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Amygdala damage impairs emotion recognition from music

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Abstract

The role of the amygdala in recognition of danger is well established for visual stimuli such as faces. A similar role in another class of emotionally potent stimuli – music – has been recently suggested by the study of epileptic patients with unilateral resection of the anteromedian part of the temporal lobe [Gosselin, N., Peretz, I., Noulhiane, M., Hasboun, D., Beckett, C., & Baulac, M., et al. (2005). Impaired recognition of scary music following unilateral temporal lobe excision. *Brain*, *128*(Pt 3), 628–640]. The goal of the present study was to assess the specific role of the amygdala in the recognition of fear from music. To this aim, we investigated a rare subject, S.M., who has complete bilateral damage relatively restricted to the amygdala and not encompassing other sectors of the temporal lobe. In Experiment 1, S.M. and four matched controls were asked to rate the intensity of fear, peacefulness, happiness, and sadness from computer-generated instrumental music purposely created to express those emotions. Subjects also rated the arousal and valence of each musical stimulus. An error detection task assessed basic auditory perceptual function. S.M. performed normally in this perceptual task, but was selectively impaired in the recognition of scary and sad music. In contrast, her recognition of happy music was normal. Furthermore, S.M. judged the scary music to be less arousing and the peaceful music less relaxing than did the controls. Overall, the pattern of impairment in S.M. is similar to that previously reported in patients with unilateral anteromedial temporal lobe damage. S.M.'s impaired emotional judgments occur in the face of otherwise intact processing of musical features that are emotionally determinant. The use of tempo and mode cues in distinguishing happy from sad music was also spared in S.M. Thus, the amygdala appears to be necessary for emotional processing of music rather than the perceptual processing itself.

Keywords: Emotion; Music; Amygdala; Fear; Arousal; Valence

1. Introduction

Emotion is an inherent part of our experience of music. Intensely pleasurable experience of music is frequently accompanied by the sensation of "chills" (Panksepp, 1995) and recruits neural regions that are involved in response to other euphoria inducing stimuli (Blood & Zatorre, 2001), such as chocolate (Small, Zatorre, Dagher, Evans, & Jones-Gotman, 2001). The power of music to engage neural networks that are important for survival is not limited to reward. Music also constitutes a highly efficient mean of signalling withdrawal or danger, as abundantly illustrated in films and videos. Recent evidence suggests that processing of scary music depends on the amygdala (Gosselin et al., 2005), a collection of subcortical nuclei in the medial temporal lobe known to be involved in triggering emotional responses, and specifically implicated in the processing of threat-related stimuli such as fear conditioning (LeDoux, 1996, 2000) and fear perception in facial expressions (Adolphs, Tranel, Damasio, & Damasio, 1994; Adolphs, Tranel, Damasio, & Damasio, 1995). The involvement of the amygdala in processing scary music derives from the study of patients with unilateral resection of the anteromedian part of the temporal lobe, resulting from neurosurgical resection for the treatment of epilepsy. These patients were found to be impaired in the recognition of scary music but exhibited spared recognition of other emotions expressed by music, such as happiness (Gosselin et al., 2005). While the results suggest that the amygdala is critical for the recognition of danger in music, they are not decisive because the resections were unilateral and included significant removal of surrounding neural tissue in the temporal lobe (i.e., hippocampus, entorhinal, perirhinal, parahippocampal cortices and temporal pole). In addition, the often long-standing epilepsy

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of the patients complicates the interpretation of their impairment. Patients with Urbach–Wiethe syndrome provide a unique exception to the above confounds due to the relative selectivity of the calcification of the amygdala (Markowitsch et al., 1994; Newton, Rosenberg, Lampert, & O'Brien, 1971; Tranel & Hyman, 1990; see also Zald, 2003). In order to ascertain the specific contribution of the amygdala, we study patient S.M., who remains to date the subject with the most selective and complete amygdala atrophy.

S.M. is a textbook case. Her detailed study has been instrumental in establishing the role of the human amygdala in the processing of stimuli related to danger. S.M. is unique in that she suffers from complete bilateral damage to the amygdala (LeDoux, 1996; Tranel & Hyman, 1990). As a result, S.M. is severely impaired in recognizing facial expressions of fear, whereas she is normal at recognizing happiness and other emotions in faces (Adolphs et al., 1994, 1995). S.M. also exhibits impaired arousal judgments notably for scary faces, whereas she has intact valence judgments (Adolphs, Russell, & Tranel, 1999). That is, S.M. finds fearful faces less arousing than normal controls whereas she judges them normally as unpleasant. Yet, S.M. is able to discriminate faces perceptually (Adolphs & Tranel, 2000). She has no difficulty to judge faces identity and gender and can discriminate facial expressions as normals do. These findings extend to humans earlier results highlighting the amygdala's role in fear processing in animals (Aggleton, 1992; LeDoux, 1996; Weiskrantz, 1956).

Curiously, S.M.'s deficit appears to be limited to facial expressions. S.M. consistently fails to recognize fear, and other emotions such as surprise, sadness, and anger, as normals do in facial expressions (Adolphs & Tranel, 2004; Adolphs et al., 1994) but she has no particular difficulty in recognizing these same emotions in emotional speech (Adolphs & Tranel, 1999; see also Adolphs & Tranel, 2000, for a detail review of S.M.'s performance across tasks and domains). In speech, S.M. judges normally the intensity of each prototypical emotion, including fear, surprise and anger, expressed by human speakers reading semantically neutral sentences. Moreover, in a follow up experiment, Adolphs and Tranel (2000) observed that S.M.'s intact recognition of emotion in prosody helped her to recognize fear in facial expressions when these were accompanied by a fearful voice. Taken together, these findings suggest that the human amygdala's role in recognizing negative emotions is limited to facial expressions. In fact, S.M. performs as normals do when presented with complex scenes in which both facial expressions, body postures, hand postures and interpersonal stances converge to express the same basic emotion (Adolphs & Tranel, 2003). Interestingly, S.M. performs best when facial expressions are erased, further supporting the notion of a deficit that is limited to facial expressions. Recently, the mechanism by which amygdala damage compromises fear recognition in facial expression in S.M. has been further elucidated (Adolphs et al., 2005). S.M.'s impairment in recognizing fear stems from her inability to direct her gaze spontaneously at the eyes region of faces, normally the most important feature for identifying fear in facial expressions.

Perhaps, facial expressions are particularly hard to decipher when there is a developmental anomaly in the normal neural wiring that sustains emotional appraisal of danger. Vocal cues might be easier to decode because these are usually accompanied by other signals, such as body gestures, language semantics and facial expressions during development, and can thus be associated with these other signals. The joint and repetitive association of vocal cues with contextual unambiguous signals may compensate for a developmental fragility in adequate neural wiring. Such a possibility makes the study of S.M. worthwhile in a musical context. Above all, there is no social pressure to respond to music in an emotionally adequate manner as long as music is experienced as an enjoyable activity. Hence, examination of S.M. with musical stimuli expressing different emotions, in particular threat, offers a unique opportunity to examine the role of the amygdala in the recognition of emotion in classes of auditory stimuli other than prosody. Indeed, the amygdala can be effectively activated in normal subjects listening to unpleasant music (Koelsch, Fritz, v Cramon, Müller, & Friederici, 2006) and deactivated by intensely pleasant music (Blood & Zatorre, 2001).

Thus, S.M. is presented here with the same material and tasks used in our prior study which proved to be diagnostic of an emotional impairment in recognizing danger in music (Gosselin et al., 2005). The material comprises 56 novel complex musical excerpts composed with the intention of being reliably recognized as expressing threat, peacefulness, sadness and happiness. The task is to judge the intensity of each emotion for each musical stimulus on 10-point scales, following a procedure similar to that used in prior studies of S.M. with facial and vocal expressions (Adolphs & Tranel, 1999; Adolphs et al., 1994). Participants are also required to assess arousal and valence on distinct 10-point scales. These latter judgments aim at assessing if S.M. exhibits impaired arousal and yet intact valence judgments in the recognition of musical expressions of threat, as she does for faces (Adolphs et al., 1999).

In order to be able to distinguish between an emotional deficit and a perceptual disorder, the ability of S.M. to process the same musical set is assessed with an error detection task. Furthermore, in order to assess whether S.M. is able to extract emotionally relevant musical characteristics, such as mode and tempo, she is tested with a different material and task in Experiment 2. The latter situation also uses complex musical excerpts. In this test, the mode and tempo of each excerpt are orthogonally manipulated so as to assess the use of these determinant cues for judging happiness and sadness in music, following the procedure adopted in a prior study of an amusic patient (Peretz, Gagnon, & Bouchard, 1998).

2. Experiment 1: recognition of scary music

2.1. Method

2.1.1. Participants

Patient S.M. is a 38-year-old woman with a high-school education and with complete bilateral damage to the amygdala. S.M. has been extensively studied by Adolphs and collaborators over the past decade (see Adolphs & Tranel, 2000, for a detailed account of her neuroanatomical and neuropsychological profile). S.M.'s damage encompasses all nuclei within the amygdala as well as anterior portions of entorhinal cortex, yet sparing all other subcortical and cortical structures. As a result, S.M. has essentially normal basic perception, memory and language, as long as it does not involve emotional material. S.M. is a typical nonmusician who occasionally listens to music.

The normal controls (NC) are four neurologically intact women matched in age (mean: 34, S.D.: 3.7), education (mean: 12.8 years; S.D.: 1.5) and music background to S.M. All participants gave their informed consent prior to their inclusion in these studies that have been approved by the ethic committees of l'Institut Universitaire de Gériatrie de Montréal and by the Institutional Review Board of the University of Iowa.

2.1.2. Emotional task

2.1.2.1. Material. Fifty-six novel musical excerpts were written by a professional composer with the intention to express fear, peacefulness, happiness, or sadness (14 excerpts per intention). The musical excerpts are conventional in that they follow the rules of the Western tonal system. The stimuli have a regular temporal structure with the exception of a few scary excerpts, as described below. All musical excerpts involve a melody with an accompaniment. The happy excerpts were written in the major mode at an averaged tempo of 137 Metronome Marking (M.M. range: 92–196), with the melodic line lying in the medium-high pitch range. In contrast, the sad excerpts were written in the minor mode at an averaged slow tempo of 46 M.M. (range: 40–60). The peaceful music was in major, intermediate in tempo (mean: 74, range: 54–100), and played with arpeggio accompaniment. The scary music was relatively fast at an average of 97 M.M. (range: 44–172) and composed with minor chords on the third and sixth degrees, hence implying the use of accidentals. Most scary excerpts are consonant and regular (see Gosselin et al., 2005, for the musical notation of the excerpts). Examples of excerpts for each emotion category can be heard on our web site at www.brams.umontreal.ca/peretz. The stimuli last on average 12.4 s (range: 9.2–16.4) and are matched in length across the four emotion categories. Short excerpts of the soundtracks of the films 'Jaws' and 'Schindler's List' serve as examples, for scary and sad music, respectively, in orienting participants to the tasks. All stimuli are computer-generated.

2.1.2.2. Procedure. Participants are presented with the two examples followed by the 56 stimuli presented in one of two different fixed random orders. For each stimulus, they are asked to judge to what extent it expresses each of four emotions (happiness, sadness, threat and peacefulness) by indicating their rating on a 10-point scale (where 0 corresponded to 'absent' and 9, 'present'). Participants are informed that a musical excerpt could express more than one emotion. For example, participants are asked to rate a peaceful stimulus with respect to happiness ('gai'), sadness ('triste') and threat ('épeurant'), and not just peacefulness ('apaisant'). They are further required to judge each stimulus on two distinct dimensions: arousal and valence. For the arousal dimension, participants rate whether the music sounds relaxing or stimulating on a 10-point scale (with 0 corresponding to 'most relaxing' and 9 to 'most stimulating'). For valence, subjects rate on a 10-point scale whether the music sounds pleasant or not (with 0 corresponding to "most unpleasant" and 9, "most pleasant"). They give judgments in this fixed order. In some rare events, it happens that the subject requests to hear the stimuli a second time, it is then repeated (this occurs rarely, and never happened for S.M.). No feedback is given, with the exception of the two examples. Subjects are tested individually in a 45 min session. S.M. and each normal participant are tested twice with a different order of stimuli on a different day.

2.1.3. Error detection task

The error detection task is devised with 24 of the 56 stimuli used in the emotional task (six happy, six sad, six scary and six peaceful). These 24 excerpts are modified so as to contain a timing error. This is done by randomly changing the timing of the tone onsets of the leading voice in an entire measure, thereby giving the impression that the pianist is suddenly losing track of what s/he is playing for a short moment. These 24 modified versions are randomly mixed with 24 intact excerpts. The task is to indicate if the pianist lost track of what s/he is playing at some point in the piece. Participants respond 'yes' if they detect an error and 'no' otherwise. There are four examples. Participants are not informed of the nature of the changes and no feedback is provided, except for the examples. The error detection task is presented following the emotional task.

3. Results

3.1. Error detection task

The percentages of correct responses are computed for S.M. and the normal controls (NC) in the error detection task. Percentages of correct responses correspond to 98% and 85% (range: 67–96) for S.M. and NC, respectively. Thus, S.M. performs in the high normal range in this non-emotional task.

3.2. Emotional tasks

Since participants were free to select as many of the four emotion labels as they wished and to provide a graded judgement for each, we first derive the best label attributed to each musical excerpt by each participant. This is done by selecting the label that has received the maximal rating. For this initial analysis, when the maximal rating corresponds to the label that matches the intended emotion of the composer, a score of 1 is given. When the maximal rating does not correspond to the intended emotion, a score of 0 is given. When the highest rating is given for more than one label, the response is considered as 'ambivalent' and receives a score of 0. As can be seen in Table 1, normal controls attribute the highest ratings to the intended emotion for the musical stimuli. Sadness tends to be somewhat confused with peacefulness, whereas threat and happiness are clearly distinguished and identified. In contrast, S.M. exhibits difficulties in recognizing both the sad ($z = -8.91$, $p < 0.001$, by a two-tailed test) and scary expressions ($z = -4.97$, $p < 0.001$). For peacefulness and happiness, S.M.'s responses are similar to the normal controls ($z = -1.05$ and 1.50, respectively, both $p > 0.05$).

Table 1
Mean percentages for the label that received the maximal rating by (A) S.M. and (B) the normal controls, as a function of the four intended emotions

Intentions	Responses				
	Scary	Peaceful	Happy	Sad	Ambivalent
(A) S.M					
Scary[a]	**64***	18	7	4	5
Peaceful	0	**61**	21	11	7
Happy	0	0	**100**	0	0
Sad	0	50	7	**39***	4
(B) Normal controls					
Scary	**87 (4.5)**	0	0	3	10
Peaceful	0	**70 (8.5)**	5	4	21
Happy	0	0	**97 (1.8)**	0	3
Sad	0	8	0	**80 (4.6)**	12

Bold type indicates the match between responses and intentions. Ambivalent responses correspond to highest ratings given to more than one label. S.D. are presented in parentheses for normal controls. An asterisk indicates that S.M.'s judgments differ significantly from controls ($p<0.001$).
[a] One stimulus was omitted because S.M. responded 0 for all labels.

Fig. 1. Mean ratings, expressed as z scores, for the four intended emotions given by S.M., 16 epileptic patients with unilateral anteromedian temporal lobe resection (UTR) and 20 normal controls (NC; including 16 controls matched to the epileptic patients and 4 matched controls to S.M.; the 4 controls matched to S.M. are represented by circles). Standard deviations are represented with bars. An asterisk indicates that S.M.'s and UTR patients' ratings differ significantly from NC.

In order to better characterize the difficulty experienced by S.M. in recognizing the scary and sad stimuli, her errors for these two emotional categories are further examined. As can be seen in Table 1, S.M. mostly confounds scary[1] with peaceful music (63% of the errors). This particular confusion never occurs in normals. S.M. also tends to confound sadness with peacefulness, and occasionally mistakes sad stimuli as happy, an error that never occurs in normal controls. Thus, both the mean accuracy of S.M. in recognizing fear and sadness, and also the pattern of errors (confusions with other emotions) that she makes, are highly abnormal.

S.M.'s performance is then compared to the previously published results from patients with unilateral resection of the amygdala and surrounding neural structures (Gosselin et al., 2005). S.M.'s scores are z-transformed in order to control for the different use of the scale across participants. Z scores are computed by considering the individuals' own mean and S.D. in rating the four labels. Controls' scores include the 16 controls tested in our prior study and the four matched controls of S.M. As can be seen in Fig. 1, S.M. and patients with unilateral amygdala damage show a recognition impairment for scary stimuli compared to normal controls ($z=-2.30$, $p<0.05$ and $z=-2.96$, $p<0.005$, respectively). Moreover, S.M. judges the happy music more intense than normal controls ($z=2.21$, $p<0.05$). No other comparison is significant. Note that the sad stimuli are judged to be less intense by S.M. as compared to her four matched controls ($z=-44.00$, $p<0.001$), but this difference is no longer significant when S.M.'s results are compared to the group of 20 normal controls ($z=-1.38$, $p>0.05$). Furthermore, S.M. does not differ from patients with unilateral amygdala damage in recognizing scary ($z=0.25$), peaceful ($z=0.86$), happy ($z=1.59$) and sad music ($z=-0.36$, all $p>0.05$). Thus, bilateral damage to the amygdala leads to a very similar deficit in emotion recognition as does unilateral damage.

The other emotional judgments, in terms of arousal and valence, are also informative. The scores are transformed to z scores relative to the individuals' own mean and S.D. of rating distribution across the arousal or valence scales. As can be seen in Fig. 2, S.M.'s ratings differ from controls in arousal judgments. S.M. judges the scary music as less arousing ($z=-3.67$, $p<0.001$) and the peaceful music as less relaxing ($z=6.33$, $p<0.001$) than controls. In contrast, S.M. judges the happy music to be more arousing than normal controls do ($z=2.37$, $p<0.05$). Nonetheless, S.M.'s arousal judgments are as sensitive to tempo variations as are those given by normals. Her ratings on the arousal dimension correlate with the tempi of the stimuli ($r=0.76$, with 56 d.f., $p<0.01$, by two-tailed test). Valence judgments are less clearly affected (see Fig. 3). The only difference to reach significance is found for the peaceful stimuli which S.M. judges to be less pleasant than the controls do ($z=-2.61$, $p<0.01$). S.M.'s pleasantness judgments are also influenced by tempo. She tends to judge faster musical tempi as more pleasant ($r=0.55$, with 56 d.f., $p<0.01$) whereas normals

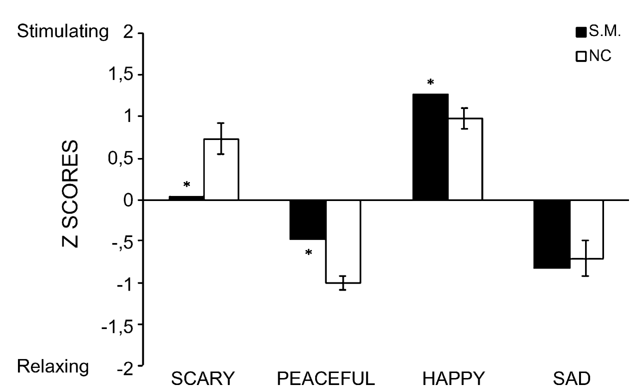

Fig. 2. Mean ratings expressed as z scores for arousal as a function of the four intended emotions for S.M. and the normal controls (NC). Standard deviations are represented with bars.

[1] Because the scary stimuli were variable in structure, by containing varying degrees of dissonance and temporal irregularities, it was deemed worthwhile to examine the possible influence of these different structures features on S.M.'s responses. However, no specific contribution of structural features could be discerned in S.M.'s judgments.

Fig. 3. Mean ratings expressed as z scores for valence as a function of the four intended emotions for S.M. and the normal controls (NC). Standard deviations are represented with bars.

controls' pleasantness judgements are unaffected by tempo ($r = -0.04$). In general, the arousal and valence judgments are similarly affected in S.M. as in patients with unilateral temporal lobe excision (Gosselin et al., 2005).

4. Discussion

S.M. is impaired in the recognition of both scary and sad music. Interestingly, she frequently mistakes scary music for peaceful music, a mistake that is never made by controls. She also confounds sad and peaceful music, a confusion that is also occasionally made by normal controls. The sad music is somewhat more difficult to identify in our set than would be expected on the basis of the literature (see Gabrielsson & Justlin, 2003; Juslin & Laukka, 2003, for recent reviews). Generally, happy and sad music are the easiest emotions to convey musically. The present difficulty to recognize sadness (with 59% correct recognition of the intended emotion when all twenty normal controls are pooled together) might be due to the fact that the sad and peaceful stimuli are written so as to differ mostly by mode and not by tempo. The mode is major in the peaceful stimuli whereas it is minor in the sad selections, both being played with a rather slow tempo. However, tempo is more salient than mode in determining sadness (e.g., Gagnon & Peretz, 2003). Hence, this might create confusion between sadness and peacefulness, a point to which we return in Experiment 2. In contrast, the recognition of musical expressions of threat is clearly impaired in S.M., as attested by her aberrant choice of peacefulness and happiness as the intended emotion for a significant proportion of the scary stimuli and by her arousal judgements indicating that she does not judge scary music as stimulating as control subjects do. The lower arousal value of the scary music cannot be due to a lack of consideration of musical cues by S.M.; her ratings are affected by tempo. Moreover, S.M. correctly judges the scary music as being unpleasant. Yet, she does not seem to be able to use this knowledge effectively in selecting the appropriate emotional label for the scary music.

This atypical behavior does not seem to arise as a consequence of impaired perceptual abilities. S.M. obtains a fairly high level of performance in the error detection task that used the same stimuli as in the emotional task. Her results suggest the presence of an emotion recognition impairment with spared perceptual music processing abilities. Further support for spared processing of musical structure in S.M. is provided in the next experiment.

5. Experiment 2: use of mode and tempo

This second experiment aims at determining the musical cues that S.M. is able to use to recognize emotion in music. Since our stimuli are computer-generated with a piano timbre, instrumentation and interpretation cannot have contributed to the judgments. In contrast, mode and tempo are two structural properties that are known to convey important emotional information (Dalla Bella, Peretz, Rousseau, & Gosselin, 2001; Gagnon & Peretz, 2003; Hevner, 1935, 1937) and are intentionally manipulated in our pool of musical selections used in Experiment 1. Slow tempi, or few beats per minute, tend to evoke sad moods whereas fast tempi, or many beats per minute, tend to evoke happy moods. Mode is related to the subset of pitches selected in a given musical segment: the minor mode is associated with a sad tone whereas the major mode is associated with a happy tone (Crowder, 1984). However, these two structural determinants are combined with other musical characteristics in the musical selections used in Experiment 1.

In order to assess the respective contribution of tempo and mode to the emotional evaluation of the musical stimuli, we exploit here another material that has been previously and successfully used with a brain-damaged patient suffering from musical impairments (Peretz et al., 1998) and with children (Dalla Bella et al., 2001). In this situation, the musical selections are taken from pre-existing music and their tempo and mode are manipulated orthogonally in three different conditions. In the tempo condition, all tempi are set to an unique median value. In the mode condition, the pieces are transcribed in the opposite mode with respect to its original mode. Finally, to examine the joint influence of mode and tempo, the two modifications applied in isolation in the mode and tempo conditions are combined. The task of the subjects is to judge on a 10-point scale whether each excerpt sounds happy or sad.

5.1. Method

S.M. and seven normal female controls matched in age (37 years) and education (13 years) participate in this experiment. Four of these matched controls also participated in Experiment 1. They are tested in four conditions using the same set of stimuli. The stimuli consist of 32 musical excerpts that are drawn from Western classical music (see Peretz et al., 1998, fore more details). These are selected so that half evoke a sense of happiness and the other half a sense of sadness. Happy selections are written in major mode (e.g., "Brindisi" from Verdi's "Traviata") and are played at a fast tempo (the quarter note value varied from 80 to 255 M.M.); sad selections are written in minor mode (e.g., Albinoni's "Adagio") and are played at a slow tempo (between 20 and 100 M.M.). All excerpts are transcribed for piano and are computer-generated. The excerpts, which do not undergo any structure modification, are referred to as the "original condition". In the "mode condition", all excerpts are transcribed in the opposite mode. That is, an excerpt in major mode is transformed into minor mode and vice versa. In the "tempo condition", all tempi are set to a unique value (with the quarter note at 84 M.M.) corresponding to the median value of the tempi used for all the excerpts in the original condition. In the "mode-tempo condition", the mode and tempo conditions are combined in order to assess the joint influence of mode and tempo manipulations.

Participants are presented with the full set of 32 excerpts in each of the four conditions and are required to judge whether each excerpt sounded happy or sad. The excerpts are presented in random order in each condition. The response is provided by means of a 10-point scale, with 1 meaning "sad" and 10 meaning "happy". The experiment lasts approximately an hour.

6. Results

The excerpts are considered as happy or sad with respect to the a priori classification of the excerpts in their original version (i.e., with "happy" corresponding to major mode and fast tempi, and "sad" corresponding to minor mode and slow tempi). The mean ratings obtained by S.M. and the matched controls are presented in Fig. 4. As can be seen, both S.M. and controls show sensitivity to the structural manipulations.

To assess these effects statistically, the ratings obtained for each selection by S.M. and normal controls are submitted to separate ANOVAs, both considering items as the random factor, and Condition (original, mode, tempo, mode and tempo) as the within-items variable. Emotional category (happy, sad) is considered as a between-items variable.

Ratings are significantly influenced by the condition presented, with a Category by Condition interaction in both S.M.'s data and controls' data ($F(3,90) = 23.23$ and 47.78, respectively, both $p < 0.001$). Comparisons between conditions were performed two by two, by separate ANOVAs, considering the same factors as in the overall ANOVA. These subsequent analyses indicate that each modification applied to the original version significantly affects the response pattern. When compared with the original version, the mode condition yields a significant interaction between Condition and response Category (with $F(1,30) = 9.04$, $p < 0.01$ and 40.25, $p < 0.001$, for S.M. and controls, respectively), as does the tempo condition (with $F(1,30) = 40.90$ and 50.46, $p < 0.001$, for S.M. and controls, respectively) and the mode + tempo condition (with $F(1,30) = 51.23$ and 80.93, $p < 0.001$, for S.M. and controls, respectively).

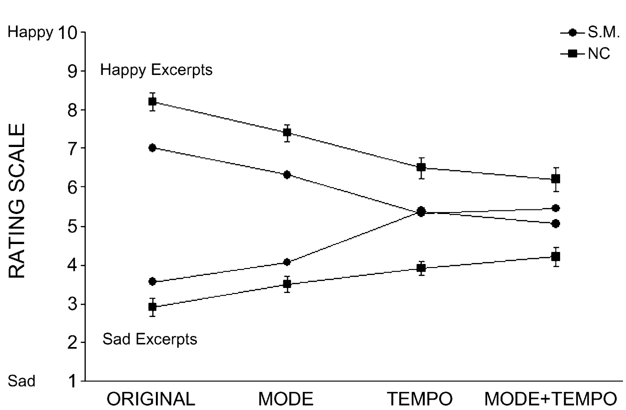

Fig. 4. Mean ratings for the happy and sad excerpts in the original, mode, tempo, and mode + tempo condition as given by S.M. and seven normal controls (NC). Standard errors are represented with bars.

7. Discussion

This second experimentation indicates that both mode and tempo modifications affect S.M.'s performance, particularly when the presented musical excerpts incorporate both modifications. Moreover, S.M.'s responses are strikingly similar to those of normal subjects, hence showing normal ability to employ tempo and mode as cues for emotional interpretation. The results suggest that S.M.'s emotional judgments are based on a normal structural analysis of the musical input, as far as the happy-sad distinction is concerned. Therefore, it is likely that S.M.'s confound between sad and peaceful stimuli in Experiment 1 is due to an inadequate weighting of the mode and tempo characteristics that are distinguishing these stimuli. Alternatively, S.M. may suffer from a genuine impairment in judging sadness in music and her apparent sparing in the present experiment might be due to the adoption of a strategy by default. S.M. may judge each stimulus relative to the happy end of the scale (i.e., as more or less happy). That is, even if S.M. has difficulties to evaluate whether musical selections express sadness as indicated in Experiment 1, she can achieve this judgment in the present setting by rating sad music relatively to the happy end of the scale, a strategy that could not be used in Experiment 1.

8. General discussion

The results show that recognition of scary music can be impaired by damage to the amygdala. The impairment is also relatively selective because recognition of happiness is normal, and recognition of peacefulness and sadness in music is less affected. The impairment does not seem to reflect task difficulty because the scary stimuli are generally easy to identify by normal participants (with 87% correct recognition of the intended emotion), and because the pattern of errors that S.M. makes for scary stimuli is quite different from the pattern of errors made by controls. S.M. chooses peacefulness for scary music while fear and peacefulness are never confused by normal controls. This abnormal pattern of errors has also been observed after right temporal resection (Gosselin et al., 2005). S.M.'s results converge with prior results obtained in epileptic patients who had undergone unilateral removal of the amygdala (Gosselin et al., 2005). Therefore, S.M.'s deficit in processing emotion is not restricted to faces, but extends to at least some classes of stimuli in other sensory modalities. This finding is also consistent with prior studies that have found positive evidence for the involvement of the amygdala in the auditory recognition of emotions in vocal sounds such as screams and yells (Scott et al., 1997) and speech prosody (Morris, Scott, & Dolan, 1999; Phillips et al., 1998; Scott et al., 1997) in other patients than

S.M.. S.M.'s difficulty to recognize scary music is also consistent with recent neuroimaging data obtain in normal subjects for unpleasant music (Koelsch et al., 2006). The amygdala appears to serve a multimodal role in processing emotions that are related to threat (see Zald, 2003, for a recent review).

The novelty of the present results is that the disorder in emotion recognition of danger can be observed in S.M. via the auditory channel. As noted in the introduction, S.M.'s impairment has been demonstrated in the recognition of facial expressions but not in the recognition of vocal emotions in speech (that are spared). Up to now, faces appear to be the prime emotional stimuli to trigger the involvement of the amygdala in S.M. (Adolphs & Tranel, 2003). Music now appears as another powerful mean to assess the neural correlates of threat-related responses in audition. There is no obvious reason why music and not prosody would be more effective to reveal a deficit in S.M. One possibility is that S.M. has difficulty to extract the emotional cues contained in the musical structure, as revealed here, but no particular difficulty with musical prosody (Juslin & Laukka, 2003; Palmer & Hutchins, 2006). Musical prosody refers to the expressive cues added to the musical structure. To test musical prosody, one needs to design a new material interpreted by real (not virtual as done here) musicians who would play the same melody in a scary, peaceful, happy and sad way. This should be the goal of future studies. At this stage, the dissociations in S.M.'s fear recognition still present a puzzle. The dissociations suggest that not all processing of the concept of fear relies on the amygdala, and they leave open the possibility that the amygdala is important for processing only a certain set of sensory cues that can signal the emotion.

The contribution of the amygdala to emotion recognition from music appears emotional in nature. Damage to the amygdala does not seem to compromise perception. Both S.M. and epileptic patients with anteromedial resection obtain a fairly high level of performance in an error detection task that uses the same stimuli as in the emotional task; patients' scores in error detection do not differ from normal ones. Moreover, the use of musical information for emotion processing, such as mode and tempo, appears normal in S.M., as shown in Experiment 2. She is able to use dynamic auditory cues related to temporal information (tempo) and pitch information (major–minor mode) to distinguish happy from sad music. Thus, lesion to the amygdala results in a relatively selective emotion recognition deficit that cannot be accounted for by a perceptual failure. The deficit seems to arise from a difficulty in associating otherwise intact perceptual processing of the structural features of the music with its emotional meaning. One possibility is that S.M.'s musical problem could be explained, like for facial expressions (Adolphs et al., 2005), by a difficulty to direct her attention to the relevant musical cues that are important to recognize emotions. If S.M.'s musical impairment is similar to her difficulty in recognizing fear in facial expressions, we should be able to direct her attention to the relevant musical emotional characteristics and enable her to perceive fear and sadness in music as normals do. While this is feasible for sadness because we know what are the perceptual determinants (i.e., mode and tempo), we do not yet know what are the structural characteristics of scary music. In our prior study (Gosselin et al., 2005), we tested different possibilities, namely irregularity, dissonance and the presence of unexpected events, but none could account for the judgments of normal subjects. Thus, the goal of future studies should be to identify what musical features signal unambiguously danger via music so as to be able to draw the attention of S.M. (or other similar patients) to these features and test the attentional account of the deficit in the musical domain.

S.M.'s inability to interpret musical information that signals potential danger is further attested by her aberrant choice of peacefulness or happiness as the intended emotion, an error never made by any control. She also judges scary music to be less stimulating than normals. Yet, S.M. judges the scary stimuli as unpleasant as the controls do. A similar pattern was also found in patients with unilateral removal of the amygdala (Gosselin et al., 2005). One possible explanation for these abnormal emotional judgments is that patients might find the scary stimuli less threatening than normals, not because they cannot perceive them as scary, but rather because they are not as aroused by the music as compared to normals. However, if this is the case, then the patients should have problems with the happy stimuli because these are even more arousing than the scary stimuli. Yet, both S.M. and epileptic patients perform as normals in recognizing happiness in a musical context. It would seem then that these two types of emotional judgments, by discrete category and by dimension, respectively, are relatively independent. However, scary music might be related to arousal in a slightly different manner. Scary music might be more salient (for normal individuals). Indeed, it has been proposed that the primary role of the human amygdala is to enhance the perception of stimuli that have emotional salience in order to achieve awareness (Anderson, Adam, Phelps, & Elizabeth, 2001). Perhaps, the scary stimuli are the most motivationally significant stimuli in the present set of stimuli because they signal aversive events (e.g., such as in the 'Psycho' or 'Jaws' films). Happy stimuli would be inoffensive in this respect and hence be less salient. In failing to note the saliency of the scary stimuli, due to a diminished arousal level, patients with amygdala damage may not predict the advent of potential danger as expressed in music.

Pleasantness judgments are similar for S.M. and for normal controls except for peaceful music. S.M. judges the peaceful stimuli as less pleasant than her matched controls. Perhaps, S.M. misinterprets slow tempi with negative emotions such as sadness. At any rate, finding a general impairment in arousal judgments and relatively preserved pleasantness judgments is not a new finding. It has been shown that the amygdala responds more strongly to the emotional arousal elicited by high-arousal odors, but does not differentiate between the pleasantness or unpleasantness of the odors (Anderson et al., 2003). This arousal-dependent response fits nicely with the present results found with music and with similar arousal-dependent amygdala responses reported previously with visual stimuli (Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000; Hamann, 2001) and with gustatory stimuli (Small et al., 2003). Moreover, some imaging studies found increased activation in the amygdala for positively valenced multimodal stimuli (see, Phan, Wager, Taylor, & Liberzon, 2002; Zald, 2003; for a review). For example, sexual stimuli (Beauregard, Levesque, & Bourgouin, 2001; Karama et al., 2002), monetary reward (Knutson, Adams, Fong, & Hommer, 2001; Knutson, Fong, Adams, Varner, & Hommer, 2001), sucrose artificial saliva (O'Doherty, Deichmann, Critchley, & Dolan, 2002), chocolate (Small et al., 2001) and cocaine (Breiter et al., 1997; Ketter et al., 1996) are associated with activation in the amygdala. However, the relation between the activation in the amygdala and pleasant stimuli is far less consistent than for aversive stimuli (Zald, 2003). For example, pleasant stimuli (euphoria induced by procaine or by music; viewing faces of loved ones; viewing happy faces) are often associated with a decreased activation in the amygdala. Thus, the present results are generally consistent with an implication of the amygdala for emotionally salient stimuli regardless of their valence.

To conclude, music is an appropriate medium to assess emotional processing because music is a powerful emotional trigger and is easy to manipulate for research purposes. In future studies, we should pay special attention to the type of musical cues that convey potential threat to the listener so as to be able to manipulate them and assess their effects on behavioral or brain responses. This type of research should provide insight into the nature of the contribution of the amygdala.

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References

Adolphs, R., Gosselin, F., Buchanan, T. W., Tranel, D., Schyns, P., & Damasio, A. R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature*, *433*, 68–72.

Adolphs, R., Russell, J. A., & Tranel, D. (1999). A role for the human amygdala in recognizing emotional arousal from unpleasant stimuli. *Psychological Science*, *10*(2), 167–171.

Adolphs, R., & Tranel, D. (1999). Intact recognition of emotional prosody following amygdala damage. *Neuropsychologia*, *37*(11), 1285–1292.

Adolphs, R., & Tranel, D. (2000). Emotion recognition and the human amygdala. In J. Aggleton (Ed.), *The amygdala: A functionnal analysis* (pp. 587–630). Oxford: Oxford University Press.

Adolphs, R., & Tranel, D. (2003). Amygdala damage impairs emotion recognition from scenes only when they contain facial expressions. *Neuropsychologia*, *41*(10), 1281–1289.

Adolphs, R., & Tranel, D. (2004). Impaired judgments of sadness but not happiness following bilateral amygdala damage. *Journal of Cognitive Neuroscience*, *16*(3), 453–462.

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*(6507), 669–672.

Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. R. (1995). Fear and the human amygdala. *The Journal of Neurosciences*, *15*(9), 5879–5891.

Aggleton, J. P. (1992). The functional effects of amygdala lesions in humans: A comparison with findings from monkeys. *The Amygdala: Neurobiological Aspects of Emotion, Memory, and Mental Dysfunction*, 485–503.

Anderson, A. K., Adam, K., Phelps, E. A., & Elizabeth, A. (2001). Lesions of the human amygdala impair enhanced perception of emotionally salient events. *Letters to nature*, *41*, 17.

Anderson, A. K., Christoff, K., Stappen, I., Panitz, D., Ghahremani, D. G., Glover, G., et al. (2003). Dissociated neural representations of intensity and valence in human olfaction. *Nature Neuroscience*, *6*(2), 196–202.

Beauregard, M., Levesque, J., & Bourgouin, P. (2001). Neural correlates of conscious self-regulation of emotion. *Journal of Neuroscience*, *21*, RC165.

Blood, A. J., & Zatorre, R. J. (2001). Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(20), 11818–11823.

Breiter, H. C., Gollub, R. L., Weisskoff, R. M., Kennedy, D., Makris, N., Berke, J., et al. (1997). Acute effects of cocaine on human brain activity. *Neuron*, *19*, 591–611.

Canli, T., Zhao, Z., Brewer, J., Gabrieli, J. D., & Cahill, L. (2000). Event-related activation in the human amygdala associates with later memory for individual emotional experience. *Journal of Neuroscience*, *20*(19), RC99.

Crowder, R. G. (1984). Perception of the major/minor distinction: 1. Historical and theoretical foundations. *Psychomusicology*, *4*(1–2), 3–12.

Dalla Bella, S., Peretz, I., Rousseau, L., & Gosselin, N. (2001). A developmental study of the affective value of tempo and mode in music. *Cognition*, *80*(3), B1–B10.

Gabrielsson, A., & Juslin, P. N. (2003). Emotional expression in music. In R. J. Davidson, H. H. Goldsmith, & K. R. Scherer (Eds.), *Handbook of affective sciences* (pp. 503–534). New York: Oxford University Press.

Gagnon, L., & Peretz, I. (2003). Mode and tempo relative contributions to "happy-sad" judgements in equitone melodies. *Cognition and Emotion*, *17*(1), 25–40.

Gosselin, N., Peretz, I., Noulhiane, M., Hasboun, D., Beckett, C., Baulac, M., et al. (2005). Impaired recognition of scary music following unilateral temporal lobe excision. *Brain*, *128*(Pt 3), 628–640.

Hamann, S. (2001). Cognitive and neural mechanisms of emotional memory. *Trends in Cognitive Sciences*, *5*(9), 394–400.

Hevner, K. (1935). The affective character of the major and minor modes in music. *American Journal of Psychology*, *47*, 103–118.

Hevner, K. (1937). The affective value of pitch and tempo in music. *American Journal of Psychology*, *49*, 621–630.

Juslin, P. N., & Laukka, P. (2003). Communication of emotions in vocal expression and music performance: Different channels, same code? *Psychological Bulletin*, *129*(5), 770–814.

Karama, S., Lecours, A. R., Leroux, J. M., Bourgouin, P., Beaudoin, G., Joubert, S., et al. (2002). Areas of brain activation in males and females during viewing of erotic film excerpts. *Human Brain Mapping*, *16*, 1–13.

Ketter, T. A., Andreason, P. J., George, M. S., Lee, C., Gill, D. S., Parekh, P. I., et al. (1996). Anterior paralimbic mediation of procaine-induced emotional and psychosensory experiences. *Archives of General Psychiatry*, *53*(1), 59–69.

Knutson, B., Adams, C. M., Fong, G. W., & Hommer, D. (2001). Anticipation of increasing monetary reward selectively recruits nucleus accumbens. *Journal of Neuroscience*, *21*, RC159.

Knutson, B., Fong, G. W., Adams, C. M., Varner, J. L., & Hommer, D. (2001). Dissociation of reward anticipation and outcome with event-related fMRI. *Neuroreport*, *12*(17), 3683–3687.

Koelsch, S., Fritz, T., v Cramon, D. Y., Müller, K., & Friederici, A. D. (2006). Investigating emotion with music: An fMRI study. *Human Brain Mapping*, *27*(3), 239–250.

LeDoux, J. E. (1996). *The emotional brain*. New York: Simon & Schuster.

LeDoux, J. E. (2000). Emotion circuits in the brain. *Annual Review of Neuroscience*, *23*, 155–184.

Markowitsch, H. J., Calabrese, P., Wurker, M., Durwen, H. F., Kessler, J., Babinsky, R., et al. (1994). The amygdala's contribution to memory-a study on two patients with Urbach-Wiethe disease. *Neuroreport*, *8*, 1349–1352.

Morris, J. S., Scott, S. K., & Dolan, R. J. (1999). Saying it with feeling: Neural responses to emotional vocalizations. *Neuropsychologia*, *37*(10), 1155–1163.

Newton, F. H., Rosenberg, R. N., Lampert, P. W., & O'Brien, J. S. (1971). Neurologic involvement in Urbach–Wiethe's disease (lipoid proteinosis). A clinical, ultrastructural, and chemical study. *Neurology*, *21*, 1205–1213.

O'Doherty, J. P., Deichmann, R., Critchley, H. D., & Dolan, R. J. (2002). Neural responses during anticipation of a primary taste reward. *Neuron*, *33*, 815–826.

Palmer, C., & Hutchins, S. (2006). What is musical prosody? In B. H. Ross (Ed.), *The psychology of learning and motivation: Advances in research and theory: Vol. 46*, (pp. 245–278). Oxford: Elsevier.

Panksepp, J. (1995). The emotional source of "chills" induced by music. *Music Perception*, *13*, 171–207.

Peretz, I., Gagnon, L., & Bouchard, B. (1998). Music and emotion: Perceptual determinants, immediacy, and isolation after brain damage. *Cognition*, *68*(2), 111–141.

Phan, K. L., Wager, T., Taylor, S. F., & Liberzon, I. (2002). Functional neuroanatomy of emotion: A meta-analysis of emotion activation studies in pet and fMRI. *NeuroImage*, *16*, 331–348.

Phillips, M. L., Young, A. W., Scott, S. K., Calder, A. J., Andrew, C., Giampietro, V., et al. (1998). Neural responses to facial and vocal expressions of fear and disgust. *Proceedings of the Royal Society of London Series B-Biological Sciences*, *265*(1408), 1809–1817.

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*(6613), 254–257.

Small, D. M., Gregory, M. D., Mak, Y. E., Gitelman, D., Mesulam, M. M., & Parrish, T. (2003). Dissociation of neural representation of intensity and affective valuation in human gustation. *Neuron*, *39*, 701–711.

Small, D. M., Zatorre, R. J., Dagher, A., Evans, A. C., & Jones-Gotman, M. (2001). Changes in brain activity related to eating chocolate: From pleasure to aversion. *Brain*, *124*(Pt 9), 1720–1733.

Tranel, D., & Hyman, B. T. (1990). Neuropsychological correlates of bilateral amygdala damage. *Archives of Neurology*, *47*, 349–355.

Weiskrantz, L. (1956). Behavioral changes associated with ablation of the amygdaloid complex in monkeys. *Journal of Comparative and Physiological Psychology*, *49*(4), 381–391.

Zald, D. H. (2003). The human amygdala and the emotional evaluation of sensory stimuli. *Brain Research Reviews*, *41*, 88–123.