Progress in Neurobiology 123 (2014) 1–17

Contents lists available at ScienceDirect

Progress in Neurobiology

journal homepage: www.elsevier.com/locate/pneurobio

The role of the medial temporal limbic system in processing emotions in voice and music

Sascha Frühholz [a,b,1,*], Wiebke Trost [a,b,1], Didier Grandjean [a,b]

[a] Neuroscience of Emotion and Affective Dynamics Lab, Department of Psychology, University of Geneva, Geneva, Switzerland
[b] Swiss Center for Affective Sciences, University of Geneva, Geneva, Switzerland

ARTICLE INFO

Article history:
Received 5 June 2014
Received in revised form 16 September 2014
Accepted 29 September 2014
Available online 5 October 2014

Keywords:
Amygdala
Hippocampus
Emotion
Music
Voice
Neuroimaging

ABSTRACT

Subcortical brain structures of the limbic system, such as the amygdala, are thought to decode the emotional value of sensory information. Recent neuroimaging studies, as well as lesion studies in patients, have shown that the amygdala is sensitive to emotions in voice and music. Similarly, the hippocampus, another part of the temporal limbic system (TLS), is responsive to vocal and musical emotions, but its specific roles in emotional processing from music and especially from voices have been largely neglected. Here we review recent research on vocal and musical emotions, and outline commonalities and differences in the neural processing of emotions in the TLS in terms of emotional valence, emotional intensity and arousal, as well as in terms of acoustic and structural features of voices and music. We summarize the findings in a neural framework including several subcortical and cortical functional pathways between the auditory system and the TLS. This framework proposes that some vocal expressions might already receive a fast emotional evaluation via a subcortical pathway to the amygdala, whereas cortical pathways to the TLS are thought to be equally used for vocal and musical emotions. While the amygdala might be specifically involved in a coarse decoding of the emotional value of voices and music, the hippocampus might process more complex vocal and musical emotions, and might have an important role especially for the decoding of musical emotions by providing memory-based and contextual associations.

Contents

1. Introduction . . . 2
2. Which emotions are expressed and perceived in voices and music and how? . . . 3
3. The auditory system and the temporal limbic system (TLS) . . . 4
4. Vocal and musical emotions activate the TLS. . . . 6
   4.1. TLS activity in response to positive and negative vocal emotions . . . 6
      4.1.1. Amygdala . . . 6
      4.1.2. Hippocampus . . . 8
   4.2. TLS activity in response to musical emotions . . . 8
5. Affective arousal, emotional intensity and multimodal processing . . . 9
   5.1. TLS sensitivity to arousing and intense vocal emotions . . . 10
   5.2. TLS sensitivity to arousing musical emotions . . . 10

Abbreviations: ABR, auditory brainstem repsonse; AC/ac, auditory cortex; acb, accessory basal nucleus of the amygdala; AMY/amy, amygdala; b, basal nucleus of the amygdala; bg, basal ganglia; BOLD, blood oxygenation level dependent; c, central nucleus of the amygdala; ca, cornu armonis; CA1, cornu ammonis, subregion 1; CA3, cornu ammonis, subregion 3; cbll, cerebellum; CN, cochlear nucleus; CN/cn, cochlear nucleus; DG/dg, dentate gyrus; ERC, entorhinal cortex; erc, entorhinal cortex; F0, fundamental frequency; fMRI, functional magnetic resonance imaging; h, healthy controls; HC/hc, hippocampus; HG, Heschls gyrus; IC/ic, inferior colliculus; l, lateral nucleus of the amygdala; m, medial nucleus of the amygdala; MGB/mgb, medial geniculate body; MNI, Montreal Neurological institute; NAc, nucleus accumbens; p, patients; pc, patient controls; PET, positron emission tomography; PHC/phc, parahippocampal cortex; PPo, planum polare; PRC/prc, perirhinal cortex; PTe, planum temporale; SOC/soc, superior olivary complex; STC/stc, superior temporal cortex; STG, superior temporal gyrus; STS, superior temporal sulcus; sub, subiculum; TLS, temporal limbic system.

* Corresponding author at: Swiss Center for Affective Sciences, University of Geneva, 9 Chemin des Mines, PO Box 60, 1211 Geneva 20, Switzerland. Tel.: +41 22 379 09 15.
E-mail address: sascha.fruehholz@unige.ch (S. Frühholz).

[1] These authors are contributed equally to this review paper.

http://dx.doi.org/10.1016/j.pneurobio.2014.09.003
0301-0082/

6. Acoustic and structural features of vocal and musical emotions . . . 10
6.1. TLS sensitivity to acoustic features of vocal emotions . . . 10
6.2. TLS sensitivity to acoustic features of music . . . 11
6.3. TLS sensitivity to structural features of music . . . 11
7. A neural framework for processing vocal and musical emotions in the TLS . . . 11
7.1. Functional pathways for the decoding of vocal emotions . . . 12
7.2. Functional pathways for the decoding of musical emotions . . . 12
8. Conclusions . . . 13
Acknowledgements . . . 14
References . . . 14

1. Introduction

In order to signal and communicate our emotional states and feelings to other social individuals, humans utilize basic as well as elaborate means for social communication in different sensory modalities. Amongst other sensory modalities, auditory signals are important means for emotional communication. The voice, for example, is a very basic channel for expressing emotions that humans also share with nonhuman primates (Belin et al., 2004, 2008; Romanski and Averbeck, 2009) and with more distant ancestors, such as song birds (Williams, 2004). The human voice is a powerful way of expressing emotions, both as nonverbal short bursts of affective exclamations, such as laughter, cries, or screams (Sauter et al., 2010; Scherer, 1994; Schrober, 2003; Szameitat et al., 2010; Wattendorf et al., 2013), and as modulation of the intonation of speech utterances. The latter is often referred to as emotional prosody (Banse and Scherer, 1996; Grandjean et al., 2006; Patel et al., 2011; Sundberg et al., 2011) and describes the suprasegmental modulations of speech intonations predominantly in terms of pitch and intensity variations, but also along other features of the voice quality (Frühholz and Grandjean, 2013c; Frühholz et al., 2014; Wiethoff et al., 2008).

Besides vocal expressions humans also have developed more elaborated means to express emotional states in the auditory modality. One such example is the musical expression of emotions (Juslin and Vastfjall, 2008; Koelsch, 2010, 2014; Trost et al., 2012; Trost and Vuilleumier, 2013). Compared to vocal expressions, music and musically expressed emotions are a rather late achievement in human phylogenesis, which largely depended on the cultural development in human societies. However, music still has some long developmental trajectory dating back to the time of the *Homo neanderthalensis* (Conard et al., 2009). Over several centuries, musical techniques became very sophisticated, and developed into a powerful mean to express and communicate emotions, especially of complex emotional states (Trost et al., 2012; Zentner et al., 2008). It seems that many of the ways to express emotions in music are shared with vocal expressions (Juslin and Laukka, 2003; Weninger et al., 2013). Moreover, at the cognitive and the neural level, human individuals might use similar mechanisms and the same brain systems to decode emotions from voices and from music (Escoffier et al., 2012; Schirmer et al., 2012).

The human brain has developed specific mechanisms for the perception and the decoding of emotional signals. One of the most important brain regions for emotional processing is the limbic system, comprising several cortical areas, but mainly structures located in the medial temporal lobe and in the brainstem (Nieuwenhuys, 1996). The amygdala is thought to be located at the center of the limbic system and the emotional brain (LeDoux, 2000, 2012). Recent studies have shown that the amygdala is sensitive to emotional signals across many sensory modalities, including auditory information. Specifically, recent studies have shown that auditory stimuli such as *vocal expressions* (Bach et al., 2008a; Beaucousin et al., 2007; Ethofer et al., 2009; Fecteau et al., 2007; Frühholz et al., 2012; Frühholz and Grandjean, 2013a; Grandjean et al., 2005; Leitman et al., 2010b; Morris et al., 1999; Mothes-Lasch et al., 2011; Phillips et al., 1998; Quadflieg et al., 2008; Sander et al., 2003b, 2005, 2007; Sander and Scheich, 2005; Schirmer et al., 2008; Wiethoff et al., 2009) and *musically expressed emotions* (Alluri et al., 2012; Ball et al., 2007; Baumgartner et al., 2006; Blood and Zatorre, 2001; Brown et al., 2004; Chapin et al., 2010; Dyck et al., 2011; Eldar et al., 2007; Engel and Keller, 2011; Khalfa et al., 2008; Kleber et al., 2007; Koelsch et al., 2006, 2008, 2013; Lehne et al., 2014; Lerner et al., 2009; Mitterschiffthaler et al., 2007; Mueller et al., 2011; Mutschler et al., 2010; Pallesen et al., 2005, 2009; Park et al., 2013; Salimpoor et al., 2013) can elicit activity in the amygdala, indicating that both vocal emotions and musical emotions share similar ways of expression, and involve similar brain mechanisms for the decoding of and adaptive response to emotional cues.

Caudally to the amygdala lies the hippocampus. The hippocampus is also part of the limbic system (Nieuwenhuys, 1996) and is mainly assumed to have an important role in different cognitive functions especially related to episodic memory processes (Maguire, 2001) and for the formation of memory associations (Henke et al., 1997). Accordingly, the hippocampus has also been suggested to be important for the formation of emotional memories, especially in connection with activity in the amygdala (Phelps and LeDoux, 2005; Richardson et al., 2004). In this functional interaction, the amygdala is supposed to provide the affective evaluation of the stimulus and to contribute to the emotional reaction, whereas the hippocampus is thought to be responsible for memory encoding. But the hippocampus seems also to specifically influence emotional processing in the amygdala, and is important for emotional and social processing in general (Immordino-Yang and Singh, 2013).

This possible role of the hippocampus for emotional processing has been partly neglected, but recent studies on processing visual (Fusar-Poli et al., 2009) and auditory emotional stimuli, such as emotional vocalizations (Alba-Ferrara et al., 2011; Beaucousin et al., 2007; Kotz et al., 2012; Leitman et al., 2010b; Mitchell et al., 2003; Phillips et al., 1998; Rota et al., 2011; Sander et al., 2005; Szameitat et al., 2010; Wiethoff et al., 2008) and musical emotions (Alluri et al., 2012; Baumgartner et al., 2006; Blood and Zatorre, 2001; Chapin et al., 2010; Dyck et al., 2011; Eldar et al., 2007; Engel and Keller, 2011; Khalfa et al., 2008; Kleber et al., 2007; Koelsch et al., 2006; Lerner et al., 2009; Mitterschiffthaler et al., 2007; Mueller et al., 2011; Pallesen et al., 2009; Plailly et al., 2007; Salimpoor et al., 2013; Trost et al., 2012; Watanabe et al., 2008) have reported an involvement of the hippocampus in these processes as well. For the latter it has been suggested that hippocampal activity during emotional processing might add episodic memories and contextual associations to the perception of musically expressed emotions of complex social meaning (Trost et al., 2012). This however might also be the case for the perception of vocally expressed emotions, which have a certain level of social importance and complexity (Alba-Ferrara et al., 2011), and sometimes depend on