paradigm and that subsequently, activation in the NAcc is low, which in turn leads to high activations in the GPi.

Figure 18 illustrates that the dopaminergic system was only observed in the separate analysis for an independent positive valence dimension from neutral to pleasantness, but failed to reach significance when data covering the full valence continuum from unpleasantness to pleasantness were analyzed. This observation suggests that the dopaminergic system does not respond linearly to the whole valence spectrum, but is engaged only for positive valence. This clearly underscores the necessity to analyse positive valence as a separate emotional dimension. However, activity in other brain areas such as the amygdala was observed more prominently in the analysis of the whole valence dimension ranging from unpleasantness to pleasantness, indicating, that these structures appear to be sensitive to valence alterations in the whole valence dimension.

4.2 Opening up to consonance – An amplification mechanism in the auditory pathway dependent on harmonic roughness

4.2.1 Introduction

A stronger engagement of auditory cortices with increasing valence was observable in the results above and is also observable in the contrast consonant music > dissonant music as depicted below.

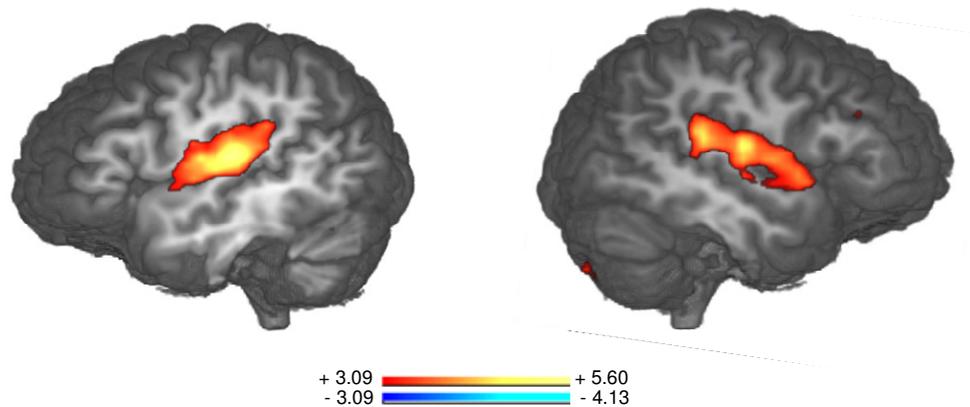


Figure 20. Depiction of consonant spectrum > dissonant spectrum. The contrast shows a stronger engagement of the auditory cortices during consonant spectrum in both hemispheres (depicted at $p < 0.001$).

Previous work has demonstrated a similarly enhanced engagement of the auditory cortex (as measured by the BOLD response) with increasing stimulus consonance, which is not easily explainable in terms of physical differences between stimuli, such as amplitude of the acoustic signal, or amount of information contained in the stimulus (Koelsch et al., 2006). This phenomenon has been attributed to top-down attentional processes (Jäncke et al., 1999; Koelsch et al., 2006), whose modes of operation however, are unclear. In this

investigation, the data acquired for the investigation of the neural correlates of the valence dimension (*Chapter 4.1*) was reanalysed, with the aim to gain a better understanding of the mechanisms that modulate auditory perception from the earliest stages of processing.

4.2.2 Methods

4.2.2.1 Participants, stimuli, procedure, image acquisition

The same data as processed in the above analysis (*Chapter 4.1.2.5*) was reanalyzed to investigate the regulation of information flow along the auditory pathway into the auditory cortex. Therefore the participants, stimuli, procedure, and image acquisition are identical with the respective sections described above (*Chapter 4.1.2 Methods*).

4.2.2.2 Data-Analysis

Applying a Psychophysiological Interaction Analysis (PPI), we examined the functional connectivity (Friston et al., 1996) of several levels of the auditory pathway and the amygdala dependent on the roughness/dissonance of the processed signals (Josephs et al., 1997). BOLD time courses of seed voxels bilaterally in the inferior colliculus and the medial geniculate body were investigated (Figure 21).

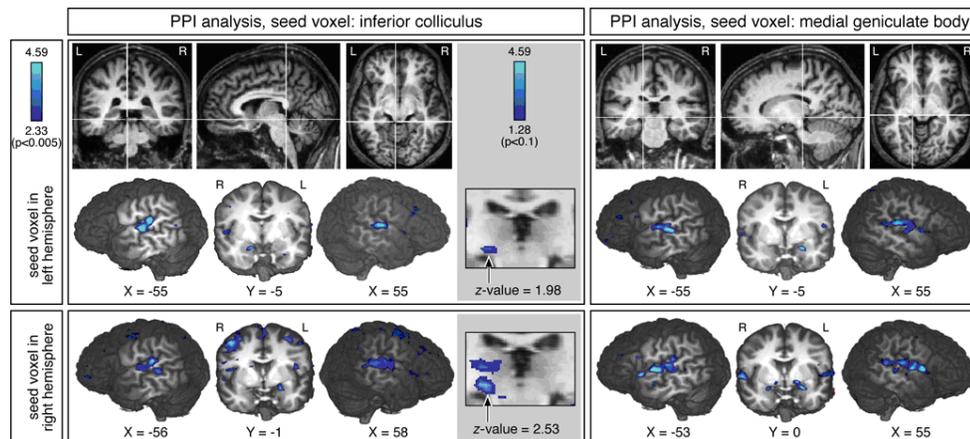


Figure 21. Patterns of functional connectivity (BOLD synchrony) that occur selectively during dissonant music with seed voxels in the left and right IC and medial geniculate body. BOLD synchrony with the IC-seed voxels also occurred the medial geniculate body (gray column), which is the main anatomical relay station to the primary auditory cortex (this is depicted at a lower threshold).

4.2.3 Results

The present data reveals that the functional connectivity between several levels of the auditory pathway (inferior colliculus, medial geniculate, primary auditory cortex) and the amygdala is dependent on the spectral order of the acoustic (music) signal: It was significantly higher during dissonant music pieces than during those with the original (consonant) spectrum (irrespective if presented forwards or backwards).

[mm] ³	max z-value	location	
Seedvoxel: left inferior colliculus			
2025	-4,06	L (-44 -26 15)	Heschl's gyrus (BA 41/42)
135	-3,77	L (-5 -50 24)	posterior cingulate cortex (BA 23)
486	-3,97	R (55 -20 9)	Heschl's gyrus (BA 41/42)

108	-3,45	R (46 19 21)	inferior frontal sulcus (BA 46)
81	-3,67	R (13 -5 -15)	amygdala
81	-3,32	R (46 4 3)	pars opercularis of inferior frontal gyrus (BA 44)
Seedvoxel: right inferior colliculus			
540	-3,9	L (-59 -29 18)	Heschl's gyrus (BA 41/42)
216	-3,96	L (-26 19 -6)	inferior anterior insula
216	-3,59	L (-65 -35 6)	posterior superior temporal sulcus (BA 22)
189	-4,01	L (-47 -5 45)	precentral gyrus (BA 6)
189	-3,38	L (-8 -26 -30)	inferior bridge
162	-3,45	L (-29 -2 54)	superior frontal sulcus (BA 8)
162	-3,22	L (-32 -23 15)	Heschl's gyrus (BA 41/42)
135	-3,81	L (-29 28 6)	anterior insula
108	-4,05	L (-26 4 -9)	amygdala
81	-3,3	L (-23 25 45)	superior frontal sulcus (BA 8)
81	-3,3	L (-23 -65 -21)	cerebellar hemisphere
81	-3,45	L (-35 -29 51)	postcentral gyrus (BA 2)
81	-3,48	L (-35 -65 51)	angular gyrus (BA 39)
1674	-4,59	R (40 -8 51)	precentral gyrus (BA 6)
864	-4,36	R (7 -53 9)	isthmus of the posterior cingulate (BA 23)
486	-4,29	R (-2 -47 27)	posterior cingulate cortex (BA 23)
324	-3,39	R (10 -83 12)	calcarine sulcus (BA 17)
324	-3,68	R (4 40 -12)	rostral sulcus (BA 12)
243	-3,42	R (58 -32 9)	posterior superior temporal gyrus (BA 22)
162	-3,71	R (28 25 -6)	H-shaped orbitofrontal sulcus (BA 25)
162	-3,45	R (34 -56 51)	intraparietal sulcus (BA 39)
162	-3,33	R (58 -23 9)	Heschl's gyrus (BA 41/42)
135	-3,68	R (1 49 36)	superior frontal gyrus (BA 9)
135	-3,38	R (40 13 24)	inferior frontal sulcus (BA 45)
135	-3,42	R (7 19 39)	cingulate sulcus (BA 24)
108	-3,71	R (1 58 -6)	frontopolar cortex (BA 10)
108	-3,49	R (13 43 12)	medial prefrontal cortex (BA 32)
81	-3,39	R (1 -50 45)	precuneus (BA 31)
81	-3,58	R (43 -2 12)	frontal operculum (BA 44)

81	-3,35	R (49 -8 3)	Heschl's gyrus (BA 41/42)
Seedvoxel: left medial geniculate body			
459	-3,87	L (-65 -35 9)	superior temporal sulcus (BA 22)
216	-4,33	L (-23 22 -3)	anterior insula
216	-4,05	L (-38 43 -9)	lateral orbital gyrus (BA 11)
108	-3,99	L (-23 -2 -12)	amygdala
108	-3,2	L (-47 -23 12)	Heschl's gyrus
459	-3,31	R (49 -26 9)	Heschl's gyrus
135	-3,96	R (43 -14 -12)	superior temporal sulcus (BA 22)
108	-3,63	R (28 25 3)	anterior insula
81	-3,39	R (34 -62 51)	angular gyrus (BA 39)
Seedvoxel: right medial geniculate body			
162	-3,84	L (-26 19 -12)	posterior orbital gyrus (BA 25)
135	-3,4	L (-56 -5 6)	superior temporal gyrus (BA 22)
108	-3,35	L (-23 -2 -12)	amygdala
243	-3,45	R (58 4 3)	frontal operculum (BA 44)
135	-3,55	R (28 34 -12)	H-shaped orbitofrontal sulcus (BA 11)
135	-3,36	R (55 -8 3)	superior temporal gyrus (BA 22)
108	-3,55	R (1 40 -9)	inferior rostral gyrus (BA 12)
81	-3,34	R (-2 28 -12)	rostral sulcus (BA 12)
81	-3,34	R (43 -38 6)	superior temporal sulcus (BA 21)

Table 4. Results from the PPI analysis

That is, if during dissonant music the BOLD response in the auditory cortex increases, so does the BOLD response in the inferior colliculus, the medial geniculate, and the amygdala. Such response synchrony more strongly occurred during stimuli with dissonant spectra than during consonant music.

4.2.4 Discussion

It has previously been shown that the processing of consonant music excerpts elicits stronger engagement of the auditory cortices (in terms of BOLD response) than the processing of their dissonant counterparts (Koelsch et al., 2006). The present data implies that this difference is due to active down regulation of auditory cortex activity during the perception of dissonance by lower-level structures within the auditory pathway, as well as the amygdala.

The involvement of the inferior colliculus at a very early stage of the auditory perceptual cascade is in line with previous evidence indicating its crucial role in the processing of roughness in several mammal species (Ehret & Schreiner, 2005; Firzlaff, Schornich, Hoffmann, Schuller, & Wiegrebe, 2006; Greenwood, 1990; Schreiner & Langner, 1997), including humans (McKinney, Tramo, & Gelgutte, 2001).

The percept of consonance and dissonance is thus intimately intertwined with a hardwired perceptual gating mechanism that is sensitive to the spectral order of the auditory signal in Western adults. Cross-cultural comparisons as outlined below indicate that the percept of consonance and dissonance is at least to some extent universal. The mechanism described at present may reflect its neural substrate.

Chapter 5

Experiment 2

Is the neurology of aversive response to violations of expectancy in chord progressions a matter of expertise?

5.1 Introduction

A number of previous functional neuroimaging studies on the processing of musical syntax used chord sequences containing chords that were harmonically either regular or irregular (Koelsch et al., 2005; Koelsch et al., 2002; Maess et al., 2001; Tillmann, Janata, & Bharucha, 2003; Tillmann et al., 2006). These studies consistently showed involvement of inferior fronto-lateral (sometimes along with anterior superior temporal) cortex (for an overview see Koelsch, 2005). However, as outlined in *Chapter 2.4 From structure building to valence percept* there is now mounting evidence that irregular musical events (such as music-syntactically irregular chords) do not only engage neural mechanisms underlying the processing of music-syntactic information, but that such chords also give rise to emotional responses.

Based on the mentioned findings, I re-analyzed a set of fMRI data that we had originally recorded to investigate music-syntactic processing with chord sequences ending on either regular or highly irregular chords (Koelsch et al.,

2005).

Whereas in that previous study a statistical threshold including FDR correction and a spatial threshold of ten voxels was applied, we tested in the present analysis the directed hypothesis that unexpected (harmonically irregular) compared to expected chords elicit activity in the amygdala, a key structure for emotional processing with regards to the generation, initiation, and termination of emotions (Baxter & Murray, 2002; Davis & Whalen, 2001; Koelsch et al., in press; Phelps, 2006; Zald, 2003). To test this directed hypothesis, a lower statistical threshold of $p < 0.05$ (uncorrected) was applied.

Moreover, we collected behavioural data from both a group of non-musicians and a group of musicians about the perceived emotional valence of regular and irregular chord sequence endings. Musicians due to their profession-specific cultural exposure to music are more familiar with irregular chord progressions as used in the present paradigm than non-musicians. Because repeated exposure to a stimulus increases the positive affect or reduces the negative affect toward the stimulus (Harmon-Jones & Allen, 2001; Zajonc, 1968), we hypothesized that non-musicians rate the irregular chord progressions as more unpleasant than musicians and that correspondingly activations within the amygdala would be stronger in non-musicians.

5.2 Methods

5.2.1 Behavioral study

5.2.1.1 Participants

Two groups of subjects were analyzed: (a) non-musicians ($n=11$; 5 females; age range 20-31 years; $M = 24.8$ years), none of them had any formal musical training (except normal school education), and none of them played a musical instrument, and (b) musicians ($n = 12$; 6 females; age range 21-32 years, $M =$

25.3 years), who had learned an instrument for 9 - 19 years ($M = 16$ years). All subjects were right-handed and reported to have normal hearing.

5.2.1.2 Stimuli and Procedure

Both stimuli and procedure were identical to the fMRI experiment as described below in *Chapter 5.2.2.2* and *5.2.2.3*, except that the task was to rate the emotional valence (pleasantness/unpleasantness) of the final chord of each chord sequence on a scale from 1 (very unpleasant) to 10 (very pleasant) by pressing response buttons. All participants were instructed not to pay attention to how “good” or “bad” the chords fitted in to the chord sequence, but only to assess their valence percept. After the rating, a post-experimental interview was performed with each participant about their experience of the experiment, especially with respect to the sometimes “musically dissonant” chords at the end of the sequences.

5.2.2 FMRI study

5.2.2.1 Participants

Two groups of subjects were investigated. Each group consisted of 10 participants (5 males and 5 females): (a) nonmusicians (age range 20–36 years, mean 25.6 years), none of them had any formal musical training (except normal school education), and none of them played a musical instrument; (b) musicians (age range 21–34 years, mean 26.8 years), who had learned an instrument for 4–18 years (mean: 9.4 years). All subjects were right-handed and reported to have normal hearing.

5.2.2.2 Stimuli

Seventy-two different chord sequences were used, each sequence consisting of five chords. There were two types of sequences: Sequences consisting of regular

chords only, and sequences ending on an irregular Neapolitan sixth chord (Figure 22). Chord sequences were presented with different melodic outlines (e.g., starting with the third, the fifth, or the octave in the top voice). Presentation time of chords 1–4 was 666.7 ms, chord 5 had a duration of 1333.2 ms (resulting in a duration of 4000 ms per chord sequence).

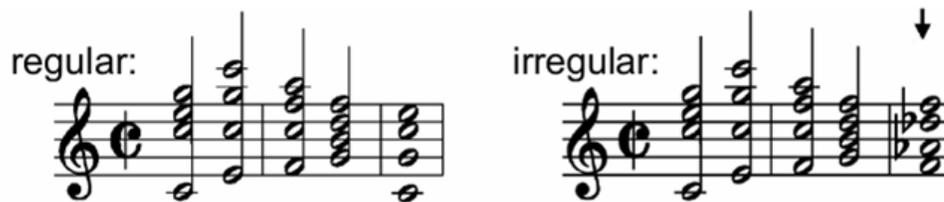


Figure 22, the arrow indicates an 'irregular' Neapolitan sixth chord.

Chords were presented using a ROLAND JV 1010 synthesizer (Roland Corporation, Hamamatsu, Japan) with a piano timbre (General MIDI #1). The musical stimulus was played with approximately 75 dB SPL using headphones with piezo-electric transmission.

5.2.2.3 Procedure

Each subject performed two runs in direct succession. For each run, 32 mini-blocks were constructed, each mini-block consisting of three sequences, resulting in a total number of 96 sequences per run. There were two types of mini-blocks: (a) mini-blocks consisting of regular sequences, and (b) mini-blocks in which sequences ended on irregular (Neapolitan) chords. 22 mini-blocks of type a and 10 mini-blocks of type b were presented in each run (that is, in each run 66 sequences ended on a tonic, and 30 sequences on a Neapolitan chord, resulting in a probability for Neapolitans of about 30%).

Both types of mini-blocks were randomly intermixed so that up to three mini-blocks of type (a) were presented before the presentation of a mini-block of type

(b). A key shift of one semitone upwards was used recurrently to prevent the musical stimulus from becoming monotonous. No key shift occurred in type b sequences. Subjects were asked to press a button on the last chord of each sequence: one button for the regular sequence ending (tonic chord) using the index finger, and another button for the irregular ending (Neapolitan chord) using the middle finger of the same hand.

5.2.2.4 Image acquisition

Functional magnetic resonance imaging (fMRI) was performed on a GE 3-T MR scanner. To minimize interferences with the MR scanner noise as well as auditory masking effects, fMRI data were acquired with an effective repetition time (TR) of 6 s using a clustered volume acquisition lasting 1.75 s. A high resolution T1 weighted scan (1 x 1 x 1.5 mm voxel size) was acquired for each subject for anatomical co-registration prior to the functional imaging experiment.

5.2.2.5 FMRI Data-Analysis

FMRI data were analyzed using the SPM99 software package (Institute of Neurology, London, UK). After realignment, co-registration, normalization, and smoothing (8 mm FWHM), condition and subject effects were estimated using a general linear model. The effects of global differences in scan intensity were removed by scaling each scan in proportion to its global intensity. Data were convolved with the hemodynamic response function (hrf), low frequency drifts were removed using a temporal high-pass filter with a cut-off of 108 s. In addition, a low-pass filter was applied. A block design analysis was used (fixed effects) to contrast the experimental condition irregular (Neapolitan chord at the end of the chord sequence) with the control condition regular (tonic chord at the end of the chord sequence).

5.3 Results

5.3.1 Behavioral Data

Means of grand-averaged valence ratings for both groups (pooled data) were 7.2 ($SD = 1.1$) for the regular and 3.4 ($SD = 1.2$) for the irregular chord sequence endings (on a scale from 1 to 10 with most unpleasant indicated by 1 and most pleasant indicated by 10). An ANOVA with factors chord (regular, irregular) and group showed an effect of chord ($F(1,20) = 147.9, p < .0001$, indicating that regular chords were perceived as more pleasant than irregular chords), but no interaction between factors ($p = .93$, indicating that the difference in valence ratings between regular and irregular chords did not differ between groups). However, the data indicated that as hypothesized the non-musicians tended to assess the unexpected Neapolitan chords as more unpleasant, than the musicians ($p < 0.05$, one-sided t-test). In the post-experimental interview, the non-musicians would typically categorize these chords as “peaking out” and “unpleasant”. The musicians, however, tended to categorize the violations more precisely, and sometimes even found the violations quite interesting. Here some examples of musicians’ statements: “I found some of the daring endings quite interesting”, “you can find an explanation for these chords”, “the dissonant chords were integrated into a system, either a Trugschluss, or Jazz - you can come up with a construction, so that it works”, “it depends on how the dissonances are derived if you perceive them as unpleasant”, “I found the late romantic resolutions to major quite a success”.

5.3.2 FMRI data

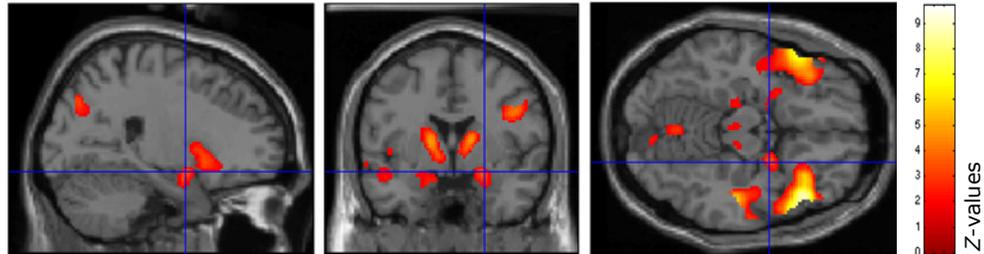


Figure 23. The figure shows the contrast unexpected chord sequence endings > expected chord sequence endings for all participants, depicted at a statistical threshold of $p < 0.005$, uncorrected.

Music-syntactically irregular chords elicited activity in the amygdala bilaterally. On the voxel level, a small volume correction (SVC) indicated that the activation of the left (Talairach coordinate: -16 -3 -18), as well as of the right amygdala (Talairach coordinate: 24 -1 -12) was significant (left: $p < 0.05$; right: $p < 0.05$, both values FWE corrected).

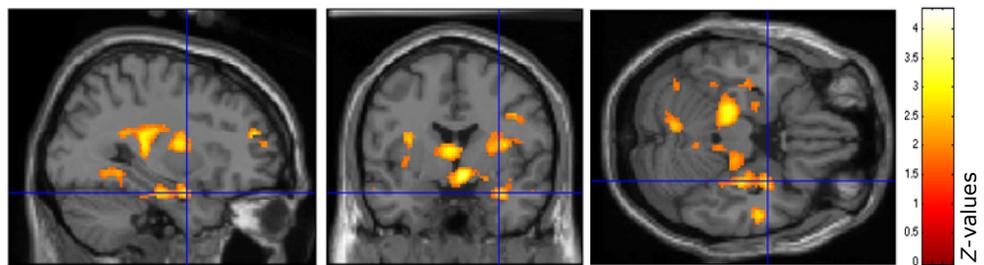


Figure 24. The figure shows the contrast non-musicians > musicians (for unexpected > expected chord progressions). This contrast reveals that the amygdala response in the participants to unexpected chords is largely driven by the response of the non-musicians. A small volume correction (SVC) indicated a significant ($p < 0.05$) engagement of the right amygdala.

Music-syntactically irregular chords elicited a stronger amygdala engagement in non-musicians. On the voxel level, a small volume correction (SVC) analysis showed that an activation in the amygdala of the right hemisphere located adjacent to the head of the hippocampus (Talairach coordinate: 32, 0, -22) was significant ($p < 0.05$, FWE corrected, search volume: sphere with radius 3 mm). No local maxima were observed within the amygdala on the left side.

5.4 Discussion

In the behavioural study, the irregular chords were judged as clearly more unpleasant than the regular chords, in both groups of subjects. The fMRI data showed that irregular chords elicited activity in the amygdala bilaterally. The finding that the activation of the amygdala was bilateral in the uncorrected SPMs, in addition to the significance indicated by the FWE-corrected SVC renders it unlikely that these amygdala activations were simply due to chance. Therefore, our data provide evidence for an involvement of the amygdala in the response to irregular chord progressions, presumably due to their unpleasantness. This finding corroborates Meyer's theory on music and emotion as outlined above, and fits nicely with previous functional imaging data on music-syntactic processing reporting activations of orbito-frontal cortex in response to irregular chords (Koelsch et al., 2005; Tillmann et al., 2006).

Previous studies have shown a decrease of rCBF in the amygdala in response to extremely pleasurable experiences during music listening (such as "chills" and "thrills" (Blood & Zatorre, 2001)), or an increase of BOLD signal in response to highly unpleasant (permanently strongly dissonant) music (Koelsch et al., 2006), or to fearful music paired with pictures (Baumgartner T, 2006) or film clips (Eldar et al., 2007). Our results show that simply a music-syntactic irregularity can elicit an amygdala response, providing further evidence for the strong impact of music on brain structures that are crucially involved in human

emotion. Notably, a Neapolitan chord itself is a consonant, “normal” chord - it is principally the music-syntactic relation (i.e., the harmonic relation) to the preceding chords of the sequence in which this chord sounds irregular and unexpected (at least for listeners familiar with major-minor tonal, i.e. “Western” music). Future neuroimaging studies on musical syntax processing should be aware that irregular chords may also elicit emotional responses, and thus ideally also assess the perceived valence of chords.

As hypothesized, the behavioural study showed that non-musicians rated the irregular chord endings as more unpleasant than musicians. Correspondingly in the fMRI data the contrast musicians > non-musicians (for unexpected > expected chords) revealed that the amygdala response to unexpected chords was more strongly driven by the amygdala response of the non-musicians. Music-syntactic expectancies are strongly dependent on the listeners exposure to rule-based stimulus material (Koelsch et al., 2002; Krumhansl, 1990; Krumhansl & Keil, 1982; Meyer, 1956; Tillmann, Bharucha, & Bigand, 2000). These findings can thus be explained by the higher exposure to music-syntactically rather unexpected chord progressions such as Neapolitan chords that musicians have, which may to them render the Neapolitan chord less unexpected than for non-musicians.

It has previously been shown that musicians more strongly involve cortical areas related to music-syntactic processing such as inferior frontal cortex in the response to music-syntactically unexpected chords (Koelsch et al., 2005). This suggests that a higher familiarity with irregular chord progressions leads to a lower involvement of the amygdala associated with less behavioural aversion but to a greater involvement of cortical areas specialized in (music-) syntactic processing.

Chapter 6

Experiments 3-4

Universal preference for consonance over dissonance and forward over backward in music

6.1 Introduction

The Mafa are one of approximately 250 ethnic groups which make up the population of Cameroon. They are located in the 'Extreme North', in the Mandara mountain range, which is culturally rather isolated due to a high regional density of endemic illnesses. Their traditional music culture is so unrelated to Western music culture that it was possible to address the investigation of music universalities by cross-cultural comparison of individuals who were thoroughly isolated from each other with respect to music culture.

Knowledge about musical regularities is largely implicit and shaped through sometimes unattended listening experience that we may not consciously recall (Tillmann et al., 2000). Therefore it was a necessity for this study that the Mafa participants were completely naïve to Western music. Western music culture mainly spreads with electricity supply (and thus the possibility to operate radios)

and Christianization (through Western Christian song). The more remote Mafa settlements do not have electrical supply, and are still inhabited by many individuals who pursue a traditional lifestyle and who have never been exposed to Western music.

Music appreciation can be addressed through an assessment of the valence percept experienced by the music listener, which is closely linked to emotional state ('core affect' (Russell, 2003)). As outlined in *Chapters 2.3 From feature extraction to valence percept* and in *Chapter 2.4 From structure building to valence percept* for Western listeners the valence dimension of a musical signal can be systematically and purposefully altered. This can be achieved by a distortion of its spectral order that is associated with the perceived harmonic order of a polyphonic sound (Ball et al., 2007; Blood et al., 1999; Koelsch et al., 2006; Sammler et al., 2007) and its temporal order (Menon & Levitin, 2005). Surprisingly, neither of these methods has yet been applied to investigate the universality of preference for consonance over dissonance or the universality of music played forward over music played backward in cross-cultural research with individuals thoroughly isolated from each other with respect to their music culture.

As argued above in *Chapter 2 From music perception to valence percept*, the most suitable means to examine music universals is cross-cultural research with participants that are naïve with regard to the respective other music culture. The present study employed a research paradigm designed to investigate the neural correlates of music appreciation and dislike (Koelsch et al., 2006; Sammler et al., 2007), and adapted it to the demands of a cross-cultural ethno-musicological investigation. We studied the universality of music appreciation of consonant vs. dissonant and forward vs. backward Western (Experiment 3) and Mafa (Experiment 4) music with listeners from both cultures.

6.2 Methods

6.2.1 Participants

22 Mafas participated in Experiment 3 with Western music (10 male; 35 to 75 years, $M = 58.0$ years), and 21 in Experiment 4 with Mafa music (12 male; 35 to 100 years, $M = 62.3$ years). The age of most Mafa participants had to be estimated because they do not have a concept of accumulated age. Only Mafas who had never before listened to radio, and had never been to or lived in the proximity of a church were accepted as participants for the experiments (see introduction). The Mafa do not have a concept of a professional musician, even though many dedicate time for musical activity on an everyday basis. Thus, Mafa participants could neither be categorized as musicians nor as nonmusicians. 20 Westerners participated in Experiments 3 and 4 (10 male; 40 to 68 years, $M = 52.9$ years). Criteria for the selection of Western listeners were that they were not familiar with African music and were aged between 40 and 70 years.

6.2.2 Stimuli

The stimulus material included Western music pieces (Experiment 3) and Mafa music recordings (Experiment 4), as well as their dissonant and reversed (played backwards) counterparts, so that four stimulus categories were included in both experiments: (1) original, (2) reversed original, (3) dissonant, (4) reversed dissonant.

The dissonant stimuli were created by rendering a multitrack arrangement, where three versions of the music excerpt, one in original pitch, one pitched a semitone higher, and one pitched a tritone lower (but all with the original tempo) played simultaneously. 14 Western and 10 Mafa music stimuli for each duration (2, 10, 30 sec.) were included for each condition. In total the Mafa

music experiment comprised 120 trials, and the Western music experiment 168 trials. Not more than two versions of the same stimulus category occurred in sequence and an equivalent number of stimuli from each category occurred in each third of the experiment. Stimuli and instructions were presented using Presentation software (version 0.70, www.neuro-bs.com) on a laptop (which was charged by a mobile solar electricity facility during the field study in Cameroon).

The instructions were presented in a standardised fashion in either German or Mafa (translated beforehand and recorded by a Mafa woman living in Europe) language. While auditory instructions were presented over headphones, the experimenter simultaneously demonstrated how to handle the interface. During the experiment only the participants could listen to the stimuli.

Western music pieces included excerpts from joyful instrumental dance music from the past four centuries (Johann Sebastian Bach – Badinerie, F. Canaro – La Punalada, P. F. Caroubel - Volte, Dvorak – Slavonic Dance No. 8 in G Minor (Op. 46), Glenn Gould – Das Wohltemperierte Klavier (nr. 5), Flook - Happy Jigs, Herb Alpert & The Tijuana Brass – Zorba the Greek, Gene Urupa - Jeepers Creepers, Riluiruairc - Leaba, J. Pastorius – Soul Intro “The Chicken”, Johann Sebastian Bach - Rejouissance, Santiago - Amarru, Shantel - Bucovina, The Ventures – Kicking Around; for more information see also Koelsch et al., 2006 and Sammler et al., 2007).

The Mafa flute music included in the experiments (Figures 25 and 26, for scores of the flute music used in the present experiment see *Appendix A Supplementary Figures*, Figure 34) plays a key role in the performance of a number of rituals. Its integrated and context dependent character in Mafa society is nicely illustrated by the observations that the Mafa do not have a word for music at all, and that music performers labelled music patterns by reference to the rituals where they were performed. To the naïve Western ear, Mafa flute music sounds bizarre.

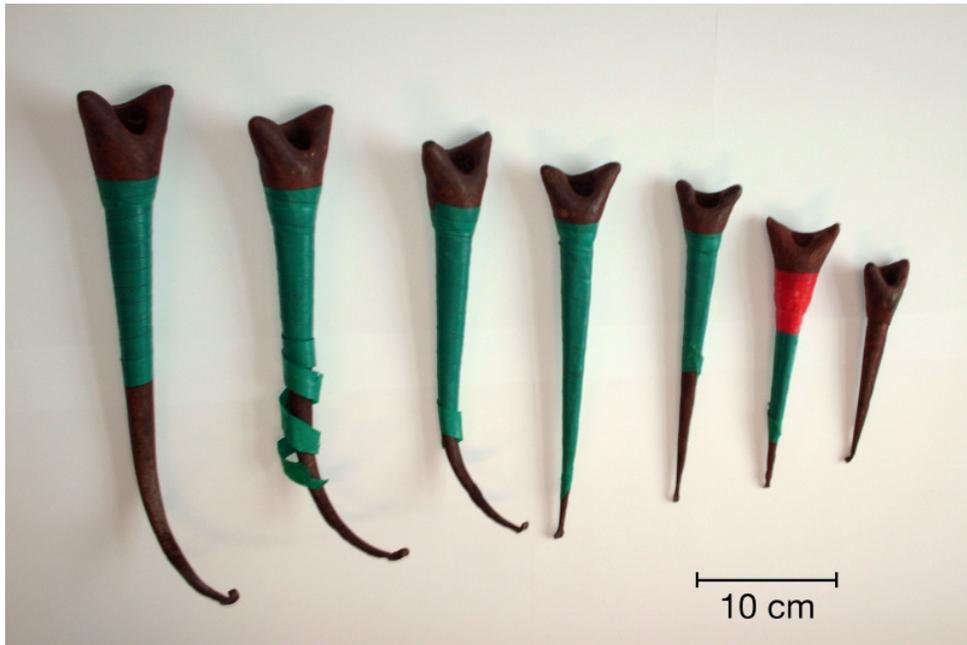


Figure 25. The mafa flutes consist of two functional components, a resonance body made out of forged iron and a mouth piece crafted with a mixture of clay and wax. The depicted set of mafa flutes is "refined" with rubber band.

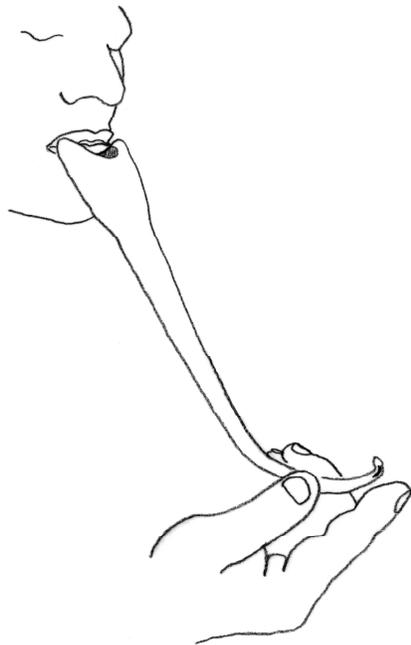


Figure 26. The mafa flutes that are manufactured from forged iron have a quite basic form, where the flute is an open tube which is blown like a bottle. At its bottom end is a small hole with which the tube can be controlled for opening and closure.

Scores of the recorded Mafa flute music that was used in Experiment 4 are depicted in *Appendix A Supplementary Figures*, Figure 34.

6.2.3 Procedure

Mafa and Western participants listened to the original (consonant) music stimuli and three categories of manipulated counterparts (reversed, dissonant, reversed dissonant) for different durations (2s, 10s, 30s). They were asked to indicate their appreciation/dislike of both Mafa and German music and the respective counterparts on a continuous scale with a slider interface.

In order to illustrate the extremes of the bipolar dimension in a universally comprehensible manner, we adapted the SAM (Self-Assessment-Manikin) that is meant to signify valence (from displeasure to pleasure), but in the original version (see *Chapter 1.1.4 dimensions*) rather characterizes a scale from unhappiness to happiness.

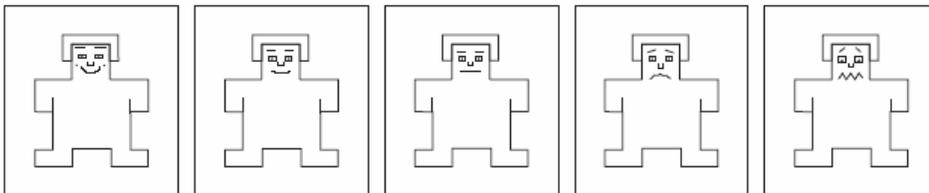


Figure 27. Adapted SAM (Self-Assessment-Manikin) for valence signifying the dimension from pleasure to displeasure.

Listeners assessed the valence (pleasantness/unpleasantness) of music excerpts with a slider interface, where both poles of the valence dimension were indicated by a Self-Assessment-Smile that was developed from the adapted SAM as depicted above because the body of the Self-Assessment-Manikin does not convey relevant information.



Figure 28. The figure shows the Self-Assessment-Smileys at the poles of the valence dimension as depicted to the left (unpleasant) and right (pleasant) of the slider.

These excerpts were either flute music recorded during Mafa rituals (see scores in *Appendix A Supplementary Figures*, Figure 34) or a variety of Western instrumental tunes from the past four centuries. As a control the participants were additionally asked to verbally express their judgement before pressing a button on the slider interface to confirm their rating. If the two responses (slider, articulation) did not match, the trial had to be repeated. 22 Mafa participated in Experiment 3, 21 Mafa participated in Experiment 4, and 20 Western listeners participated in Experiments 3 and 4. We compared consonant vs. dissonant (cacaphonic) versions of these music pieces which were played either in forward or reversed direction.

The experiment instructions were presented both to the participant and an experimenter (an assisting translator) over a system with two closed headphones. It could thus be ensured that the translator always exactly knew which experiment was currently conducted. During the presentation of the stimuli and during the rating the headphone of the experimenter was switched off to avoid him biasing the response of the participant.

6.2.4 Data-Analysis

For the statistical evaluation, the rating values for each participant were z -transformed, to eliminate individual assessment tendencies. With these values, four ANOVAs with the within-subject-factors *direction* (forward vs. reversed), *spectrum* (consonant vs. dissonant), and *length* (2, 10, and 30 sec) were computed for each subgroup and each musical culture separately (Table 5).

These four models were used, since the investigation of the subgroup specific responses to the music from both cultures were central to our focus of interest. Furthermore, we observed interactions for *direction* \times *subgroup* as well as for *spectrum* \times *subgroup* for both, Western and Mafa music (see *Appendix B Supplementary Tables*, Table 9 (z -transformed values) and Table 10 (non-transformed values)). In the mixed-model ANOVAs used in these analyses, *direction* (forward vs. reversed), *spectrum* (consonant vs. dissonant), and *length* (2, 10, and 30 sec) served as within-subject-, and *subgroup* (Western vs. Mafa listeners) as between-subjects-factor. Since not all Mafa participants took part in both Experiment 3 and 4, we had to compute two separate ANOVAs for Western and Mafa music respectively. These ANOVAs were computed for the z -transformed (*Appendix B Supplementary Tables*, Table 9) as well as for the non-transformed values (*Appendix B Supplementary Tables*, Table 10). The latter analysis was necessary, since the main effect of subgroup could not be evaluated for the z -transformed values (where the mean within each subject was zero, resulting in a mean of zero in the two subgroups). A significant main effect of *subgroup* was revealed in both ANOVAs (with the non-transformed values), for Western as well as for Mafa music. Apart from these differences, the ANOVAs (for z -transformed and non-transformed values) revealed relatively similar results.

6.3 Results

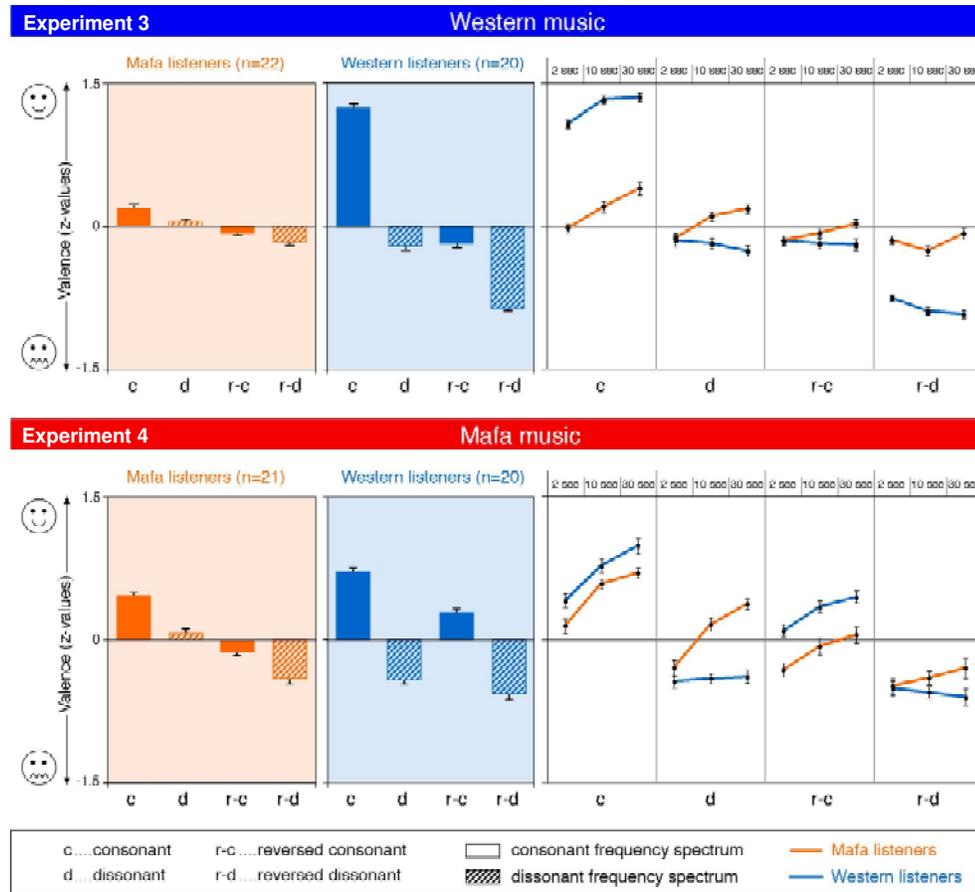


Figure 29. The figure shows z-values of the ratings for Experiment 3 and 4. Mean values are depicted for each entire stimulus category (c, d, r-c, r-d), and each stimulus duration (2, 10, 30 sec) respectively. Error bars indicate SEM (for values see corresponding Table in additional online material).

The results of the music appreciation rating (Figure 29) with non-transformed values are depicted in *Appendix A Supplementary Figures* (Figure 35). A table showing the z-values depicted in Figure 29 is shown in *Appendix B Supplementary Tables* (Table 8).

	Mafa listeners				Western listeners			
	Mafa music		Western music		Mafa music		Western music	
direction	$F_{(1,20)} = 82.28$	$p < 0.001$	$F_{(1,21)} = 19.32$	$p < 0.001$	$F_{(1,19)} = 48.93$	$p < 0.001$	$F_{(1,19)} = 313.85$	$p < 0.001$
spectrum	$F_{(1,20)} = 44.94$	$p < 0.001$	$F_{(1,21)} = 6.14$	$p = 0.022$	$F_{(1,19)} = 141.65$	$p < 0.001$	$F_{(1,19)} = 322.01$	$p < 0.001$
length	$F_{(2,19)} = 12.37$	$p < 0.001$	$F_{(2,20)} = 6.48$	$p = 0.007$	$F_{(2,18)} = 8.17$	$p = 0.003$	$F_{(2,18)} = 0.47$	$p = 0.633$
direction × spectrum	$F_{(1,20)} = 0.96$	$p = 0.339$	$F_{(1,21)} = 0.06$	$p = 0.806$	$F_{(1,19)} = 29.76$	$p < 0.001$	$F_{(1,19)} = 44.27$	$p < 0.001$
direction × length	$F_{(2,19)} = 4.23$	$p = 0.030$	$F_{(2,20)} = 5.65$	$p = 0.011$	$F_{(2,18)} = 4.44$	$p = 0.027$	$F_{(2,18)} = 11.79$	$p = 0.001$
spectrum × length	$F_{(2,19)} = 0.28$	$p = 0.757$	$F_{(2,20)} = 2.84$	$p = 0.082$	$F_{(2,18)} = 16.12$	$p < 0.001$	$F_{(2,18)} = 10.27$	$p = 0.001$
direction × spectrum × length	$F_{(2,19)} = 0.92$	$p = 0.417$	$F_{(2,20)} = 0.80$	$p = 0.461$	$F_{(2,18)} = 0.06$	$p = 0.941$	$F_{(2,18)} = 3.17$	$p = 0.066$

Table 5. ANOVAs with the within-subject factors direction (forward vs. reversed), spectrum (consonant vs. dissonant) and length (2, 10, and 30 sec) that were computed separately for each subgroup and each musical culture; standardized values, significant main effects are printed in black.

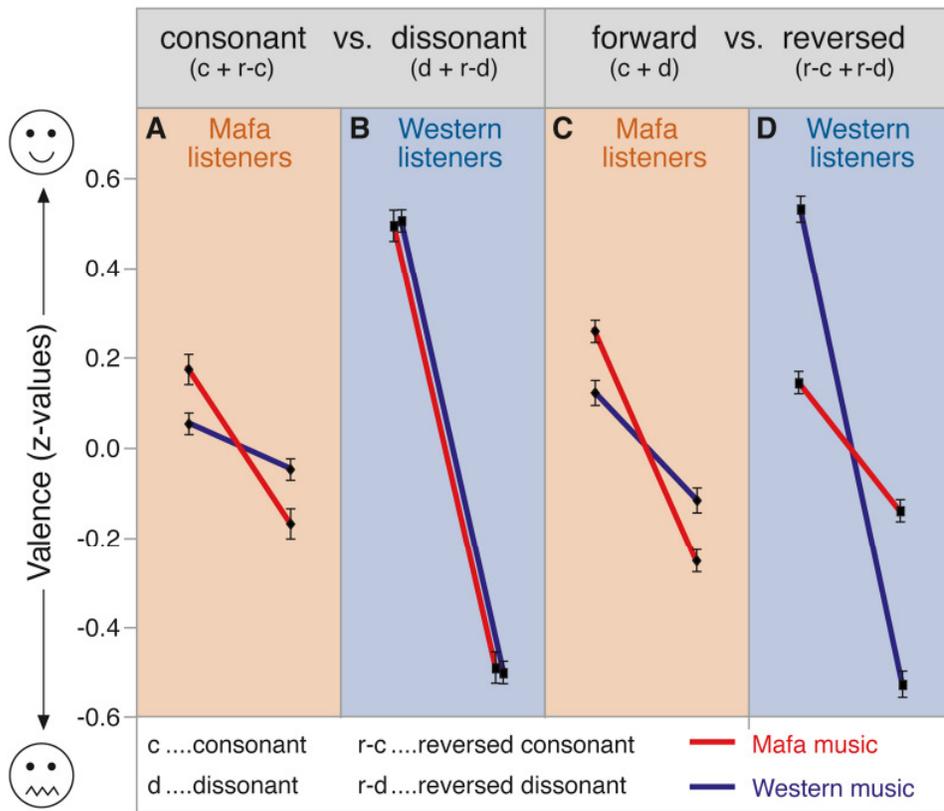


Figure 30. Mean values of valence ratings for the main effects of direction and spectrum. Error bars indicate SEM.

6.4 Discussion

Both Mafa and Western listeners showed a significant preference for excerpts with their original spectrum as opposed to those with dissonant spectra, not only for their own music, but also for the music of the respective other music culture. This clearly demonstrates that there must be, at least to some extent, a universal perceptual mechanism underlying the preference of consonance over continuous dissonance.

On the other hand, Figure 29 and Figure 30A/B illustrate that Western listeners respond more strongly (in terms of valence rating) to a distortion of the spectral order of the music (original spectrum vs. cacophonous spectrum) than Mafa listeners (see also Table 5, and interaction *spectrum* × *subgroup* in *Appendix B Supplementary Tables*, Tables 9 and 10). This is likely to correspond to different consonance-dissonance concepts learned through cultural exposure (see also below), in that the dynamic of alteration between consonance and dissonance may play a more important role in Western music culture. Since in nonmusicians the consonance/dissonance percept likely interacts with the valence percept (Bugg, 1933), these findings thus indirectly also lend support to cultural theories of consonance (Cazden, 1945; Lundin, 1947).

As described in detail in *Chapter 2.3 From feature extraction to valence percept*, two types of dissonance can be distinguished: the first, sensory or psychoacoustical, arising from inharmonicity in the acoustical signal (deriving from multiple frequency components interacting within a critical bandwidth; (Braun, 1999; Greenwood, 1991; Helmholtz, 1885/1954; Kameoka & Kuriyagawa, 1969; Plomp & Levelt, 1965; Sethares, 1993; Terhardt, 1974)), and thus bearing a principled relationship to the operation of the human auditory system: and a second, musical, arising from cultural musical practice (Cazden, 1945; Lundin, 1947; Terhardt, 1984), wherein certain tones or simultaneous combinations of tones are perceived to be syntactically 'unstable', requiring resolution by being temporally succeeded by 'stable' tones or tone-combinations (Apel, 1972; Burns & Ward, 1982; Cazden, 1945; Terhardt, 1983).

Our data support a model that includes both universal sensory dissonance and culturally acquired musical dissonance. We suggest that the observed universal preference for consonance over dissonance reflects universalities in the workings of the auditory pathway of Mafa and Western listeners, and corresponds to an effect of sensory dissonance. On the other hand, it is probable that the difference between the Mafa and Western rating is due to differences in music acculturation, and thus a culturally altered perception of musical dissonance.

One reason for the smaller valence difference between harmonious and cacophonous music for Mafa listeners may be that Western listeners are through cultural experience more accustomed to listen to long and variable polyphonic music sequences (bare in mind: the Mafa music is extremely repetitive, usually based on two-measure patterns). They may therefore be more trained in the perception of harmonies through probabilistic learning, and thus may also more strongly perceive a difference between consonance and dissonance (and their dynamic alteration that may also be a more important structural component to Western music pieces).

That the Mafa seem to more strongly appreciate the dissonant pieces when compared to the Western listeners needs further explanation that strongly considers the background of Mafa music performance. The Mafa appreciate a powerful music performance. This may be due to the circumstance that Mafa flutes are exhausting to play, involving long phases of hyperventilation controlled by the size and rhythm of the different flutes. A powerful music performance seems to be largely characterized by the number of performing participants and the liveliness and duration of the music pieces (which is e.g. why longer music pieces and their counterparts were probably more appreciated by the Mafa, see Figure 29). This is a reasonable explanation for why Mafa rather appreciate the dissonances when compared to the Western listeners - it

sounds like a music performance with more participants motivated to join in the strenuous performance. That the Mafa compared to Westerners rather appreciate the dissonant excerpts is thus probably a secondary, cultural effect, which is also observable in many other non-western cultures (see e.g. Stobart, 1996) where musical sounds that appear strongly sensorily dissonant may be perceived as musically consonant.

Differences in culturally learned consonance-dissonance concepts may also account for the finding that only Western listeners show a significant interaction of *spectrum* \times *direction* (Table 5). Thus, for Western, but not for Mafa listeners, the valence difference between original and cacophonous music pieces was significantly greater than the difference between reversed original and reversed cacophonous music pieces. In other words, for the Mafa listeners the effect of the distortion of the spectral order is merely additive, i.e., similar when forward and when reversed stimuli were manipulated. For Western listeners, however, the effect is stronger when original music excerpts were manipulated than when reversed music excerpts were manipulated.

Both Mafa and Western listeners preferred forward to reversed music stimuli when assessing the music of their own culture, and interestingly also when assessing music of the respective other culture (Figure 29, see also results of ANOVAs in Table 5). The latter finding is striking, considering the fact that neither the Western listeners, nor the Mafa, had ever before listened to music of the respective other culture, and did not know that the stimulus sample contained manipulated music pieces. Time reversed envelopes of natural sounds seem to generally make sounds less pleasant to listen to, presumably because we are used to hearing rapid onsets and gradual decays. Although it appears that the reversal manipulation creates rather unnatural sounds, the Mafa listeners tended to attribute the manipulated Mafa music excerpts to real people. Typical Mafa comments were: “you shouldn’t let children play the flutes, this is no good”, or “I know this, this is from the people of the Gouzda village, I really don’t like how they play the flutes”. One of the reasons for this may be that the Mafa have

no concept for technically manipulated natural sounds, another may be that the on- and offsets of the Mafa flute tones are rather prompt and symmetric (~ 30 ms), so that the single flute tones sound quite similar in either direction. This implies that the temporal order of music mediates a coherence that is perceivable even in completely unknown music of another culture played with unknown instruments, and the distortion of this coherence by playing the music in a backward direction is universally perceived as unpleasant.

While Mafa listeners showed a significant interaction between length and valence (the longer the music, the stronger the pleasantness ratings), Western listeners only showed such an interaction for the Mafa (and not for Western) music. That Mafa listeners showed a significant interaction between length and valence may be explained by the observation that a flute performance for only a short duration is generally regarded as a bad performance among Mafas (the Mafa listeners would often attribute the short stimuli to unmotivated performers or children trying to play the flute), which is probably connected to the fact that playing the Mafa flutes is a vigorous, physically challenging activity, and in a natural setting a longer performance corresponds to higher skill and fitness (Fitch, 2005; Huron, 2001) of the players. Why Western listeners show a significant interaction between length and valence for the unknown Mafa music, but not their own Western music, remains to be answered.

In conclusion, the results show there is a universal component to the preference for consonant over dissonant music and music played in forward direction over music played in backward direction. However, both Western and Mafa listeners perceived a greater difference (in terms of valence) between original vs. cacophonous spectrum and forward vs. backward stimuli respectively in their own music compared to when they listened to the music of the other culture (see Figure 29 and Figure 30). This indicates that the percept of pleasantness/unpleasantness mediated by music perception is primarily determined by a universal perceptual mechanism engaged in response to physical stimulus

properties, and that this perceptual process is likely to be secondarily modulated by cultural imprinting.

Chapter 7

Experiment 5

Recognition of emotional expression in unknown music of another culture modulates the valence of the music percept

7.1 Introduction

The investigation of an attribution of emotional expressions to music of other cultures has rarely been addressed (Balkwill & Thompson, 1999; Balkwill et al., 2004; Gregory & Varney, 1996). These studies intended to investigate cues that transcend cultural boundaries, and the investigators made an effort to include listeners with little prior exposure to the music presented (e.g. Westerners listening to Hindustani music). Although these participants were exposed to mass media and thus also inadvertently to emotional cues of the respective foreign music (for example by the association of this music with film), these studies have importantly enhanced our understanding of how cultural influence may modulate music perception. Other authors have argued for a relatively basic perceptual mechanism underlying the decoding of emotional expressions which is shared by Western listeners of different age groups, including 5-year old

children (Terwogt & Grinsven, 1991). However, in order to draw clear conclusions about music universals it is necessary to address music listeners thoroughly culturally isolated from each other.

The mediation of emotional expressions plays an important role in Western music culture and the capacity of a musical piece to convey emotional expressions is often regarded a prerequisite to its appreciation. This is not necessarily the case in a variety of other music cultures that do not similarly emphasize an importance of emotional expressivity.

To my knowledge, it has never been addressed how the capability to decode emotional expressions from Western music pieces is related to the valence percept of the music listener, probably because Western listeners are quite good at decoding emotional expressions from Western music. Whether listeners completely naïve to Western music can decode emotional expressions from Western music at all has never been conclusively shown. If they could, then it would be interesting to understand, whether the knowledge they have about the emotional expressivity in the music (as outlined in *Chapter 2.5 From a-referential meaning to valence percept* this can be considered a form of semantic knowledge) modulates their appreciation (valence percept) of the music and of temporally and spectrally corrupted counterparts of the same music.

The present study employed two research paradigms designed to quantify how listeners

1. recognize emotional expressions in Western music, using music pieces that have been used to investigate deficiencies in brain damaged patients (Gosselin, Peretz, Johnsen, & Adolphs, 2006; Gosselin et al., 2005).

2. appreciate or dislike Western music pieces and their temporally and spectrally corrupted counterparts as investigated in Experiment 3 (see also Koelsch et al., 2006).

The outcomes were then correlated in order to determine, whether the capability to decode emotional expressions from Western music pieces modulates a listeners' appreciation (valence percept) of the music and of temporally and spectrally corrupted counterparts of the same music.

7.2 Methods

7.2.1 Participants

21 Mafas participated in a musical emotion expression recognition experiment (13 males; 37 to 90 years old; $M = 62.3$ years). 10 of these participants (4 male; 37 to 70 years, $M = 56$ years) also participated in Experiment 3 (*Chapter 6 Universal preference for consonance over dissonance and forward over backward in music*). This is relevant, because with the data of these participants a performance correlation between both experiments was performed.

Like in Experiment 3 only Mafas who had never before listened to radio, and had never been to or lived in the proximity of a church were accepted as participants for the experiments, because exposure to Western music mainly spreads with electricity supply (and the possibility to operate radios) and Christianization (i.e., Western Christian song). The age of most Mafa participants had to be estimated because they do not have a concept of accumulated age. Similar as in Experiments 3-4 the Mafa participants could neither be categorized as musicians nor as nonmusicians, because they do not have a concept of professional musicianship.

20 Westerners participated in the musical emotion expression recognition experiment (non-musicians; 10 male; 40 to 68 years old; $M = 52.4$ years), of whom 18 (10 male; 40 to 68 years, $M = 52.9$ years) also participated in Experiment 3 (*Chapter 6 Universal preference for consonance over dissonance and forward over backward in music*). Criteria for the selection of Western listeners were that they were not familiar with African music and matched approximately the age range of the Mafa participants (between ~40 and ~70 years).

7.2.2 Stimuli

Stimuli were Computer-generated piano music excerpts with durations between 9-15 seconds, which were specifically designed to express the emotions happy, sad, and scary according to Western conventions such that they varied with respect to mode, tempo, pitch range, tone density and rhythmic regularity (Gosselin et al., 2006; Gosselin et al., 2005). They were controlled for timbre, tone volume, tone attack, tone decay, tone release, and tempo fluctuation. No Mafa flute music was included in this experiment, as the Mafa music recorded locally was not unambiguously assigned by its performers to any particular emotional expressions.

7.2.3 Procedure

An emotional expression recognition experiment with computer-generated piano music excerpts (happy, sad, scary) was performed, where the music stimuli had to be classified to the according depictions of facial expressions from the Ekman archive (Ekman, 1976). The experiment was conducted with a group of Mafa and German participants. Before the experiment they were asked to verbally identify the three emotional expressions depicted and an agreement was

achieved about which emotional expression corresponded to which depiction (three Mafa participants had difficulties recognizing facial expressions on the two-dimensional paper sheet presentations and had to be excluded from the test).

During the experiment, the participants had to indicate which facial expression fitted best with the expression of each music excerpt (forced choice). Additionally they were asked to vocally label the corresponding expression in order to ensure that they remained attentive during the experiment and that their response did not arise from a faulty recognition of the facial expressions. If the two responses (indication of facial expression and verbalization of the emotional expression) did not match, the trial was repeated. If the participants had problems recognizing facial expressions on the paper sheets, and accordingly had several mismatches in a row, they were excluded from the experiment. 14 stimuli from each category (42 in total) were presented from a CD player (two pseudorandomized sequences). During the experiment the stimuli were only audible to the participant (over headphones) to avoid response biases through the experimenter.

7.2.4 Data-Analysis

Test results were considered to be significant when the probability of error was lower than 0.05 (two-tailed). When necessary, a Bonferroni correction was applied. A *t*-test against chance (1/3) was calculated to test for significance of the recognition rates of emotional expression in Western piano music excerpts (Figure 31). In addition, a binomial distribution test (with the assumption that above a percentile rank of 95 the result is not chance) was calculated to determine the percentage of Mafa and Western participants that performed above this criterion in the experiment (see also *Appendix A Supplementary Figures*, Figure 36). An ANOVA for the percentages of correct responses was

computed with the within-subject factor “emotional expression” (happy vs. sad vs. scary) and the between-subjects factor “experimental group” (Mafa vs. Western listeners). A paired-samples *t*-test was conducted to test whether the choice of the non-target categories in attributing the emotional expression were biased towards one of these two emotions (i.e., it was determined, if one of the two non-target categories was chosen significantly more often than the other) (*Appendix A Supplementary Figures, Figure 37*).

We wanted to investigate whether the capability to decode putatively a-referential semantic information such as emotional expressions (see also *Chapter 2.4 From structure building to valence percept*) from Western music corresponded to a higher appreciation of Western music (as opposed to its manipulated counterparts) as investigated in Experiment 3 (*Chapter 6 Universal preference for consonance over dissonance and forward over backward in music*). Therefore, a correlation analysis was calculated in which each participant’s performance in the emotion recognition experiment was used as a dependent variable, and the differences between the individual ratings (*z*-values) of forward vs. reversed and consonant vs. cacophonous Western music excerpts in Experiment 3 were used as independent variables.

7.3 Results

All emotional expressions were recognized above chance level by both Western and Mafa listeners (*Figure 31*), although the Mafa listeners had never before been exposed to Western music and piano sound.

An ANOVA with the within-subject factor “emotional expression” (happy vs. sad vs. scary) and the between-subjects factor “experimental group” (Mafa vs. Western listeners) was used to evaluate the percentage of correct responses. It revealed a main effect of “emotional expression” ($F_{(2,39)} = 15.48$; $p < 0.001$),

reflecting the difference in recognition performance between the emotion categories: Happy music was recognized better than scary ($F_{(1,40)} = 24.52$; $p < 0.001$) and sad pieces ($F_{(1,40)} = 12.55$; $p = 0.001$) by members of both cultures. Moreover, a main effect of “subgroup” ($F_{(1,40)} = 117.83$; $p < 0.001$) indicates a different recognition performance between the two groups (with Western listeners performing better than Mafa listeners).



Figure 31. The figure shows the mean performance (*M*) in percent for the

*recognition of each emotional expression (*** $p < 0.001$, ** $p < 0.05$) in Western music excerpts, standard error (SEM), t -values ($df = 20$ for the Mafa listeners and $df = 19$ for the Western listeners), p -values.*

For the data acquired in the emotional expression recognition experiment all (but two) variables conformed to a standard normal distribution (as tested by means of Kolmogorov-Smirnov tests). The deviations resulted from ceiling effects: Western listeners recognized happy and sad pieces in almost all cases (98.93 and 92.50 percent correct recognition).

The analysis investigating correlations between the participants' performances in the emotion recognition experiment and the effects of direction and spectrum on their rating behaviour (assessing Western music and its manipulated counterparts) in Experiment 3 yielded the following results: For Western listeners, no significant correlations were found (neither for the manipulations on direction, $r = 0.17$, nor on these of spectrum, $r = -0.11$). For the Mafas, the analysis revealed a positive correlation between the performance in the emotional expression recognition experiment and the extent to which they differentiated (in terms of valence) between forward and reversed Western music excerpts ($r = 0.74$; $p = 0.015$; $N = 10$). No correlation was observed between the performance in the emotion recognition experiment and the extent to which the Mafa differentiated between music excerpts with original and cacophonous spectrum ($r = 0.12$; $p = 0.737$; $N = 10$).

7.4 Discussion

In a first part of the experiment it was investigated whether emotional expression in music is universally perceived or its decoding is crucially dependent on cultural conventions. Figure 31 showed that both Western and Mafa listeners could successfully decode the intended emotional expressions

from the Western music, indicating that the emotional expressions conveyed by the Western music excerpts can indeed be recognized universally.

The mechanism underlying the mediation of emotional expressions with Western musical phrases in Mafa listeners completely naïve to Western music is not yet evident. Here we suggest that it may reside in a recognition of nonverbal patterns of emotional expressiveness found in both music and speech (Eckerdal & Merker, 2009), thus in a mechanism closely associated or even identical with the mechanism underlying the largely universal recognition of emotional expression in affective prosody (K. R. Scherer, 1997), which is in line with the notion that instrumental music may at least partly derive its capacity to convey emotions by imitating features of the human voice (Juslin, 2001).

Western listeners decoded the intended emotional expressions from the music at a higher rate (Figure 31). This could either reflect that they discerned a set of culturally determined cues not perceived by the Mafa listeners, or simply the unfamiliarity of Mafas with the abstract nature of the face and music presentations without a social context of music production and perception which is customary in Mafa culture.

In a second part of the experiment it was tested whether the capability to decode emotional expressions from Western music excerpts interacts with an appreciation (as indicated by valence) of Western music as opposed to manipulated music (distortion of direction and spectrum) as investigated in Experiment 3. For Western listeners, no significant correlations were found (neither for a manipulation of direction nor for a manipulation of spectrum), presumably, due to the low error rates the Western listeners displayed in the present musical emotion expression recognition experiment.

For the Mafas, the analysis revealed a positive correlation between the performance in the emotional expression recognition experiment and the extent to which they differentiated (in terms of valence) between forward and reversed Western music excerpts ($r = 0.74$; $p = 0.015$; $N = 10$) as investigated in

Experiment 3. In contrast, no correlation was observed between the performance in the emotional expression recognition experiment and the extent to which they differentiated between music excerpts with original and cacophonous spectrum ($r = 0.12$; $p = 0.737$; $N = 10$). This suggests that Mafa participants who better recognized the emotional expressions in Western music were more sensitive to a distortion of the temporal order of the music excerpts, and showed a greater preference for the original Western music excerpts as opposed to the manipulated versions than participants who showed a poor performance in the emotional expression recognition experiment.

This finding can be interpreted as follows: Musical emotional expression is a form of semantic information (as laid out in the *Chapter 2.5 From a-referential meaning to valence percept*), contributing to a meaningfulness of the music (Koelsch et al., 2004; Patel, 2007). Music may be appreciated at least partly for its meaningfulness. A temporal corruption of the Western music by playing it backwards strongly corrupts the meaningfulness of the musical signal, but only for individuals for whom the original Western music was meaningful (e.g. by coding emotional expressions). On the other hand, the Mafa may not perceive a distortion of the meaningfulness of the music (for example the coded emotional expressions) as strongly by a spectral corruption of the Western music.

Chapter 8

Summary and General Discussion

The main objective of this dissertation was to develop (further) experimental paradigms in the field of cognitive research that effectively address the investigation of emotional processing with music. Theoretical considerations outlined in *Chapter 1 (What is emotion?)* led to the conclusion that presently the most appropriate way to advance towards a proficient understanding of emotional processing as elicited by music perception is achieved by a systematic variation of the valence percept in the listener. This emotional dimension, unlike other putative emotional dimensions like for example arousal, can easily be assessed by self-report of the participants.

It was investigated how the valence percept is influenced by an alteration of stimulus properties and cultural background at the level of several modules of music processing (as described in the ‘Neurocognitive model of music perception’, see *Chapter 2 From music perception to valence percept*), namely ‘feature extraction’, ‘structure building’, and ‘meaning’. The findings gathered in the present work thus provide an empirical basis for the only poorly substantiated functional interlinking between these music processing modules and emotion, and importantly reveal novel insights about the susceptibility of

functional music processing modules (or the interconnection between functional modules) to cultural shaping.

8.1 Experiment 1

The neurology of the valence dimension as investigated with pleasant and unpleasant music

The neurology of the valence dimension as investigated in *Chapter 4.1* has not yet been intelligibly exposed. Especially the putative workings of the amygdala in the mediation of both positive and negative valence percept remains puzzling. The findings from the first analysis conducted in Experiment 1 delineate the neural substrate involved in mediating the valence percept elicited by the perception of pleasant music excerpts and their variously unpleasantly manipulated counterparts.

It is widely believed that the amygdala deals only with unpleasant emotional experience. This idea largely derives from the history of emotion research in neuroscience, where unpleasant emotions such as fear and stress have been easier to operationalize in animal experiments. Recent evidence of amygdala functionality indicates that it has a greater role in the processing of positive valence than formerly believed, although the underlying physiology is not yet clear. Emotional processes putatively correspond to a highly precise physiological pattern of temporally coordinated procedures. The neurophysiological mechanism underlying such an elaborate synchronization needs to be fast and connected to putatively various emotion mediating networks. It is probably a structure or a small network of structures in a position to exert an immediate influence on the hormonal system. I have argued that the amygdala is anatomically well qualified to be involved in such a mechanism, and have accordingly investigated its role in the orchestration of neuronal

engagement during emotional response in terms of valence percept to musical stimuli.

The design of the scanning paradigm applied in Experiment 1 was optimized to investigate for engagement of amygdala subregions during various valence percept mediated by musical stimuli with 3T functional magnetic resonance imaging (fMRI).

Results showed that two separate amygdala subregions are involved in the mediation of a response to musical stimuli with increasing and decreasing pleasantness. The functional connectivity network of each of these regions was investigated, revealing that each behaves synchronously with a corresponding putatively largely valence-specific network. This finding contributes importantly to our knowledge about the organization of the brain physiology of emotions, especially with respect to how valence specific functional networks may be orchestrated in association with amygdala subregions.

It was further investigated whether activity of certain brain regions may be related to separate positive and negative valence dimensions (Lewis et al., 2007), and not to valence as a continuous scale from unpleasantness to pleasantness. The dopaminergic system was observed to be exclusively responsive to alterations of positive valence, underscoring the necessity to separately analyse positive valence as an independent emotional dimension. Importantly however, other brain areas, such as the amygdala, showed more prominent activity when the whole valence dimension was considered in the analysis, indicating that these brain areas are sensitive to alterations of valence across the whole valence spectrum.

Opening up to consonance – an amplification mechanism in the auditory pathway dependent on harmonic roughness

Whether the percept of consonance and dissonance is hardwired in the auditory perceptual pathway, or an effect of late cognitive processing, is still an

unresolved issue.

Contrasting the brain's response to consonant music with its response to dissonant music revealed a stronger engagement of the auditory cortex in response to consonant music. This rather supports the view that a distinction between the processing of consonant and dissonant music is hardwired in the auditory pathway. However, previously, such enhanced engagement of auditory cortex during consonant music has been attributed to attentional processes (Koelsch et al., 2006) that are known to modulate auditory processing (Jäncke et al., 1999).

In order to investigate the mechanism underlying such an amplification of consonant over dissonant musical information, in section 2 of Experiment 1 a psycho-physiological interaction (PPI) analysis was conducted. This was aimed at identifying a neural network sensitive to dissonance that determines how much musical sound engages the auditory cortex dependent on its harmonic roughness.

The findings demonstrate that spectral order is a key feature determining the responsiveness of our auditory pathway to music. They indicate the existence of a perceptual gating mechanism in the auditory domain, illustrating that several levels of the auditory pathway interact with each other and the amygdala to regulate information flow into the auditory cortex.

8.2 Experiment 2

Is the neurology of aversive response to violations of expectancy in chord progressions modulated by musical expertise?

A number of previous fMRI studies investigated the processing of musical syntax using chord sequence paradigms with harmonically regular and irregular chords (see introduction). However, recent evidence indicates that unexpected ('irregular') chords also trigger an emotional response (Steinbeis et al., 2006),

which may confound an investigation of music-syntax.

According to the theoretical considerations outlined in *Chapter 1.3 Elements*, emotional responses are possibly always associated with a valence percept. However, to my knowledge Experiment 2 was the first to apply chords with variable regularity to investigate neural substrates of the valence percept.

In a behavioural study, the valence percept elicited by music-syntactically regular and irregular chords was assessed by a group of listeners comprising musicians and non-musicians. The valence ratings clearly differed, with the irregular chords being perceived as more unpleasant, and the regular chords as more pleasant.

An fMRI study investigating the amygdala response during music-syntactically regular and irregular chords in a group of listeners comprising musicians and non-musicians showed increased BOLD signal changes bilaterally in the amygdala during irregular chords. This demonstrates that syntactically irregular chords not only elicit brain responses related to the processing of musical structure (as it has been reported in a previous study (Koelsch et al., 2005)), but also brain activity related to emotional processing. The findings imply that in addition to intensely pleasurable music or highly unpleasant music, activity changes in the amygdala can be elicited even by single chords that are perceived as unexpected in their musical context, and thus as unpleasant.

A question that may here arise to the reader conscious of the putatively valence specific subregions of the amygdala, as outlined in the findings of the first section of Experiment 1 (*Chapter 4.1 The neurology of the valence dimension as investigated with pleasant and unpleasant music*), is whether the results of Experiment 2 confirm the valence specific anatomical subregions as described above. In Experiment 2 we report only an amygdala engagement in response to the negative valence. This is not surprising, however, because Experiment 1 was

specifically optimized for an investigation of amygdala subregions, presenting short music pieces in a sparse temporal sampling design with oversampling. In contrast to this paradigm, the block design of Experiment 2 was rather designed for an investigation of cortical differences in the processing of chords differing in their context specific regularity, results that have been described in detail in Koelsch, Fritz et al., 2005. A possible relevance of the amygdala in the processing of chords with differing regularity was not hypothesized until it had been shown that the processing of irregular chords is associated with alterations of the skin conductance response (SCR) (Steinbeis et al., 2006), and thus likely with an emotional response.

The data was consequently subjected to further analysis, addressing the investigation of a possible involvement of emotional processing. Furthermore, I investigated a possible role of cultural imprinting in terms of musical education in a modulation of the mediated valence percept. Behavioural data indicated that as hypothesized, musicians assessed the irregular chords to be less unpleasant than the non-musicians (one-sided t-test). It was argued that this probably corresponds to their higher exposure to unusual chord progressions during their musical training, and thus in a wider sense resembles a music cultural effect. Contrasting the brain response of musicians and non-musicians during the processing of irregular chords revealed that this processing more strongly engages the amygdala in non-musicians than in musicians, corresponding to the behavioural findings.

This suggests that a higher familiarity with irregular chord progressions leads to a reduced involvement of the amygdala, possibly due to less aversion towards the stimulus, and instead, as reported in Koelsch, Fritz, et al. (2005) to a greater involvement of cortical areas specialized in (music-) syntactic processing (mostly inferior fronto-lateral cortex).

8.3 Experiments 3 and 4

Universal preference for consonance over dissonance and forward over backward in music

As with Experiment 2, Experiments 3 and 4 investigate the modulating role of cultural imprinting on the valence percept mediated by music listening. Additionally, for the first time, they also systematically address the question of universals of music appreciation (*Chapter 6*).

It has long been debated which aspects of music perception are universal, and which are developed only after exposure to a specific musical culture (Trehub, 2003). Unfortunately, opportunities for intercultural comparisons between individuals exposed to completely incongruent music cultures are becoming increasingly rare, due to globalization. Insights from developmental studies are constrained, because infants never completely lack exposure to music of their culture (given that music perception begins in utero during the third trimester of pregnancy). Experiments 3 and 4 are cross-cultural studies with participants from a native African population (Mafa) and Western participants, both groups naïve to the music of the respective other culture. We investigated the effects of spectral and temporal distortions on the appreciation of Mafas and Westerners listening to both Western music (Experiment 3) and music from the Mafa culture (Experiment 4). It could be demonstrated that preference for consonant as opposed to dissonant music, as well as preference for music played forward as opposed to music played backward, are based on perceptual mechanisms that are universal, although the impact of the respective distortion is modified by the listeners' music cultural imprinting. Cultural influence has the consequence that modifications performed on music of ones own music culture more strongly alter the valence percept than modifications performed on the music of another music culture. Furthermore the data show that Western listeners are more susceptible to a corruption of the spectral order than Mafa listeners, their valence percept differing more strongly between consonant and dissonant

versions of the same tunes. This is indicative of a culturally developed sensitivity to spectral order in Western music culture, which is not present in all music cultures. Thus, a preference for harmony over disharmony is primarily hardwired in the human brain, but secondarily depends on culture-specific experience that modulates the intensity of the valence percept. This data hence support a model that includes both universal sensory dissonance and culturally acquired musical dissonance: The observed universal preference for consonance over dissonance appears to reflect universalities in the workings of the auditory pathway of Mafa and Western listeners, and corresponds to an effect of sensory dissonance. On the other hand, it is probable that the difference between the Mafa and Western ratings is due to differences in music acculturation, and thus a culturally altered perception of musical dissonance.

Furthermore the findings indicate that music universally mediates a coherence that is perceivable even in completely unknown music of another culture played with unknown instruments, and that the distortion of such coherence by a corruption of the temporal order of the music is universally perceived as unpleasant.

8.4 Experiment 5

Recognition of emotional expression in unknown music of another culture modulates the valence of the music percept

Experiment 5 addresses the modulating influence of a capacity to decode a form of a-referential semantic information, emotional expressions, from Western music on the appreciation of Western music and its manipulated counterparts in Mafa listeners entirely naïve to Western music (*Chapter 7*). A-referentially expressive gesture of music comprises the mediation of emotional expressions such as happiness, sadness, and fear. However, it is not clear cut, how much the

decoding of such emotional expressions actually depends on referential information such as culturally learned musical clichés. The experiment consisted of two sections: First, it was investigated how good Mafa listeners naïve to Western music recognize the emotional expressions happy, sad and scary in Western music, using music pieces that have previously been used to investigate deficiencies in brain damaged patients (Gosselin et al., 2006; Gosselin et al., 2005). In a second section of the experiment, the emotion expression recognition performance of those Mafa individuals who had also participated in Experiment 3 (appreciation of Western music and its counterparts) was correlated with their assessment behavior recorded in Experiment 3 in order to determine whether the capability to decode emotional expressions from Western music pieces modulates a listeners' appreciation (valence percept) of the music, and of temporally and spectrally corrupted counterparts of the same music. It was shown that Mafa listeners and a Western control group with success (over chance) decoded the intended emotional expressions from the Western music. This finding thus indicates that the emotional expressions conveyed by the Western music excerpts can be recognized universally, similar to the largely universal recognition of human emotional facial expression (Ekman, Sorenson, & Friesen, 1969). None of the previous cross-cultural studies on emotional expressions in music had been conducted with listeners thoroughly isolated from the respective foreign music, rendering it impossible to draw clear conclusions about music universals from this evidence. The present finding is thus the first unambiguous evidence demonstrating that music is a universal non-verbal channel for the expression of emotion.

For Western listeners, no significant interactions were found between their performance in this emotion expression recognition experiment and the data from Experiment 3 (neither for a manipulation of direction nor for a manipulation of spectrum), presumably due to the low error rates the Western listeners displayed in the musical emotion expression recognition experiment. For the Mafas, the analysis revealed a positive correlation between the performance in the emotion expression recognition experiment and the extent to

which they differentiated (in terms of valence) between forward and reversed Western music excerpts (but not the extent to which they differentiated between music excerpts with original and cacophonous spectrum). This suggests that Mafa participants who better recognized the emotional expressions in Western music were more sensitive to a distortion of the temporal order of the music excerpts, and showed a greater preference for the forward Western music excerpts as opposed to the manipulated versions than Mafa participants who showed a poor performance in the emotion recognition experiment.

These findings indicate that the capacity to decode emotional expressions from Western music entails its increased appreciation. As described above in the introduction (*Chapter 2.5 From a-referential meaning to valence percept*) and in *Chapter 7 (Recognition of emotional expression in unknown music of another culture modulates the valence of the music percept)* emotional expression is a form of a-referentially semantic information, contributing to a meaningfulness of the music. It is thus possible that the findings of Experiments 3, 4, and 5 partly correspond to our appreciation of meaningfulness of music⁵⁵.

Consequently, not only the capacity to decode emotional expressions, as a form of a-referentially semantic information from music, may alter the valence percept of a listener, but the capacity to decode semantic information from the music in general. Note that this is a mechanism of how emotion may be elicited by music that has not been elaborated in such detail before, and is only seldomly addressed (Fritz & Koelsch, in press; Juslin & Västfjäll, in press; Menon & Levitin, 2005).

⁵⁵ Note however that our appreciation of music may also correspond to the content of the meaning mediated by music. For example, music has often been considered unpleasant when regarded to be the music of the devil (e.g. Vienna Waltz, Rock'n'Roll).

8.5 Conclusions arising from an integration of the findings, and future questions to address

The experiments investigating the valence percept as it relates to music perception indicate that how valence is attributed to musical sounds may differ considerably. It appears that the valence percept of a listener can be modulated through physical stimulus manipulation at the level of several modules of music processing, namely 'feature extraction', 'structure building', and 'meaning'. It is plausible that the connections between the 'emotion' module, which is closely associated with valence percept, and the modules 'feature extraction', 'structure building', and 'meaning' are reciprocal so that emotional state may in turn alterate their operation. Consequently, a deeper knowledge about the modulating influence of emotional states on music perceptual processes is necessary to avoid confounds in the design of experiments addressing music perceptual processes. However, research into how emotional processes alterate perceptual processes is still largely unclaimed territory.

The current findings furthermore bear important implications for the neuroscience of emotion research. It has been shown that whereas some brain structures such as the amygdala are responsive to alterations in the whole valence spectrum, others like the dopaminergic system may respond rather selective to a confined subdivision of the valence spectrum (e.g. only positive valence). Accordingly, the experimentally defined valence space should be well chosen corresponding to the neural system investigated.

The investigation of the amygdala subregions at 3 Tesla has yielded some success. However, an examination of the functional role of numerous small brain structures putatively especially important to emotional processing - such as the amygdala, the nucleus accumbens, the periaqueductal grey, the ventral tegmental area, the raphe nucleus, the substantia nigra, and the hypothalamus – needs to be addressed with an investigative technology that allows for a more fine grained signal resolution. Current developments in neuroimaging with

higher field strengths such as 7 Tesla point the way to such a methodological option with fMRI.

The investigation of cultural influence on the valence percept has yielded important insights on music universals. Experiments 3, 4, and 5 suggest that certain musical features are perceived in members of both music cultures, Mafa and Western, and are thus likely to be music universals, although they seem to have developed more strongly or possibly exclusively in only one of the investigated music cultures. Accordingly, musical universals cannot simply be determined by specifying the common denominator between the musical features of all cultures.

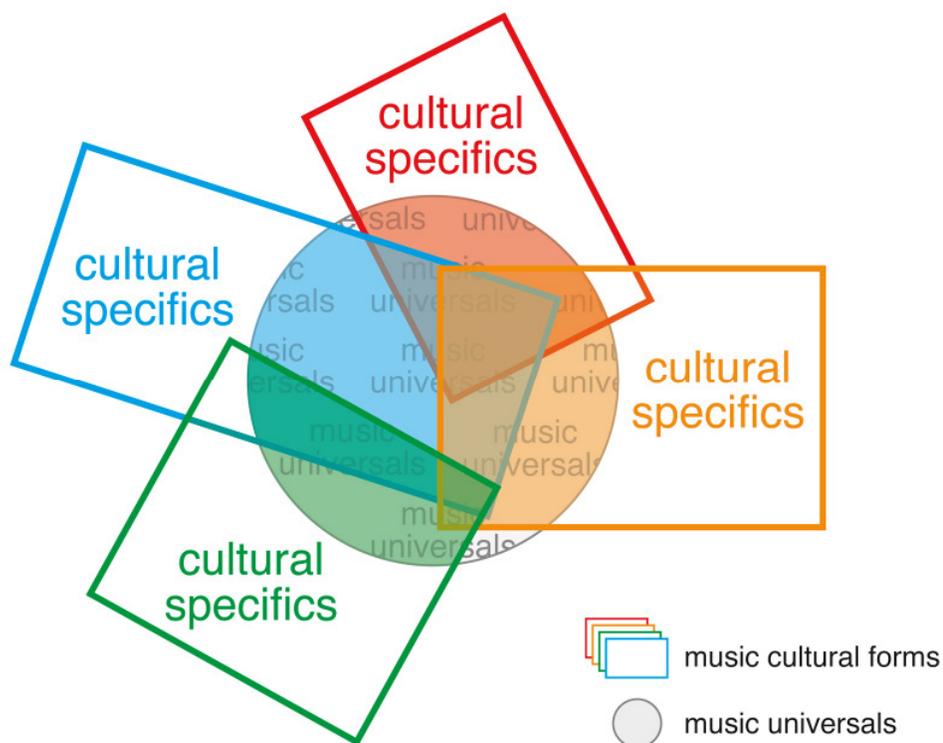


Figure 32. Anchor model of musical culture: The model suggests that all music cultures contain both music universals and cultural specifics. The more cultures share a music cultural influence, the more their musical codes overlap. It suggests that despite a universally shared understanding of a partly common

musical code, not all music cultures have implemented the whole set of universal musical features in their musical repertoire (here labelled music cultural form).

This is also nicely illustrated by a possible absence of a variety of emotional expressions in Mafa music as described in Experiment 5 (*Chapter 7*), although the Mafa are able to identify a variety of emotional expressions from Western music. Furthermore, an absence of a comparable variety of emotional expressions in Mafa music would have important implications: If music were in its essence indeed a universal language of emotions, how come that Mafa music seems not to express a variety of emotions comparable to Western music? The appropriate answer is that although emotional expressions in music are perceived universally, this may not be the principal function of music (as already pointed out by Hanslick in his 1854 essay (Hanslick, 1980)). Despite the observed universals of emotional expression recognition one should thus be careful to conjure the idea of music as a universal language of emotion, which is largely a legacy of the period of romanticism.

The experience of sensory dissonance may arise from a universal, physiologically determined architecture of hearing, beginning with the cochlea, to the sound analysis suppression mechanism for sounds with high roughness, investigated in the present study, which engages several stages of the auditory pathway and the amygdala. However that gives no clue about why our nervous systems should interpret properties of sound such as roughness as pleasant or unpleasant. It is probable that our auditory preferences serve a much higher purpose to mankind through evolution. One possibility is that sounds with high roughness are better avoided, because they often imply danger for the individual (corresponding e.g. to a typically high roughness of aggressive vocalizations) or offspring (so that crying babies are better appeased in order not to endanger themselves and the group through an attraction of predators). Another possibility is that human appreciation of consonance (as opposed to dissonance) corresponds to a key evolutionary divergence promoting human musical

capacities, possibly as a factor increasing the motivation to engage in musical activity. This issue still needs to be addressed in future investigations.

A field of research calling for further investigation in continuation of the present work is the ethnomusicological field study with physiological measures. We are currently in the process of developing advanced experimental paradigms to understand the influence of music on the physiology, including the immunology, of the music listener and performer. This enables us to address important questions: What is it about music, that makes us feel good, and may even increase our health and bodily fitness through passive listening (Koelsch & Fritz, 2007)?

The Mafa flute music ritual is observed to be an elaborate method that putatively enables the music performers to manipulate their mental states by employing different rhythms and depths of hyperventilation. It is a good example of how we could learn about the medical applicability of music by elaborately investigating musical practice in other cultures with physiological measures. Before we can apply physiological measures in an ethnomusicological investigation, however, we must assess the practicability of performing them in the field. Furthermore, it would be very helpful to be able to classify participants' mental states from these physiological patterns. In fMRI research the multivariate statistical methods that enable such 'brain reading' have already advanced considerably (Haynes, Rees, Box, & Contact, 2006). This methodology is not restricted to fMRI, but can also be applied to EEG and peripheral physiological measures.

However, when considering the present results it seems reasonable to conclude that an ultimate ethnomusicological methodology to pursue might be fMRI. Experiment 2 this technique was used, showing that the level of amygdala response to music-syntactical violations varied according to musical expertise acquired through specific music cultural exposure (musical training). Yet this study could only address cultural differences between groups of participants

with largely overlapping music cultural imprinting, and does not provide conclusive evidence regarding music universals.

An issue that can only be investigated with such a neuro-ethno-musicological approach using fMRI is whether the hardwired amplification mechanism for consonant music, which was characterized in the second section of Experiment 1, is innate or established through music cultural imprinting. A PPI-analysis similar to the one conducted in Experiment 1 (*Chapter 4.2 Opening up to consonance – an amplification mechanism in the auditory pathway dependent on harmonic roughness*), but with Mafa participants, would yield the answer.

The endeavour of ethnomusicological field work with fMRI clearly entails great organisational challenges, and possibly also some ethical considerations, because participants would need to travel to an operational MR-facility that allows for functional investigation. However, I consider such a venture possible. If it is addressed, then I suggest the sooner the better, because the spread of media technology to even remote areas of settlement in Africa and other appropriate destinations (such as for example Western New Guinea) currently happens very rapidly.

Appendix A

Supplementary Figures

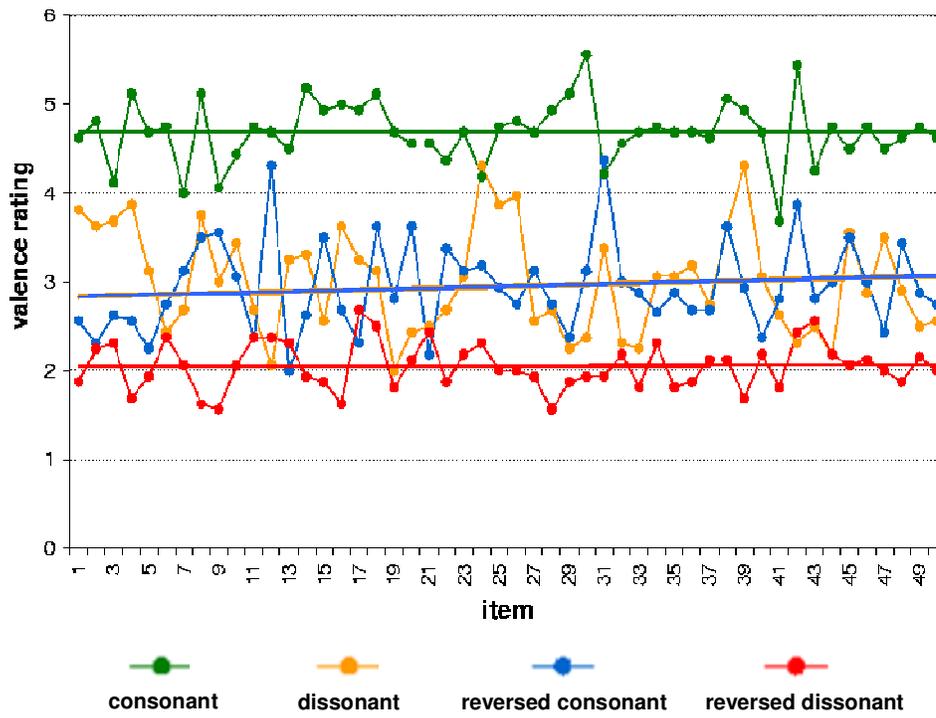


Figure 33. Valence rating during the fMRI experiment

The figure displays seven traditional instruments used in Mafa music, arranged from largest to smallest: Mdegem, Tcegem, Gsa, Maill, Mbege, Paleyga, and Chechega. A 10 cm scale bar is provided for reference. Below the instrument images are four musical scores, each consisting of two staves for each of the seven instruments:

- Houdok:** A score for the instruments Chechega, Paleyga, Mbege, Maill, Gsa, Tcegem, and Mdegem.
- Maray:** A score for the instruments Chechega, Paleyga, Mbege, Maill, Gsa, Tcegem, and Mdegem.
- Zavad Nouveau:** A score for the instruments Chechega, Paleyga, Mbege, Maill, Gsa, Tcegem, and Mdegem.
- Zavad Traditionell:** A score for the instruments Chechega, Paleyga, Mbege, Maill, Gsa, Tcegem, and Mdegem.

Figure 34. Scores of the recorded Mafa music played with the instruments depicted above and in Figures 25 and 26, each pattern is presented twice (Mafa players perform these patterns repetitively).

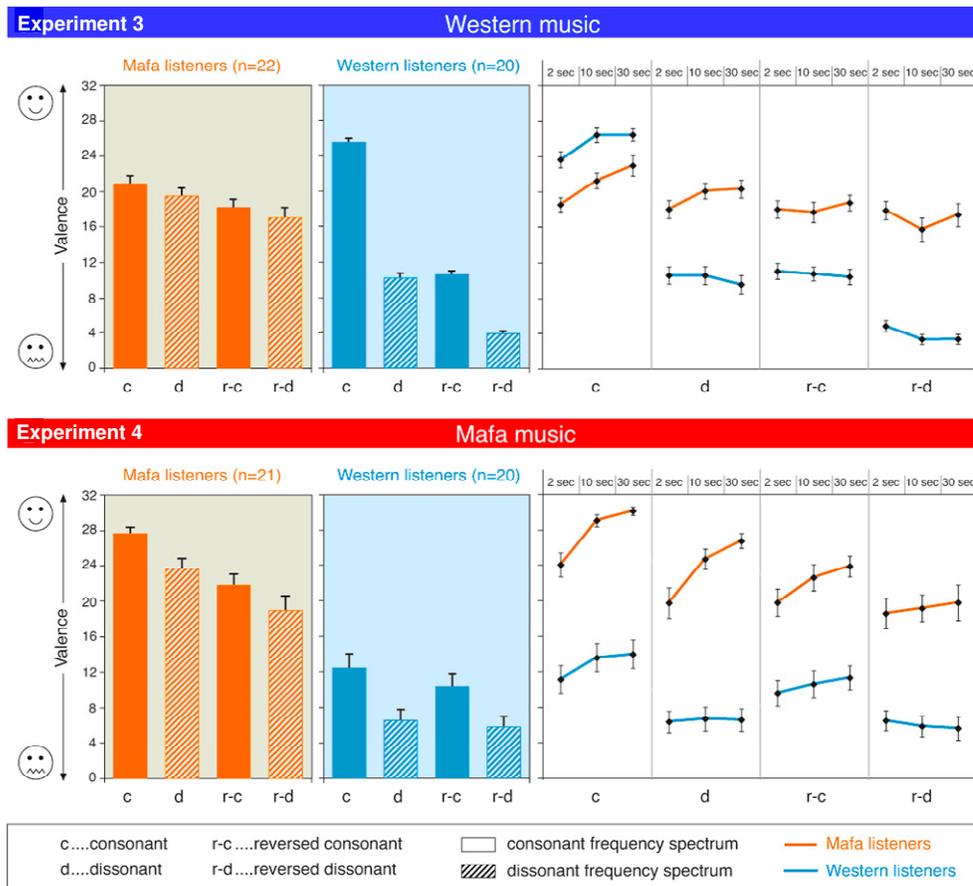


Figure 35. The figure shows non-transformed values of the ratings conducted in the music appreciation experiment. Mean values are depicted for each entire stimulus category (c, d, r-c, r-d), and each stimulus duration (2, 10, 30 sec) respectively. Error bars indicate SEM.

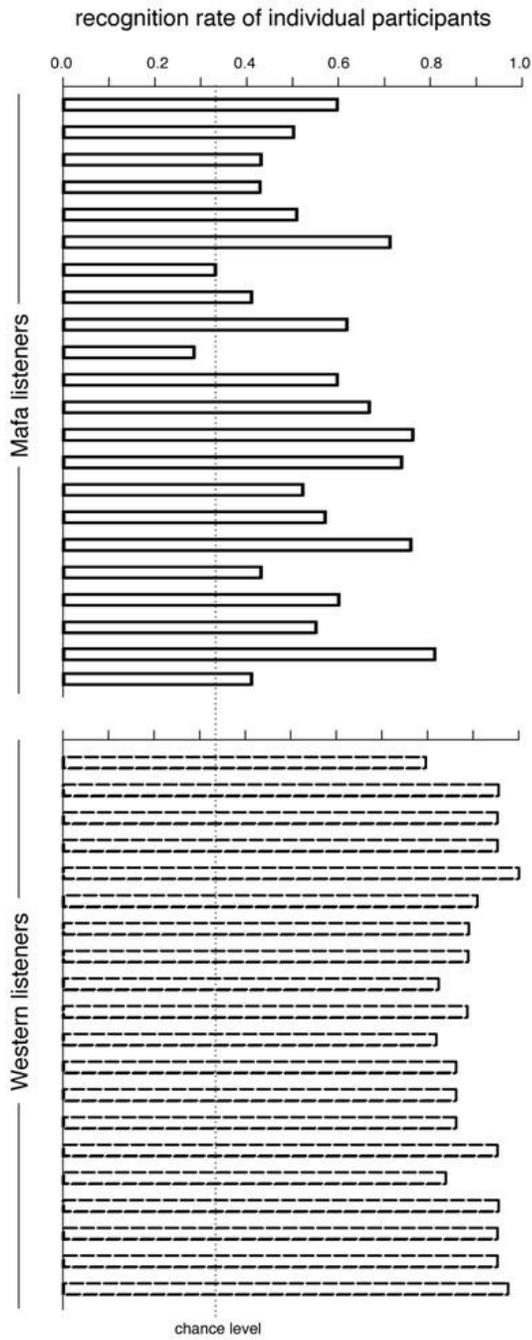


Figure 36. Depiction of the mean emotional expression recognition rates for the participants of Experiment 5.

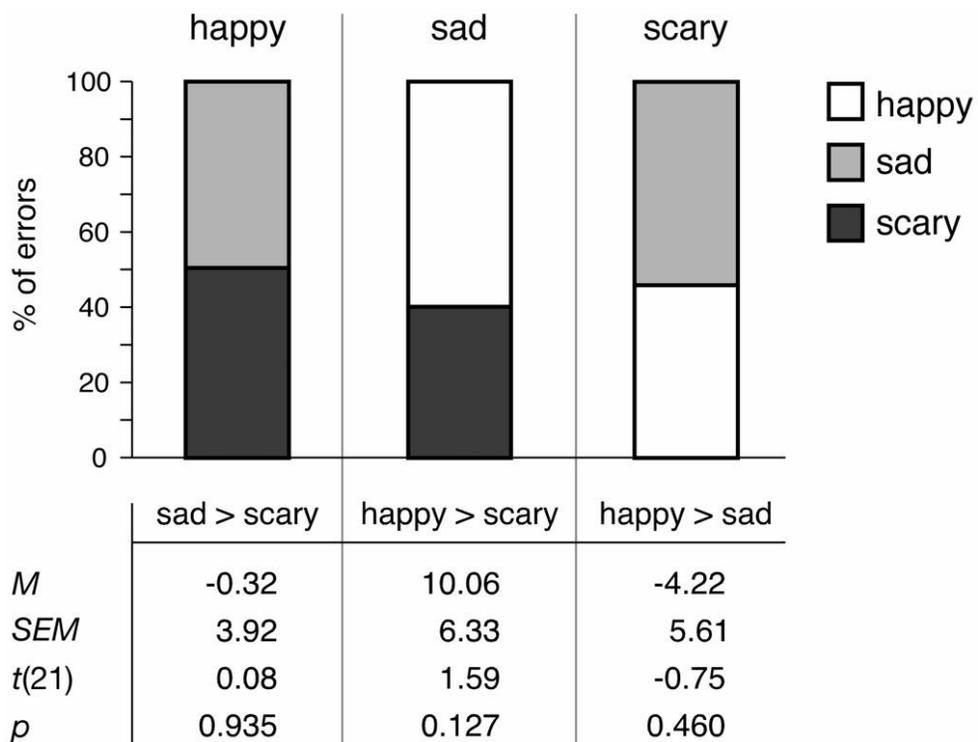


Figure 37. Mafa error rates (i.e. non-target choices) in percentage for the recognition of each emotional expression. The table shows mean differences in percentages of choices of non-target categories (*M*), standard error (*SEM*), *t*-values, *p*-values.

Appendix B

Supplementary Tables

mm ³	z-values	location	
<i>Increasing pleasantness</i>			
7344	4,47	L (-53 -18 15)	planum temporale, Heschl's gyrus, BA 41,42
1134	4,05	L (-23 0 6)	medial putamen
351	3,38	L (-5 0 51)	rostral SMA, BA 6
297	3,66	L (-2 33 -12)	ventromedial prefrontal cortex, BA12
135	3,94	L (-20 -3 -6)	dorsal and extended amygdala/substantia innominata
108	3,74	L (-2 -51 -30)	vermis cerebelli
81	3,41	L (-32 -21 3)	postero-lateral putamen/clastrum
5562	4,47	R (43 -18 6)	Heschl's gyrus, (planum temporale), BA 41,42
216	3,6	R (4 -57 -39)	cerebellar tonsil
162	3,53	R (13 27 -6)	H-shaped sulcus (orbitofrontal cortex) BA11
135	3,92	R (10 -6 0)	medial pallidum/hypothalamus
54	3,21	R (16 0 6)	pallidum
54	3,31	R (4 -3 6)	anterior thalamus
<i>Increasing unpleasantness</i>			
189	-3,57	L (-29 6 48)	superior precentral sulcus, BA6
162	-3,64	L (-35 24 42)	medial frontal gyrus (post, dorsolat, prefront.), BA8
54	-3,18	L (-23 15 42)	superior frontal sulcus, BA8
54	-3,40	L (-29 -78 36)	IPS, horizontal part, BA7/39
54	-3,20	L (-35 -36 33)	IPS, ascending part
54	-3,59	L (-26 3 30)	IFJ (crossing point of precentral & inf, frontal sulci)
675	-3,80	R (10 -51 51)	precuneus, BA7
216	-4,00	R (4 -36 57)	marginal segment of the cingulate sulcus, BA5/7
81	-3,18	R (25 6 57)	medial frontal gyrus (post, dorsolat, prefront.), BA8
81	-3,28	R (22 -21 54)	central sulcus (omega shaped knob), BA4
54	-3,31	R (31 27 36)	medial frontal gyrus (post, dorsolat, prefront.), BA8
54	-3,14	R (22 -3 -15)	central amygdala (basolateral)
54	-3,33	R (49 -21 -18)	ant, inferior temp, sulcus, BA20/21

Table 6. BOLD response correlating with increasing and decreasing valence; minsize: 2 voxels = 54 mm³, threshold $p < 0.001$.

mm ³	z-value	location	
Seed Voxel central amygdala (R)			
324	4,73	L (-35 -3 -15)	ant, mesial temporal lobe (planum polare) BA 38
162	4,62	L (-41 3 -24)	temporal pole BA 38
81	4,31	L (-17 -33 15)	dorsal postero-lateral Thalamus (Pulvinar?)
81	4,51	L (-35 -21 -15)	collateral sulcus BA 36
54	4,61	L (-20 -30 -9)	anterior parahippocampal gyrus BA 36
54	4,38	L (-23 -12 -15)	head of the hippocampus
54	4,47	L (-44 -27 -15)	anterior temporo-occipital sulcus BA 20
54	4,36	L (-14 -33 -18)	pontine nuclei
567	5,16	R (22 -18 -15)	head of the hippocampus
378	4,82	R (16 -36 -9)	posterior parahippocampal gyrus BA 36
297	4,86	R (40 15 -18)	temporal pole BA 38
81	4,70	R (7 -30 -18)	pontine nuclei
81	4,37	R (16 -48 6)	isthmus of the cingulate gyrus
54	4,80	R (7 -30 -9)	mesencephal tegmentum
54	4,52	R (7 -27 12)	dorsal postero-medial Thalamus (Pulvinar?)
54	4,44	R (10 -33 12)	dorsal postero-medial Thalamus (Pulvinar?)
Seed Voxel dorsal amygdala (L)			
1269	5,45	L (-20 -2 -6)	(seed voxel + stretching into ventral striatum)
297	5,24	L (-11 -26 -18)	pontine nuclei
216	4,46	L (-38 10 -15)	temporal pole BA 38
54	4,50	L (-53 22 0)	pars orbitalis BA 47
54	4,28	L (-11 40 -3)	sulcus cinguli BA 32 ("limbic" cortex)
54	4,39	L (-5 28 -12)	medial orbitofrontal cortex BA 12
54	4,66	L (-26 16 -12)	sulcus arcuatus (h-shaped orbital sulcus) BA 11
756	4,99	R (13 -5 -9)	contralateral dorsal amygdala/ventral striatum
162	5,22	R (31 -71 -33)	cerebellum, lobus posterior
135	4,35	R (28 -71 -18)	cerebellum, lobus posterior
108	4,57	R (40 13 -24)	temporal pole BA 38
54	4,54	R (22 22 -9)	sulcus arcuatus (h-shaped orbital sulcus) BA 11
54	4,47	R (13 -23 -9)	substantia nigra
54	4,33	R (7 -83 -15)	cerebellum, lobus posterior
54	4,29	R (-2 -5 9)	anteromedial thalamus

Table 7. Networks functionally connected to seedvoxels in the left dorsal and the right central amygdala; minsize: 2 voxels = 54 mm³, threshold $p < 0.00001$.

	category	Mafa music				Western music			
		c	d	r-c	r-d	c	d	r-c	r-d
Mafa listeners	value	0.46	0.07	-0.12	-0.41	0.19	0.05	-0.07	-0.16
	SEM	0.03	0.04	0.04	0.06	0.04	0.02	0.02	0.03
Western listeners	value	0.71	-0.42	0.28	-0.57	1.24	-0.20	-0.18	-0.86
	SEM	0.05	0.04	0.04	0.06	0.04	0.06	0.05	0.03
		cconsonant	ddissonant	r-c....reversed consonant	r-d ...reversed dissonant				

Table 8. Z-values as depicted in Figure 29.

General Linear Model				
	Mafa music		Western music	
direction	$F_{(1,39)} = 128.88$	$p < 0.001$	$F_{(1,40)} = 259.21$	$p < 0.001$
direction × subgroup	$F_{(1,39)} = 10.47$	$p = 0.002$	$F_{(1,40)} = 103.46$	$p < 0.001$
spectrum	$F_{(1,39)} = 190.39$	$p < 0.001$	$F_{(1,40)} = 261.78$	$p < 0.001$
spectrum × subgroup	$F_{(1,39)} = 44.93$	$p < 0.001$	$F_{(1,40)} = 175.00$	$p < 0.001$
length	$F_{(2,38)} = 19.60$	$p < 0.001$	$F_{(2,39)} = 2.54$	$p = 0.092$
length × subgroup	$F_{(2,38)} = 2.44$	$p = 0.101$	$F_{(2,39)} = 4.89$	$p = 0.013$
direction × spectrum	$F_{(1,39)} = 10.54$	$p = 0.002$	$F_{(1,40)} = 40.29$	$p < 0.001$
direction × spectrum × subgroup	$F_{(1,39)} = 2.30$	$p = 0.138$	$F_{(1,40)} = 37.63$	$p < 0.001$
direction × length	$F_{(2,38)} = 7.00$	$p = 0.003$	$F_{(2,39)} = 12.41$	$p < 0.001$
direction × length × subgroup	$F_{(2,38)} = 1.30$	$p = 0.286$	$F_{(2,39)} = 0.55$	$p = 0.583$
spectrum × length	$F_{(2,38)} = 8.50$	$p = 0.001$	$F_{(2,39)} = 11.02$	$p < 0.001$
spectrum × length × subgroup	$F_{(2,38)} = 6.55$	$p = 0.004$	$F_{(2,39)} = 0.90$	$p = 0.416$
direction × spectrum × length	$F_{(2,38)} = 0.21$	$p = 0.812$	$F_{(2,39)} = 2.38$	$p = 0.106$
direction × spectrum × length × subgroup	$F_{(2,38)} = 0.69$	$p = 0.507$	$F_{(2,39)} = 1.72$	$p = 0.193$
Factors:	direction (forward vs. reversed).....(c + d) vs. (r-c + r-d)		length.....2 vs. 10 vs. 30 sec	
	spectrum (consonant vs. dissonant)..... (c + r-c) vs. (d + r-d)		subgroup.....Mafa vs. Western listeners	

Table 9. Overview of the results from the ANOVA calculated with z-values for Mafa and Western music; significant main effects are printed in black.

General Linear Model				
	Mafa music		Western music	
subgroup	$F_{(1,39)} = 71.48$	$p < 0.001$	$F_{(1,40)} = 30.54$	$p < 0.001$
direction	$F_{(1,39)} = 58.11$	$p < 0.001$	$F_{(1,40)} = 157.85$	$p < 0.001$
direction × subgroup	$F_{(1,39)} = 17.67$	$p < 0.001$	$F_{(1,40)} = 54.41$	$p < 0.001$
spectrum	$F_{(1,39)} = 71.56$	$p < 0.001$	$F_{(1,40)} = 165.91$	$p < 0.001$
spectrum × subgroup	$F_{(1,39)} = 3.63$	$p = 0.064$	$F_{(1,40)} = 97.56$	$p < 0.001$
length	$F_{(2,38)} = 10.18$	$p < 0.001$	$F_{(2,39)} = 2.11$	$p = 0.134$
length × subgroup	$F_{(2,38)} = 4.36$	$p = 0.020$	$F_{(2,39)} = 5.25$	$p = 0.010$
direction × spectrum	$F_{(1,39)} = 5.65$	$p = 0.023$	$F_{(1,40)} = 31.51$	$p < 0.001$
direction × spectrum × subgroup	$F_{(1,39)} = 0.38$	$p = 0.542$	$F_{(1,40)} = 27.49$	$p < 0.001$
direction × length	$F_{(2,38)} = 8.84$	$p = 0.001$	$F_{(2,39)} = 11.17$	$p < 0.001$
direction × length × subgroup	$F_{(2,38)} = 2.25$	$p = 0.120$	$F_{(2,39)} = 0.58$	$p = 0.567$
spectrum × length	$F_{(2,38)} = 6.00$	$p = 0.005$	$F_{(2,39)} = 9.87$	$p < 0.001$
spectrum × length × subgroup	$F_{(2,38)} = 1.00$	$p = 0.379$	$F_{(2,39)} = 0.52$	$p = 0.598$
direction × spectrum × length	$F_{(2,38)} = 1.74$	$p = 0.190$	$F_{(2,39)} = 3.85$	$p = 0.030$
direction × spectrum × length × subgroup	$F_{(2,38)} = 2.03$	$p = 0.146$	$F_{(2,39)} = 2.58$	$p = 0.089$
Factors:	direction (forward vs. reversed).....(c + d) vs. (r-c + r-d)		length.....2 vs. 10 vs. 30 sec	
	spectrum (consonant vs. dissonant)..... (c + r-c) vs. (d + r-d)		subgroup.....Mafa vs. Western listeners	

Table 10. Overview of the results from the ANOVA calculated with non-transformed values for Mafa and Western music; significant main effects are printed in black.

mm ³	z-values	location	
<i>Increasing pleasantness</i>			
11367	4.96	L (-50 -18 6)	auditory cortex
7830	4.72	L (-5 -27 3)	VTA / periaqueductal grey
567	3.83	L (-11 30 27)	ACC
297	3.89	L (-5 -15 15)	dorsal thalamus / stria medullaris
270	3.75	L (-35 -18 3)	posterior insula
270	3.96	L (-32 27 -6)	posterior lateral orbitofrontal cortex
216	3.63	L (-29 12 -9)	posterior orbitofrontal cortex
189	3.65	L (-11 -84 -27)	cerebellum
108	3.67	L (-38 42 33)	anterior medial frontal gyrus
54	3.47	L (-26 39 24)	ant. superior frontal sulcus
54	3.40	L (-50 18 27)	inferior frontal sulcus
54	3.68	L (-8 0 27)	corpus callosum
54	3.71	L (-41 0 21)	IFG, opercular part
54	3.33	L (-35 27 15)	IFG, triangular part
54	3.09	L (-35 21 6)	anterior insula
7155	4.55	R (43 -18 9)	auditory cortex
945	4.77	R (28 -57 -18)	cerebellum
351	3.86	R (-2 -48 -30)	cerebellum
243	3.45	R (1 30 12)	ACC
243	3.70	R (22 6 -6)	ventral caudate
189	3.45	R (1 -6 57)	SMA
162	3.35	R (58 -30 24)	planum temporale
162	3.29	R (37 -36 9)	STS
108	3.34	R (7 -63 -9)	cerebellum
108	4.07	R (1 -60 -24)	cerebellum
108	3.59	R (46 -66 -30)	cerebellum
108	3.56	R (4 -36 -33)	pons
108	3.30	R (22 -63 -42)	cerebellum
81	4.07	R (34 -87 -18)	cerebellum
54	3.22	R (7 6 36)	cingulate sulcus
54	3.32	R (40 9 12)	IFG, opercular part
54	3.79	R (19 -21 3)	ventrolateral thalamus
54	3.36	R (4 36 -9)	medial orbitofrontal cortex
54	3.41	R (1 -27 -15)	pontomesencephalic transition area
54	3.87	R (52 -63 -24)	cerebellum
54	3.30	R (10 -63 -36)	cerebellum
<i>Decreasing pleasantness</i>			
108	-3.25	L (-32 6 51)	superior precentral sulcus
945	-3.85	R (25 12 51)	superior frontal sulcus

Table 11. Areas responding to increasing and decreasing pleasantness from the parametric analysis investigating an independent positive valence dimension from neutral to pleasant.

mm³	z-values	location	
<i>Increasing unpleasantness</i>			
162	-3.23	L (-35 24 42)	medial frontal gyrus
81	-3.49	L (-29 15 36)	superior frontal sulcus
54	-3.14	L (-29 -6 30)	white matter
54	-3.24	L (-20 15 12)	caudate nucleus
270	-3.51	R (7 6 18)	caudate nucleus
216	-3.63	R (31 39 33)	medial frontal gyrus
135	-3.54	R (19 -21 51)	motor cortex, hand field
81	-3.34	R (22 24 9)	white matter
54	-3.12	R (31 33 36)	medial frontal gyrus
<i>Decreasing unpleasantness</i>			
1161	3.93	L (-59 -12 6)	auditory cortex
189	3.82	L (-5 12 -9)	infragenual cortex
162	3.81	L (-35 -18 66)	motor cortex, hand field
54	3.28	L (-47 3 36)	precentral sulcus
486	3.61	R (61 -12 9)	primary auditory cortex
297	3.64	R (49 0 45)	precentral gyrus
270	3.62	R (43 27 18)	IFG, triangular part
135	3.90	R (22 27 -6)	posterior orbitofrontal cortex (H-shaped sulcus)
54	3.33	R (64 -24 12)	STG
54	3.30	R (16 -69 21)	cuneus
54	3.77	R (34 15 18)	IFG, opercular part

Table 12. Areas responding to increasing and decreasing unpleasantness from the parametric analysis investigating an independent negative valence dimension from unpleasant to neutral.

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List of Abbreviations

AB - accessory basal nucleus of the amygdala

ACC – anterior cingulate cortex

AC – anterior commissure

ANOVA - analysis of variance

ANS - autonomic nervous system

B - basal nucleus of the amygdala

BA - Brodmann area

BOLD - blood oxygenated level dependent

CE - central nucleus of the amygdala

CS - Conditioned stimulus

EPI – Echo Planar Imaging

fMRI - functional Magnetic Resonance Imaging

FOV – field of view

FWE – family wise error

FWHM – full-width at half-maximum

GLM - general linear model

GPI – globus pallidus interna

HPA - hypo-thalamic-pituitary axis

Hrf – hemodynamic response function

HRP - Horseradish peroxidase

Hz - hertz

HT – hypothalamus

IC - inferior colliculus

ICC – central nucleus of the inferior colliculus

IFG – inferior frontal gyrus
LA - lateral nucleus of the amygdala
LHb – lateral habenular nucleus
MDEFT – modified driven equilibrium fourier transform
MGm/PIN - medial division of the medial geniculate body
MGv - medial geniculate body
NAcc – nucleus accumbens
PC – posterior commissure
PET - Positron Emission Tomography
PFC – prefrontal cortex
PRh - perirhinal cortex
Raphe – raphe nucleus
RF - radio frequency
ROI - region of interest
SD - standard deviation
SE - standard error
SMA – supplementary motor area
SN – substantia nigra
SPL – sound pressure level
SPM – statistical parametric mapping
STS – superior temporal sulcus
SVC – small volume correction
TE – spin echo time
TE1 - primary auditory cortex
TE3 - auditory association cortex
TR – repetition time
VTA – ventral tegmental area