

## POSITIVE AND NEGATIVE MUSIC RECOGNITION REVEALS A SPECIALIZATION OF MESIO-TEMPORAL STRUCTURES IN EPILEPTIC PATIENTS

STÉPHANIE KHALFA

*Inserm U751 and Aix Marseille Université,  
Marseille, France*

CHARLES DELBE & EMMANUEL BIGAND

*Aix Marseille Université, Marseille, France*

EMMANUELLE REYNAUD, PATRICK CHAUVEL,  
& CATHERINE LIÉGEAIS-CHAUVEL

*Inserm U751 and Aix Marseille Université,  
Marseille, France*

AMYGDALA INVOLVEMENT IN FACIAL NEGATIVE EMOTION processing seems to be lateralized. The aim of the present study was to verify the existence of this phenomenon in the music domain and to study asymmetrical processing of emotions by the anteromedial temporal structures. Thirteen epileptic patients with left unilateral resection in the temporal lobe including the amygdala, hippocampus, parahippocampal gyrus, and anterior temporal pole, and fourteen patients with the same right-sided temporal resection, were asked to identify the emotion conveyed by music selections (happiness, sadness, or anger), and to assess their arousal (relaxing/stimulating aspects) and valence (pleasantness/unpleasantness aspects). The results demonstrated asymmetrical processing of positive emotions towards the left whereas negative (sad and angry) excerpts were either less recognized or confounded in both right and left operations. It seems that this impairment of music emotion recognition is not linked to an impairment of arousal and valence judgments.

*Received June 28, 2007, accepted November 1, 2007.*

**Key words:** music, emotion, amygdala, epilepsy, lateralization

**D**UE TO THE POWERFUL ABILITY OF MUSIC TO evoke emotions, experiments have increasingly used music excerpts to explore the cerebral basis of emotion processing.

Recently, several studies in brain lesioned patients have focused on the role of unilateral anteromedial temporal

structures (including the amygdala, the anterior temporal pole, and a part of the adjacent structures, i.e., hippocampus, parahippocampus gyrus, entorhinal, and perirhinal cortex) in assessment of music emotion recognition, valence (pleasantness/unpleasantness aspects), and arousal (relaxing/stimulating aspects). A first study showed impaired recognition of scary music following either right or left unilateral temporal lobe excision including the amygdala (Gosselin et al., 2005). Arousal ratings were also impaired by right temporal resection for scary and sad music that was judged less extreme in arousal, and by left temporal resection for peaceful music (less relaxing). Pleasantness judgments were spared in the operated patients. However, the larger the removal of parahippocampal cortex, the more impaired (i.e., the more pleasant) the valence ratings for scary music, i.e., music inducing fear (Gosselin et al., 2006). The amygdala appears thus to be involved in scary music recognition, while the parahippocampal gyrus seems to contribute to the unpleasantness judgements.

Other studies have also shown the involvement of the amygdala in positive emotion processing (Garavan, Pendergrass, Ross, Stein, & Risinger, 2001; Hamann & Mao 2002; Schneider et al., 1997). However, the amygdala essentially seems to be devoted to negative emotion processing such as fear (Adolphs, Tranel, Damasio, & Damasio, 1995; Davidson, 2002; LeDoux, 1992; ), and less frequently anxiety (Halgren, Walter, Cherlow, & Crandall, 1978), sadness (Schneider et al., 1997; Wang, McCarthy, Song, & Labar, 2005), and anger (Adolphs, Russell, & Tranel, 1999; Dougherty et al., 1999; Sato, Kubota, Okada, Murai, Yoshikawa, & Sengoku, 2002).

Amongst the many studies dealing with the role of the amygdala in emotion processing, unilateral amygdala involvement has frequently been explored and the most recent review of functional neuroimaging studies on this issue (Baas, Aleman, & Kahn, 2004) indicates that the left amygdala is more often activated than the right in response to emotional stimuli. The metaanalysis of findings from neuroimaging (Wager, Luan Phan, Liberzon, & Taylor, 2003) also did not support the classical hypothesis of overall right lateralization of emotional function (Erhan, Borod, Tenke, & Bruder, 1998; Levine & Levy, 1986; Spence, Shapiro, & Zaidel, 1996), but rather

found that amygdala activations were lateralized to the left, particularly for negative emotions, although the left amygdala may also respond to happy faces (Killgore & Yurgelun-Todd, 2001). Finally, the review from Zald (2003) included both neuroimaging and lesion studies, and confirmed that the amygdala responds to positively valenced stimuli, although these responses are less consistent than those induced by aversive stimuli. Regarding the laterality issue, a greater left amygdala involvement in association with negatively valenced stimuli was observed, whereas no clear pattern of lateralization emerged for positive stimuli.

On the contrary, a recent experiment has shown that direct intracerebral stimulation of the right human amygdala induces only negative emotions (especially fear and sadness) while the same electric stimulation of the left amygdala induces both positive (happiness) and negative (fear, anxiety, sadness) emotions (Lanteaume, Khalfa, Marquis, Chauvel, & Bartolomei, 2007). Happiness processing may thus involve the left amygdala, whereas negative emotions could involve both right and left amygdala.

The aim of the present study was thus to further explore this laterality issue in the music domain, and clarify whether the left temporal structures are involved in positive emotion processing, as well as whether both right and left anteromedial temporal structures respond to negatively valenced stimuli. In addition, we also aimed to study whether deficits in emotion recognition following unilateral temporal resections can be related to deficits in valence and arousal processing, knowing that this two-dimensional affective space defined by affective valence and arousal dimensions (Lang, Bradley, & Cuthbert, 1998) has already been found to be asymmetrically processed by the mesio-temporal structures (Gläscher & Adolphs, 2003).

According to the results obtained by Gläscher and Adolphs (2003), the arousal judgment might rely upon left anterior mesio-temporal lobe (including the amygdala) activity. They used subliminal and supraliminal emotional stimuli, and recorded skin conductance

responses in parallel to arousal ratings in responses to affective pictures. From their results, they hypothesized that the left amygdala may decode the stimulus arousal, while the right amygdala may provide a global level of autonomic activation by any arousing stimulus. We thus expected left temporal resection to decrease the ability to discriminate between relaxing and stimulating music.

In the present experiment, epileptic patients who underwent right or left anteromedial temporal lobe excision were presented with orchestral music intended to be strongly emotional (Bigand, Vieillard, Marozeau, & Dacquet, 2005) that conveyed the positive emotion of happiness and the negative emotions of sadness and anger.

## Method

### Participants

Twenty-seven seizure-free epileptic patients with unilateral resection either in the left temporal lobe ( $n = 13$ ) or in the right temporal lobe ( $n = 14$ ) participated in the experiment, which was carried out 6 to 18 months post-operatively. All patients coming for their postoperative medical check-up were included in the study if they had no additional neurological or psychiatric disease. They were matched as closely as possible on age, gender, handedness, education, and music training (only one or two participants per group had more than four years of music training) to 26 normal participants, recruited by advertisement, who had no history of neurological or psychiatric disease (see Table 1).

All patients were operated on for the treatment of temporal lobe epilepsy in La Timone Hospital (Marseille, France). An illustration of a representative excision is displayed in Figure 1. The right and the left antero-medial temporal lobe resections (RTR and LTR respectively) included the temporal pole, the whole amygdala, the whole entorhinal and perirhinal cortex, and a part of the hippocampus, the parahippocampal gyrus, and the superior temporal gyrus (T1). However, in five patients the

TABLE 1. Demographics for Right Temporal Resection (RTR), Left Temporal Resection (LTR), and Control Participants.

Groups	N	Age (years) (mean $\pm$ SE)	Males/ Females	Left-/right- handers	Education (years) (mean $\pm$ SE)	IQ (mean $\pm$ SD)
RTR	14	34.3 $\pm$ 10.4	4/10	4/10	12.3 $\pm$ 2.7	89.3 $\pm$ 12.0
LTR	13	28.7 $\pm$ 8.4	5/8	3/10	10.6 $\pm$ 2.07	80.6 $\pm$ 14.9
Controls	26	31.7 $\pm$ 11.3	11/15	4/22	12.7 $\pm$ 2.6	—

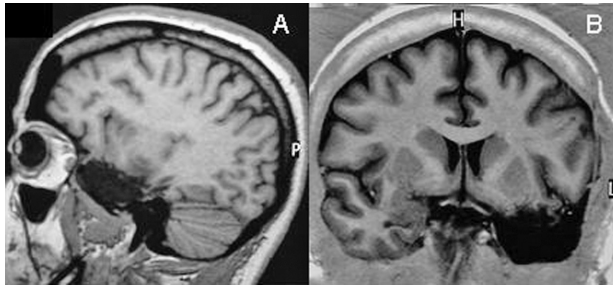


FIGURE 1. Sagittal (A) and frontal (B) MRI of a left operated epileptic patient with typical anterior mesio-temporal resection including the amygdala, the hippocampus, the parahippocampal gyrus, and the anterior temporal pole.

central amygdala nucleus was partially preserved as described in Table 2. Table 2 also indicates length of resected structures as compared to contralateral intact structures. Structure length was measured by two confirmed neuroradiologists on postsurgical MRI (3D T1 weighted images, 1 mm thickness) performed after 6 to 12 months (not available in 6 patients). Complete resection of the amygdala was assessed on coronal, axial, and sagittal images; T1, hippocampus, and parahippocampal gyrus were measured on sagittal images. We found no significant difference between RTR and LTR patients for T1, hippocampus, and parahippocampal gyrus ratios.

All participants gave written informed consent before testing, in accordance with the Declaration of Helsinki.

### Stimuli

Thirty music excerpts of 20-s duration were selected by music theorists and psychologists in order to elicit intense and homogeneous emotional experience. Most of these excerpts have already been precisely described in Bigand et al. (2005), and all of them are available online (<http://leadserv.u-bourgogne.fr/wave>). The chosen

music selections were intended to strongly and clearly evoke happiness (10 excerpts), sadness (10 excerpts), and anger (10 excerpts). The excerpts were chosen from the key musical periods of Western classical music (baroque, classic, romantic, and modern), and from the most important instrumental groups (solo, chamber music, orchestra).

### Procedure

During their clinical evaluation, participants were asked to relax in a comfortable armchair, listen attentively to the thirty musical excerpts, and concentrate as much as possible on the emotion conveyed by the music. The stimuli were presented in pseudorandomized order using the E-studio software (e-prime v 1.1), through two free field Yamaha NS10M loudspeakers. After each unique stimulus presentation, participants had to choose in a forced choice paradigm which emotion (happiness, sadness, or anger) best represented the excerpt they just heard. They then had to verbally rate the pleasantness (valence) and arousal they perceived in the music on two 10-point scales ranging from 1 (unpleasant) to 10 (pleasant), and from 1 (relaxing) to 10 (stimulating). Participants were told to base their emotional judgments on their own feelings. The emotional session lasted on average 25 to 40 min since some participants commented lengthily on each of their emotional ratings.

### Data Quantification and Analyses

Emotional ability was assessed by calculating the percentage of emotion recognition for sadness, happiness, and anger per participant. Arousal and valence rating means were also calculated for happy, sad, and angry music. In order to test for the Population (3 groups), Emotion (3 types), and Population  $\times$  Emotion interaction effects on the emotion recognition percentage,

TABLE 2. Postsurgical MRI Analysis Assessing the Extent of Resected Structures.

Populations	Central Nucleus of the Amygdala	T1 Ratio (mean $\pm$ SD)	Hippocampus Ratio (mean $\pm$ SD)	Parahippocampus Gyrus Ratio (mean $\pm$ SD)
RTR group	3/14	0.55 $\pm$ 0.10	0.49 $\pm$ 0.26	0.50 $\pm$ 0.20
LTR group	2/13	0.63 $\pm$ 0.11	0.39 $\pm$ 0.25	0.46 $\pm$ 0.20

Note: The length of resected superior temporal gyrus (T1), hippocampus, and parahippocampal gyrus is compared in each participant with the length of intact contralateral T1, hippocampus, and parahippocampal gyrus respectively.

arousal ratings, and valence ratings, two-way repeated measures ANOVAs were performed. When the ANOVAs reached significance, student *t*-tests or paired *t*-tests with Bonferroni corrections were performed as post hoc comparison tests.

## Results

### *Asymmetrical Impairment of Emotion Recognition*

Control participants' mean percentage of emotion recognition appears, on average, superior to 90% (see Figure 2). The selected music proved to evoke the intended emotions. Contrary to the controls, however, emotion recognition was diminished in patients. There was a significant Population  $\times$  Emotion interaction,  $F(4, 10) = 2.71, p < .05$ . The RTR specifically diminished sad excerpt recognition,  $t(38) = 2.72, p < .01$ , whereas the LTR compromised both happiness,  $t(37) = 3.35, p < .01$ , and anger recognition,  $t(37) = 2.94, p < .01$ , as compared to controls.

In patients with RTR, the sad excerpts (18.57%) that were not labelled as expected were instead incorrectly identified as angry. Therefore, the diminished recognition of sadness after RTR also revealed a deficit in anger judgments. However, for patients with RTR, positive emotion recognition was completely spared. In contrast, for patients with LTR, the happy excerpts (22.80%) not recognized as expected were instead identified as sad (13.10%) and angry (9.70%) excerpts. In addition, angry excerpts (23.00%) not recognized by these patients



FIGURE 2. Means and standard error bars of percentage of emotion recognition for the happy, sad, and angry excerpts in controls, patients with left temporal resection (LTR), and patients with right temporal resection (RTR). A \* indicates a significant difference between controls and patients.

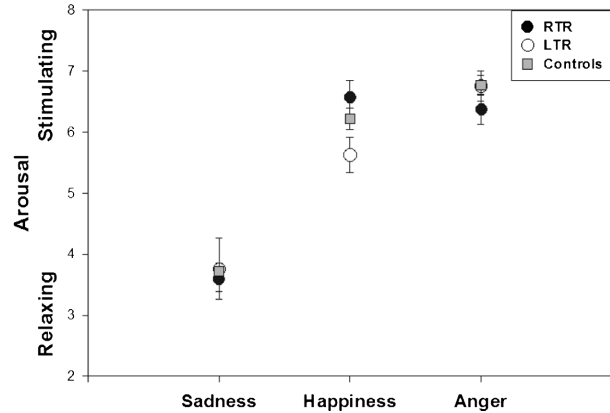


FIGURE 3. Means and standard error bars of arousal ratings for the musical selections conveying sadness, happiness, and anger in controls, patients with left temporal resection (LTR), and patients with right temporal resection (RTR).

were equally considered to be either happy (11.30%) or sad (11.70%). After LTR, the decreased recognition of happiness and anger was due to false emotion attribution distributed among sadness, happiness, or anger. Both positive and negative musical emotion recognition as compared to controls were therefore affected by LTR.

### *Non-Modified Arousal and Valence Judgments*

The ANOVA performed on the arousal ratings only displayed a significant Emotion effect,  $F(2, 98) = 138.49, p < .01$ ; the happy and angry excerpts were more stimulating than the sad excerpts,  $t(51) = 12.99, p < .0001$ , and  $t(51) = 15.30, p < .0001$ , respectively, as illustrated by Figure 3. The right and left operations did not modify the arousal evaluation. In addition, the valence rating only varied according to the Emotion,  $F(2, 100) = 4.13, p < .01$ . As expected, Figure 4 shows that happy music was found to be more pleasant than sad and angry music,  $t(52) = 6.87, p < .0001$ , and  $t(52) = 9.57, p < .0001$ , respectively irrespective of the participants' group.

## Discussion

Our first aim was to verify the existence of lateralized emotion recognition at the level of antero-mesial temporal structures. As hypothesized, our results seem to demonstrate left mesio-temporal structure involvement in positive emotion recognition (i.e., happiness). This result is consistent with previous experiments in other

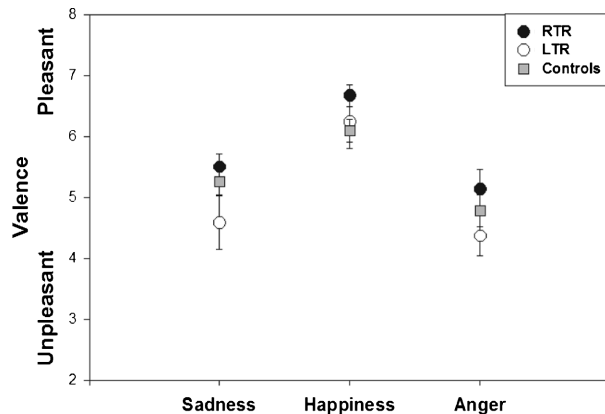


FIGURE 4. Means and standard error bars of percentage of valence ratings for the happy, sad, and angry music in controls, patients with left temporal resection (LTR), and patients with right temporal resection (RTR).

sensory domains demonstrating specific left amygdala activation when viewing happy faces (Schneider et al., 1997) or positive photographs (Hamann & Mao, 2002). Electrical stimulations of the left amygdala but not of the right amygdala also evoked happy feelings (Lanteaume et al., 2007). Thus, despite the inability of Zald's review (2003) to show clearly lateralized processing of positive stimuli by the amygdala, the more recent results cited above, as well as our results, argue in favour of lateralized amygdala (and/or adjacent structure) involvement towards the left in happiness processing, and particularly in happiness recognition in music. Since our patients' surgical resection included the amygdala but also the anterior temporal pole, the parahippocampal gyrus, and the hippocampus, and since these structures are interconnected (Charbardes, Minotti, Hoffman, & Benabid, 2002; Lavenex & Amaral, 2000; Pitkanen, Kelly, & Amaral, 2002; Wilson, Isokawa, Babb, & Crandall, 1990; Wilson, Isokawa, Babb, Crandall, Levesque, & Engel, 1991), it remains difficult to define which structure is responsible for the decrease in emotion recognition. The anterior temporal pole has rarely been demonstrated to participate in emotion processing (Royet et al., 2000). By contrast, several previous neuropsychological, electrophysiological, and neuroimaging studies have shown the role of the amygdala in emotion processing (Lanteaume et al., 2007; Scott, Young, Calder, Hellawell, Aggleton, & Johnson, 1997; Wager et al., 2003). Further investigations may yield more evidence of the role of each anteromedial temporal structure in emotion recognition.

Concerning the recognition of negative musical emotions, right temporal structures appeared to intervene

in sadness recognition while the left ones were related to anger recognition. However, given that in RTR patients the unrecognized sad excerpts were all misidentified as angry excerpts, the anger label was also not attributed as expected. It would thus be more accurate to conclude that RTR reduced both sadness and anger processing, which is in accordance with some previous experiments showing right or bilateral amygdala involvement in anger processing. In one study using direct intracerebral electrical stimulations of the amygdala, a feeling of anger was never evoked (Meletti, Tassi, Mai, Fini, Tassinari, & Lo Russo, 2006), while in two other studies, anger was rarely elicited following right amygdala stimulation (Halgren et al., 1978; Lanteaume et al., 2007). An event-related fMRI experiment also revealed a right amygdala response to anger prosody (Sander et al., 2005). On the contrary, anger in facial expressions (Adolphs, Tranel, Damasio, & Damasio, 1994; Graham, Devinsky, & LaBar, 2007; Sato et al., 2002), as well as anger in vocal affect (Scott et al., 1997) have been shown to be affected by bilateral amygdala lesions. A PET study did not provide evidence that angry expressions generate a signal in the amygdala (Blair, Morris, Frith, Perrett, & Dolan, 1999), nor an fMRI study (Sprengelmeyer, Rausch, Eysel, & Przuntek, 1998), while in another experiment, anger evoked by scripts of participants' past personal events activated the bilateral anterior temporal poles (Dougherty et al., 1999).

In patients with LTR, even if sadness was as well recognized as in controls, half of the non identified angry and happy stimuli were confounded with sad excerpts. This confusion also suggests a disruption of sad excerpt processing in these patients. These results parallel those of intracerebral amygdala stimulation in humans showing sadness elicitation by both right and left stimulations (Lanteaume et al., 2007).

However, it should be underlined that although the patients' ability in recognizing musical emotions decreased, the mean percentage of emotion recognition remained superior to 75%. The unilateral resection was not sufficient to completely disrupt emotion recognition in music as compare to controls.

The present study also intended to confirm the role of left mesio-temporal structures in arousal assessment, and to study the role of the mesio-temporal structures in valence evaluation. Contrary to a previous study with emotional pictures (Gläscher & Adolphs, 2003), arousal judgments of musical excerpts were not modified by the unilateral resections. The same result was observed with valence judgments. It is unexpected to note that the deficits observed in emotion recognition do not appear

to rely upon deficits in evaluating the valence and arousal emotional dimensions. The emotion categorization may then be at least partially independent from the two emotional determinants.

Finally, this study extends to the music domain the notion of mesio-temporal lobe involvement in anger processing, since LTR impaired anger recognition as compared to controls, and since RTR led to problems in identifying sad and angry music. Bilateral damage to amygdala has been shown to impair the recognition of emotional arousal for facial expressions, words, and sentences depicting anger (Adolphs et al., 1999). In addition, arousal was modified for scary and sad excerpts following unilateral anteromedial resection (Gosselin et al., 2005). On the contrary, in the present experiment, unilateral mesio-temporal damage including the amygdala solely reduced the recognition of anger but not of its arousal. Arousal deficits may therefore be more evident following bilateral amygdala damage, and when shorter and less emotional excerpts are employed. The strength of a stimulus' emotional content may improve the ability of operated patients to perceive arousal levels. However, it remains that despite the current use of such longer, complex (including orchestral music) stimuli, and despite the fact that many studies have not found mesio-temporal structure involvement in anger processing (Aftanas, Reva, Savotina, & Makhnev, 2006; Blair et al., 1999; Grandjean et al., 2005), anger recognition in music was decreased by the temporal lesions. This result reinforces previous studies showing the participation of medial temporal structures in anger processing in faces and voices (Dougherty et al., 1999; Sander et al., 2005; Sato et al., 2002; Scott et al., 1997; Graham et al., 2007).

In summary, positive happy music appears to be preferentially processed at the level of the left anteromedial temporal structures whereas negative (sad and angry) excerpts appear to be bilaterally processed. It seems that this decrease of music emotion recognition is not linked to a decrease of the two emotional determinants assessments, i.e., arousal and valence. Although emotion recognition tends to be very stable (Bigand et al., 2005), these results must be interpreted with the caveat that many factors such as the participant's mood may influence the reaction to music and then the subsequent emotional judgments. Further studies are also required to precisely determine which anteromedial structures are involved in music emotion processing, and why anger processing is not always related to mesio-temporal structure activity. It also would prove useful to study the extent to which asymmetrical emotional processing in limbic structures is linked to lateralized activity in the orbitofrontal cortex.

#### Author Note

We thank all the participants for their cooperation, and the medical team of the Epileptic unit of La Timone hospital (especially Patrick Marquis). This work was supported by a grant (ACI Neurosciences intégratives et computationnelles) from the French government.

*Correspondence concerning this article should be addressed to Dr. Stéphanie Khalifa, Laboratoire de Neurophysiologie et Neuropsychologie, Inserm U 751, Université de la Méditerranée, Faculté de médecine Timone 27, Bd Jean Moulin 13385 Marseille cedex 5-France. E-MAIL: skhalifa@skhalifa.com*

#### References

- ADOLPHS, R., RUSSELL, J. A., & TRANEL, D. (1999). A role for the human amygdala in recognizing emotional arousal from unpleasant stimuli. *Psychological Science, 10*, 167-171.
- ADOLPHS, R., TRANEL, D., DAMASIO, H., & DAMASIO, A. R. (1994). Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature, 372*, 613-614.
- ADOLPHS, R., TRANEL, D., DAMASIO, H., & DAMASIO, A. R. (1995). Fear and the human amygdala. *Journal of Neuroscience, 15*, 5879-5891.
- AFTANAS, L. I., REVA, N. V., SAVOTINA, L. N., & MAKHNEV, V. P. (2006). Neurophysiological correlates of induced discrete emotions in humans: an individually oriented analysis. *Neuroscience and Behavioral Physiology, 36*, 119-130.
- BAAS, D., ALEMAN, A., & KAHN, R. S. (2004). Lateralization of amygdala activation: a systematic review of functional neuroimaging studies. *Brain Research Review, 45*, 96-103.
- BIGAND, E., VIEILLARD, S., MAROZEAU, J., & DACQUET, A. (2005). Multidimensional scaling of emotional responses to music: the effect of musical expertise and of the duration of the excerpts. *Cognition and Emotion, 19*, 1113-1139.
- BLAIR, R. J. R., MORRIS, J. S., FRITH, C. D., PERRETT, D. I., & DOLAN, R. J. (1999). Dissociable neural responses to facial expressions of sadness and anger. *Brain, 122*, 883-893.

- CHABARDES, S., MINOTTI, L., HOFFMANN, D., & BENABID, A. L. (2002). Anatomy of the temporal pole region. *Epileptic Disorders, 4*, S9-15.
- DAVIDSON, R. J. (2002). Anxiety and affective style: Role of prefrontal cortex and amygdala. *Biological Psychiatry, 51*, 68-80.
- DOUGHERTY, D. D., SHIN, L. M., ALPERT, N. M., PITMAN, R. K., ORR, S. P., LASKO, M., ET AL. (1999). Anger in healthy men: A PET study using script-driven imagery. *Biological Psychiatry, 46*, 466-472.
- ERHAN, H., BOROD, J. C., TENKE, C. E., & BRUDER, G. E. (1998). Identification of emotion in a dichotic listening task: Event-related brain potential and behavioral findings. *Brain and Cognition, 37*, 286-307.
- GARAVAN, H., PENDERGRASS, J. C., ROSS, T. J., STEIN, E. A., & RISINGER, R. C. (2001). Amygdala response to both positively and negatively valenced stimuli. *Neuroreport, 12*, 2779-2783.
- GLÄSCHER, J., & ADOLPHS, R. (2003). Processing of the arousal of subliminal and supraliminal emotional stimuli by the human amygdala. *Journal of Neuroscience, 23*, 10274-10282.
- GOSSELIN, N., PERETZ, I., NOULHIANE, M., HASBOUN, D., BECKETT, C., BAULAC, M., & SAMSON, S. (2005). Impaired recognition of scary music following unilateral temporal lobe excision. *Brain, 128*, 628-640.
- GOSSELIN, N., SAMSON, S., ADOLPHS, R., NOULHIANE, M., ROY, M., HASBOUN, D., BAULAC, M., & PERETZ, I. (2006). Emotional responses to unpleasant music correlates with damage to the hippocampal cortex. *Brain, 129*, 2585-2592.
- GRAHAM, R., DEVINSKY, O., & LABAR, K. S. (2007). Quantifying deficits in the perception of fear and anger in morphed facial expressions after bilateral amygdala damage. *Neuropsychologia, 45*, 42-54.
- GRANDJEAN, D., SANDER, D., POURTOIS, G., SCHWARTZ, S., SEGHER, M. L., SCHERER, K. R., & VUILLEUMIER, P. (2005). The voices of wrath: Brain responses to angry prosody in meaningless speech. *Nature Neuroscience, 8*, 145-146.
- HALGREN, E., WALTER, R. D., CHERLOW, D. G., & CRANDALL, P. H. (1978). Mental phenomena evoked by electrical stimulation of the human hippocampal formation and amygdala. *Brain, 101*, 83-117.
- HAMANN, S., & MAO, H. (2002). Positive and negative emotional verbal stimuli elicit activity in the left amygdala. *Neuroreport, 13*, 15-9.
- KILLGORE, W. D., & YURGELUN-TODD, D.A. (2001). Sex differences in amygdala activation during the perception of facial affect. *Neuroreport, 12*, 2543-2547.
- LANG, P. J., BRADLEY, M. M., & CUTHBERT, B. N. (1998). Emotion and motivation: Measuring affective perception. *Journal of Clinical Neurophysiology, 15*, 397-408.
- LANTEAUME, L., KHALFA, S., MARQUIS, P., CHAUVEL, P., & BARTOLOMEI, F. (2007). Emotion induction after direct intracerebral stimulations of human amygdala. *Cerebral Cortex, 17*, 1307-13.
- LAVENEX, P., & AMARAL, D. G. (2000). Hippocampal-neocortical interaction: A hierarchy of associativity. *Hippocampus, 10*, 420-430.
- LEDoux, J. E. (1992). Brain mechanisms of emotion and emotional learning. *Current Opinion in Neurobiology, 106*, 274-85.
- LEVINE, S. C., & LEVY, J. (1986). Perceptual asymmetry for chimeric faces across the life span. *Brain and Cognition, 5*, 291-306.
- MELETTI, S., TASSI, L., MAI, R., FINI, N., TASSINARI, C. A., & LO RUSSO, G. (2006). Emotions induced by intracerebral electrical stimulation of the temporal lobe. *Epilepsia, 47*, 47-51.
- PITKANEN, A., KELLY, J. L., & AMARAL, D. G. (2002). Projections from the lateral, basal, and accessory basal nuclei of the amygdala to the entorhinal cortex in the macaque monkey. *Hippocampus, 12*, 186-205.
- ROYET, J. P., ZALD, D., VERSACE, R., COSTES, N., LAVENNE, F., KOENIG, O., & GERVAIS, R. (2000). Emotional responses to pleasant and unpleasant olfactory, visual, and auditory stimuli: A Positron Emission Tomography Study. *Journal of Neuroscience, 20*, 7752-7759.
- SANDER, D., GRANDJEAN, D., POURTOIS, G., SCHWARTZ, S., SEGHER, M. L., SCHERER, K. R., & VUILLEUMIER, P. (2005). Emotion and attention interactions in social cognition: Brain regions involved in processing anger prosody. *NeuroImage, 28*, 848-858.
- SATO, W., KUBOTA, Y., OKADA, T., MURAI, T., YOSHIKAWA, S., & SENGOKU, A. (2002). Seeing happy emotion in fearful and angry faces: Qualitative analysis of facial expression recognition in a bilateral amygdala-damaged patient. *Cortex, 38*, 727-742.
- SCHNEIDER, F., GRODD, W., WEISS, U., KLOSE, U., MAYER, K. R., NÄGELE, T., GUR, R. C. (1997). Functional MRI reveals left amygdala activation during emotion. *Psychiatry Research. Neuroimaging Section, 76*, 75-82.
- SCOTT, S. K., YOUNG, A. W., CALDER, A. J., HELLAWELL, D. J., AGGLETON, J. P., & JOHNSON, M. (1997). Impaired auditory recognition of fear and anger following bilateral amygdala lesions. *Nature, 385*, 254-257.
- SPENCE, S., SHAPIRO, D., & ZAIDEL, E. (1996). The role of the right hemisphere in the physiological and cognitive components of emotional processing. *Psychophysiology, 33*, 112-122.
- SPRENGELMEYER, R., RAUSCH, M., EYSEL, U. T., & PRZUNTEK, H. (1998). Neural structures associated with recognition of facial expressions of basic emotions. *Proceedings of the Royal Society of London—Biological Sciences, 265*, 1927-1931.
- WAGER, T. D., LUAN PHAN, K., LIBERZON, I., & TAYLOR, S. F. (2003). Valence, gender, and lateralization of functional brain

- anatomy in emotion: a meta-analysis of findings from neuroimaging. *NeuroImage*, 19, 513-531.
- WANG, L., MCCARTHY, G., SONG, A. W., & LABAR, K. S. (2005). Amygdala activation to sad pictures during high-field (4 tesla) functional magnetic resonance imaging. *Emotion*, 5, 12-22.
- WILSON, C. L., ISOKAWA, M., BABB, T. L., & CRANDALL, P. H. (1990). Functional connections in the human temporal lobe. I. Analysis of limbic system pathways using neuronal responses evoked by electrical stimulation. *Experimental Brain Research*, 82, 279-292.
- WILSON, C. L., ISOKAWA, M., BABB, T. L., CRANDALL, P. H., LEVESQUE, M. F. & ENGEL, JR., J., (1991). Functional connections in the human temporal lobe. II. Evidence for a loss of functional linkage between contralateral limbic structures. *Experimental Brain Research*, 85, 174-187.
- ZALD, D.H. (2003). The human amygdala and the emotional evaluation of sensory stimuli. *Brain Research Reviews*, 41, 88-123.



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.