



Recognition of facial emotion in nine individuals with bilateral amygdala damage

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Received 14 September 1998; accepted 2 March 1999

Abstract

Findings from several case studies have shown that bilateral amygdala damage impairs recognition of emotions in facial expressions, especially fear. However, one study did not find such an impairment, and, in general, comparison across studies has been made difficult because of the different stimuli and tasks employed. In a collaborative study to facilitate such comparisons, we report here the recognition of emotional facial expressions in nine subjects with bilateral amygdala damage, using a sensitive and quantitative assessment. Compared to controls, the subjects as a group were significantly impaired in recognizing fear, although individual performances ranged from severely impaired to essentially normal. Most subjects were impaired on several negative emotions in addition to fear, but no subject was impaired in recognizing happy expressions. An analysis of response consistency showed that impaired recognition of fear could not be attributed simply to mistaking fear for another emotion. While it remains unclear why some subjects with amygdala damage included here are not impaired on our task, the results overall are consistent with the idea that the amygdala plays an important role in triggering knowledge related to threat and danger signaled by facial expressions. © 1999 Elsevier Science Ltd. All rights reserved.

1. Introduction

Studies in animals have demonstrated the amygdala's importance in behaviors elicited by stimuli with high emotional significance. Recently, the amygdala's role has also been explored in humans, using both the lesion method and functional imaging. Several reports found that bilateral damage to the human amygdala impairs the recognition of emotions in facial expressions, especially in the case of fear [6,7,12,13,25,26]. Similarly, functional imaging studies

have found activation of the amygdala when viewing facial expressions of fear, as compared to neutral faces [11,19,20,21], even under conditions of subliminal presentation [24]. These studies provide strong support for the idea that the amygdala, in humans as in animals, plays a key role in triggering behaviors and knowledge retrieval in response to biologically salient stimuli, especially those related to possible danger and threat.

However, comparisons between different studies have been difficult, because different sets of stimuli, and different methods, have been used. For example, several studies by Young and colleagues [12,13,25,26] have used certain sets of face stimuli, and a labeling task, whereas other studies [6,7,15] have used a different set of stimuli and a task in which subjects' ratings

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Table 1
Background data for bilateral amygdala subjects^a

Subject	Age	Lesion			Etiology	Ref.
		Left amyg	Right amyg	Other		
SM	31	Complete	Complete	Minimal	Congenital	[6,7,22]
JM	67	Complete	Complete	Extensive	Encephalitis	[5]
RH	42	Complete	Complete	Extensive	Encephalitis	[5]
SE	65	Complete	Complete	Extensive	Encephalitis	[13]
DR	57	Partial	Minimal	Minimal	Surgical	[25]
GT	59	Complete	Complete	Extensive	Encephalitis	[15]
EP	73	Complete	Complete	Extensive	Encephalitis	[15]
SP	52	Partial	Complete	Moderate	Lobectomy	[9,10]
DBB	28	Complete	Partial	None	Surgical	[17,18]

^a Age at testing. Lesion: extent of lesion from neuroanatomical analyses. Readers are referred to prior publications for more detailed information.

were correlated with normal ratings. Moreover, the study by Hamann et al. [15] reported intact recognition of facial emotion in two subjects with complete bilateral amygdala damage.

The present report is a collaboration between all the different laboratories that have published data on facial emotion recognition in subjects with bilateral amygdala damage, with the aim of examining subjects from several research groups on the same task, so as to permit direct comparisons. We report findings from six individuals who have been described in prior reports, and from three whose facial recognition was studied here for the first time. All nine subjects were administered identical stimuli in an identical task that provided a detailed and quantitative assessment of their ability to recognize emotion in facial expressions (identical to that used in [6,7,15]). We addressed the following specific issues:

1. We re-investigated the hypothesis that bilateral amygdala damage would impair the recognition of fear in facial expressions by comparing the group of nine individuals with bilateral amygdala damage with a group of 16 brain-damaged controls, all tested on the same task. This provided sufficient power to permit a direct statistical test of the hypothesis.
2. We further hypothesized that impairments in recognizing facial emotion would not be restricted to fear, but rather would encompass a class of emotions related to threat and danger. Again, our sample size permitted a statistical test of this possibility.
3. Finally, we wished to explore the reasons that individuals with bilateral amygdala damage might be impaired in recognizing facial emotion. In particular, did they consistently mistake one facial emotion for another, or did they simply give a more incon-

sistent performance on certain facial emotions? To determine performance consistency, a subset of subjects participated in replications of the experiment.

2. Methods

2.1. Participants

2.1.1. Target subjects

Neuroanatomical data on all individuals with bilateral amygdala lesions included in this study have been described previously. A summary of their etiology and background biographical information is given in Table 1. Subjects SM [6,7], EP and GT [15] have previously been tested on the same task used here; SP has been tested on a subset of the stimuli with an identical analysis [9,10]. Subjects DR and SE [13,25,26] have previously been tested on different tasks requiring choice of emotion labels from a list, and using different stimuli. Data on facial emotion recognition from JM, RH, and DBB are presented here for the first time. Subjects were tested by several, different individuals, depending on the research group from which the data were obtained.

2.1.2. Brain-damaged controls

An additional 16 brain-damaged subjects without bilateral amygdala damage were tested to provide a group to control for the possible effects of brain damage per se. All these subjects were selected from the Patient Registry of the University of Iowa and had chronic, focal brain lesions. Previous studies [2] have shown that lesions in certain sectors of neocortex in right hemisphere also impair recognition of emotional facial expressions, and subjects with lesions in these regions were therefore excluded.

Data from participants with bilateral amygdala lesions, and from brain-damaged controls, were correlated with those from a group of seven normal individuals who have been used as a reference group in previous publications [6,15], in order to permit comparisons to the extant data. An additional, separate group of five normal subjects was also tested for the replicate experiments described below. All people had given informed consent to participate in this study.

2.2. Task

We used stimuli and procedures identical to those published in [6,7]. Subjects were shown slides of the faces of 6 different individuals each displaying six different basic emotions (happiness, surprise, fear, anger, disgust, sadness), and three neutral faces, for a

total of 39 stimuli. All 39 stimuli were presented in random order with no time limit. The 39 stimuli were shown six times in separate blocks, and subjects rated the stimuli with respect to the intensity of each of the six basic emotions, rating one emotion in each of the six blocks. Thus, for a particular facial expression of, say, happiness, subjects would be asked to rate the face with respect to the intensity shown of happiness, surprise, fear, anger, disgust, and sadness. Ratings were given on a scale of 0 (least) to 5 (most). No feedback was given to the subject to indicate what emotion the stimuli were showing. Subject SP was administered a subset of the stimuli (two happy and two surprised faces; three faces of all other emotions) under identical task conditions, due to time constraints.

Five of the subjects with bilateral amygdala damage, nine of the brain-damaged controls, and an additional group of five normal controls (separate from the seven normals that served as the group with which all data were correlated) were administered the same task twice, on different testing dates, to investigate the consistency with which subjects rated the faces. Repeated testing was administered by the same individual, except in the case of SM, who was administered the task twice by each of two testers.

2.3. Data analysis

In addition to presenting raw data, we calculated Pearson correlation scores as follows. The rating profile given to each face by each brain-damaged subject was correlated with the mean rating profile given to that face by the group of seven normal individuals. Thus, correlations near 1 indicate that the subject rated the stimulus normally; correlations near 0 (or negative) indicate that the subject rated the stimulus very abnormally. This procedure controls for the possibility that different individuals may have different judgments of absolute intensity (for example, some subjects might find all the stimuli very intense, whereas others might find them all rather weak); thus, the procedure essentially prevents floor and ceiling effects, and controls for idiosyncratic global response biases.

To calculate averages for correlations over several faces (e.g., the average correlation for all six happy faces), a subject's correlation for each individual face was *Z*-transformed, the *Z*-transformed correlations were averaged over all 6 faces that expressed a given emotion, and the average was then inverse *Z*-transformed to obtain the mean correlation for that emotion (cf. [6,7]).

To obtain a measure of the consistency with which a person rated the faces, in those cases where the task had been administered twice, we calculated the absolute difference in the correlation obtained for each face on the two testing sessions.

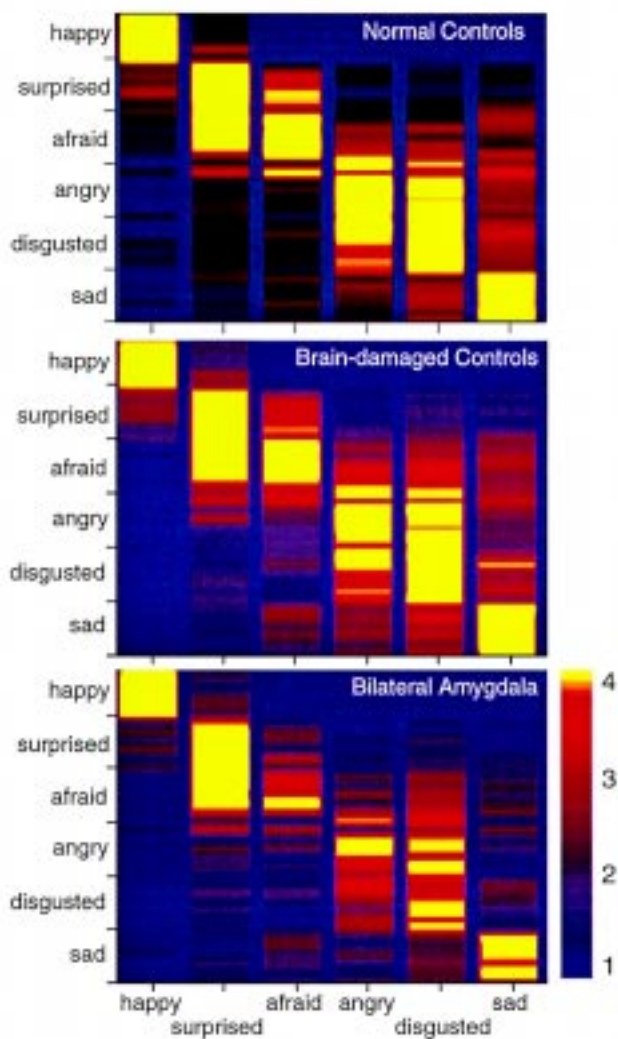


Fig. 1. Raw rating scores of facial expressions of emotion. The emotional stimuli (36 faces; six each of each of the six basic emotions indicated) are ordered on the *y*-axis according to their perceived similarity (stimuli perceived to be similar, e.g., happy and surprised faces, are adjacent; stimuli perceived to be dissimilar, e.g., happy and sad faces, are distant; cf. [7]). The six emotion labels on which subjects rated the faces are displayed on the *x*-axis. Color encodes the mean rating given to each face by a group of subjects, as indicated in the scale. Thus, a red line would indicate a lower mean rating than a yellow line for a given face; and a thin yellow line for a given emotion category would indicate that few stimuli of that emotion received a high rating, whereas a thick yellow line would indicate that many or all stimuli within that emotion category received high ratings. Because very few mean ratings were <1 or >4 , we truncated the graphs outside these values. For subjects who were tested multiple times, we used only the first performance score in calculating group means. Data are shown for eight of the nine amygdala subjects (excluding SP), and indicate abnormally low ratings of negative emotions (thinner yellow color bands across any horizontal position corresponding to an expression of a negative emotion).

3. Results

The raw data for the group of seven normal con-

Table 2
Summary of results^a

	Happy	Sad	Disgusted	Angry	Afraid	Surprised	Correlation
SE		-0.6	-0.8		-2.8		Surprised
DR	-3.1	-2.0	-5.5	-2.3	-4.4		Angry, disgusted
EP	-1.2		-4.3	-0.3	-1.2		Angry
GT	-0.1		-0.2				Surprised
DBB	-0.9	-1.2		-0.2	-1.5		None
SM	-1.3		-0.6	-0.8	-7.2	-3.3	Afraid
RH		-0.3		-4.3	-0.7	-0.7	Angry, surprised
SP	-0.9	-2.8	-3.2		-6.4		Sad, anger, fear
JM		-2.2	-2.3	-5.5	-3.6		Afraid, Disgusted

^a For each emotion category, we show S.D. below the mean of brain-damaged control ratings, where we consider only the intensity rating of each emotion on its prototypical label (e.g., rating how happy happy faces look, how sad sad faces look, etc.). Values < -2 are in bold. The correlation column lists those emotions on which the subject's correlation was more abnormal than the correlation of any of the 16 brain-damaged controls.

trols, the 16 brain-damaged controls, and eight of the nine individuals with bilateral amygdala damage are shown in Fig. 1. (SP's raw data are not shown in the figure. This subject was not administered a complete set of stimuli, and we wished to avoid uneven weighting of different stimuli.) Normal and brain-damaged controls gave very similar performances, as indicated by the nearly identical data graphs. By contrast, subjects with bilateral amygdala damage gave abnormally low rating scores to most negative emotions (cf. Table 2). While ratings of happy faces appear entirely normal, ratings of afraid, angry and disgusted faces were not judged to express intense emotions (either with respect to the correct emotion, or any other emotion). Surprised and sad faces were judged to exhibit the prototypical emotion, but were not judged to also show

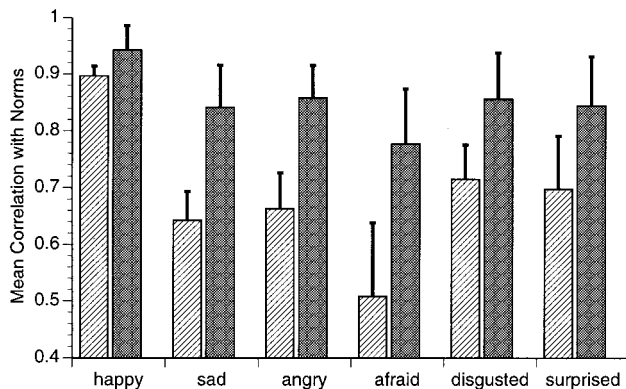


Fig. 2. Mean (\pm SD) correlations of all nine subjects with bilateral amygdala damage (hatched bars) and of 16 brain-damaged controls (grey bars). Averages were first calculated over all subjects for each face, and then averaged over all faces within an emotion category. While amygdala subjects gave somewhat abnormal rating profiles for all emotions except happiness, they differed the most from controls in the case of fear.

some overlapping fear, anger, or disgust. This examination of the raw data is consistent with the different impairments that have been reported for subjects with bilateral amygdala damage: fear, anger, and, to a lesser extent, disgust have all been found to be variously impaired [6,7,12,13,25,26].

For subsequent analyses, we calculated correlation scores for all subjects (see Section 2), to obtain a single measure of performance that avoided floor and ceiling effects, as we have done in prior reports [6,15]. This correlation measure is calculated from the rating profile one sees across a horizontal band of an emotion category in Fig. 1. The correlation scores are correlations with the mean normal ratings; consequently all statistical comparisons below are between subjects with bilateral amygdala damage and brain-damaged controls (Fig. 2).

We first tested the hypothesis that individuals with bilateral amygdala damage would be more impaired in their ratings of faces that express fear than would brain-damaged controls. A Mann-Whitney *U*-test showed that the scores given by subjects with bilateral amygdala damage were significantly impaired compared to the scores given by brain-damaged controls, when rating faces that express fear (one-tailed $P < 0.05$).

To investigate performances given by subjects with bilateral amygdala damage across all the different emotions, we next carried out a 2×6 ANOVA, with lesion group (bilateral amygdala damage or brain-damaged control) as a between-subjects factor, and the basic emotion expressed by the stimuli as a within-subjects factor, using the *Z*-transformed correlation scores as the dependent variable. There was a highly significant effect of the type of emotion ($F(5)=13.8$; $P < 0.0001$), and a significant group effect (type of lesion) ($F(1)=7.8$; $P < 0.005$). There was no significant interaction between emotion type and subject group ($F(5)=0.89$; n.s.). The ratings given by subjects with bilateral amygdala damage generally correlated less well with normal ratings than did the ratings given by brain-damaged controls (Fig. 2). Scheffe post-hoc tests revealed that, across all subjects, happy expressions were rated differently from all other emotions, and expressions of fear were rated different from all other emotions except surprise.

To summarize the pattern of impairments, we calculated both the deviations from the brain-damaged control mean of the intensity ratings that subjects with bilateral amygdala gave, as well as the correlations which were more abnormal than those of any of the brain-damaged controls. Consistent with the ANOVA, several trends were apparent: (1) No subject was notably impaired in recognizing any happy face; (2) subjects' impairments varied over the other emotional expressions, but (3) were most severe in the case of



Fig. 3. Inconsistency in subjects' scores. Five subjects with bilateral amygdala damage (filled symbols), nine brain-damaged controls (open symbols), and five normal controls (grey squares; separate from the group of seven normals to whom data were correlated) participated in a replication of the experiment. Inconsistency was calculated as the absolute value of the difference in correlation scores between each subject's two datasets.

anger and fear. These conclusions are summarized in Table 2.

We wanted to address two further issues. Were subjects impaired when rating fearful faces because there were a few specific faces expressing fear that were consistently rated most abnormally? To address this possibility, we calculated Spearman rank correlations between the performance scores given to each face by different subjects. Subjects with amygdala damage did not show any evidence that specific faces were rated most abnormally (Spearman rank correlations between ratings given to the faces, averaged over correlations between all subjects and over all stimuli within an emotion category: $-0.15 < r < 0.15$).

Did amygdala subjects perhaps mistake fear for another emotion? That is, did they consistently make an abnormal rating, or did they simply not know what emotion was being expressed? To test directly the possibility that the impairment might be attributable primarily to inconsistent performance, as opposed to a consistently erroneous performance, we repeated the entire experiment with a subset of subjects. Replicate datasets from five subjects with bilateral amygdala damage, from nine of the brain-damaged controls, and from five normal controls, showed that there was significantly less consistency in the data from subjects with bilateral amygdala damage than from controls, and that this inconsistency was largest for fear and anger, the two emotions whose ratings were most impaired (Fig. 3). While amygdala subjects always gave ratings that were impaired, the actual ratings were highly inconsistent. A 2×6 ANOVA with factors as above, but with inconsistency as the dependent measure, showed significant effects of both emotion type ($F(5) = 5.87$; $P < 0.001$) and lesion group

($F(1) = 28.7$; $P < 0.001$), as well as an interaction between the two ($F(5) = 2.62$; $P < 0.05$). Post-hoc Scheffé tests showed that subjects with bilateral amygdala damage were significantly less consistent in rating anger than were brain-damaged controls ($P < 0.01$).

4. Discussion

This study provided a unique opportunity to compare a relatively large number of rare individuals with bilateral amygdala damage ($N = 9$) on a single, standardized task. The findings permit some conclusions that have not been possible from prior reports that studied subjects separately.

On the basis of previous lesion and functional imaging studies, we had hypothesized that bilateral damage to the human amygdala would impair the recognition of fear in facial expressions. An examination of this hypothesis was especially important, because no prior study has had sufficient statistical power to test the hypothesis at the group level, and because two individuals with such damage (both included in the present study) had been reported to recognize faces of fear normally [15]. A direct statistical test supported the hypothesis: bilateral amygdala damage impairs recognition of fear in facial expressions.

A further issue concerns the specificity of the impairment. An ANOVA showed that subjects with bilateral amygdala damage were impaired in rating facial emotion, compared to brain-damaged controls. Furthermore, across all normal and brain-damaged subjects, happy expressions and fearful expressions stood out as being rated differently from the other emotions. One interpretation of these results could thus be that fear is simply the most difficult emotion to recognize, and happiness the easiest. A second interpretation is that impaired recognition of fear is due to damage to a more general neural system for recognizing emotions that signal potential harm to the organism, and would include fear and anger. A third possibility is that the amygdala is critical specifically for recognition of fear.

While distinguishing among these possibilities will require further investigation, we believe the data of the present study are most consonant with the second alternative. An examination of the raw data (Fig. 1), as well as the summary of Table 2, clearly argues against option No. 3. A strong argument against option No. 1 comes from findings of double-dissociations in humans: recognition of expressions of disgust can be selectively impaired [14], as can recognition of fear [6]. These data make it unlikely that impaired recognition of specific emotions can be explained by task difficulty alone. This leaves option No. 2 as the most plausible, and one which is also

most consistent with the large body of work from animal studies that implicate the amygdala in the detection of potentially harmful or threatening stimuli [8,16,23]. Taken together, the data argue that the human amygdala is a component of a neural system specialized for triggering physiological states related to stimuli that signal threat or danger [4]. Such physiological states involve both specific sets of behavioral responses, as well as the retrieval of related knowledge.

From an analysis of the consistency of ratings, it appeared that subjects with bilateral amygdala damage were impaired because they could not recognize the emotions signalled by certain facial expressions. They did not consistently mistake certain emotions for others, but rather became inconsistent in their ratings. This effect was statistically significant, and suggests that the underlying mechanism of the impairment is an inability to trigger retrieval of knowledge concerning the emotion, when presented with certain, negative emotional expressions. That is, amygdala subjects simply did not know what emotion was signalled by certain facial expressions.

It remains unclear why certain individuals with bilateral amygdala damage should be impaired, and others not. There is no single factor that distinguishes between the two cases: impaired subjects did not have larger lesions, were not older, did not have lower IQ, and were not from any one research group. Several of these factors have been discussed in previous publications [1,3,5,12,15], but no consensus has been reached. The issue is also puzzling in view of the generally consistent findings from functional imaging, which have reliably reported activation of the amygdala when normal subjects view facial expressions of fear [11,19–24]. One plausible explanation could be that (a) the amygdala is activated when processing facial expressions of fear, but that (b) it may not be essential to give normal performance on recognition tasks, because the subject may adopt alternate strategies that allow retrieval of knowledge about the emotion using anatomical routes other than the amygdala. A direction for future research should be the design of experimental tasks that force the subject to engage in a specific strategy for knowledge retrieval, for example by imposing time constraints on the task.

Acknowledgements

We thank Larry Squire for making subjects EP and GT available, and for comments on the manuscript. We thank Denise Krutzfeldt for help with scheduling subjects, and Kristofer Kinsey and Jeremy Nath for help with testing. Supported in part by NINDS grant NS19632 and a grant from the Mathers Foundation (A.R.D.), a Sloan Foundation Fellowship and NIMH

grant MH57905 (R.A.), the U.K. Medical Research Council (A.W.Y. and A.J.C.), and NIMH grant R29-MH50812 (E.P.).

References

- [1] Adolphs R. The human amygdala and emotion. *The Neuroscientist*, 1999;5:125–37.
- [2] Adolphs R, Damasio H, Tranel D, Damasio AR. Cortical systems for the recognition of emotion in facial expressions. *Journal of Neuroscience* 1996;16:7678–87.
- [3] Adolphs R, Lee GP, Tranel D, Damasio AR. Bilateral damage to the human amygdala early in life impairs knowledge of emotional arousal. *Soc Neurosci Abstr* 1997;23:1582.
- [4] Adolphs R, Russell JA, Tranel D. A role for the human amygdala in recognizing emotional arousal. *Psychological Science* 1999;10:167–71.
- [5] Adolphs R, Tranel D, Damasio AR. The human amygdala in social judgment. *Nature* 1998;393:470–4.
- [6] Adolphs R, Tranel D, Damasio H, Damasio A. Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature* 1994;372:669–72.
- [7] Adolphs R, Tranel D, Damasio H, Damasio AR. Fear and the human amygdala. *The Journal of Neuroscience* 1995;15:5879–92.
- [8] Aggleton JP. *The amygdala: neurobiological aspects of emotion, memory, and mental dysfunction*. New York: Wiley, 1992.
- [9] Anderson AK, Phelps EA. Production of facial emotion following unilateral temporal lobectomy. *Soc Neurosci Abstr* 1997;23:2113.
- [10] Anderson AK, Phelps EA. Bilateral amygdala damage impairs evaluation of facial but not vocal expressions of fear. *Annual Meeting of the Cognitive Neuroscience Society* 1998;109.
- [11] Breiter HC, Etcoff NL, Whalen PJ, Kennedy WA, Rauch SL, Buckner RL, Strauss MM, Hyman SE, Rosen BR. Response and habituation of the human amygdala during visual processing of facial expression. *Neuron* 1996;17:875–87.
- [12] Broks P, Young AW, Maratos EJ, Coffey PJ, Calder AJ, Isaac C, Mayes AR, Hodges JR, Montaldi D, Cezayirli E, Roberts N, Hadley D. Face processing impairments after encephalitis: amygdala damage and recognition of fear. *Neuropsychologia* 1998;36:59–70.
- [13] Calder AJ, Young AW, Rowland D, Perrett DI, Hodges JR, Etcoff NL. Facial emotion recognition after bilateral amygdala damage: differentially severe impairment of fear. *Cognitive Neuropsychology* 1996;13:699–745.
- [14] Gray JM, Young AW, Barker WA, Curtis A, Gibson D. Impaired recognition of disgust in Huntington's disease gene carriers. *Brain* 1997;120:2029–38.
- [15] Hamann SB, Stefanacci L, Squire LR, Adolphs R, Tranel D, Damasio H, Damasio A. Recognizing facial emotion. *Nature* 1996;379:497.
- [16] Le Doux J. *The Emotional Brain*. New York: Simon and Schuster, 1996.
- [17] Lee GP, Bechara A, Adolphs R, Arena J, Meador KJ, Loring DW, Smith JR. Clinical and physiological effects of stereotaxic bilateral amygdalotomy for intractable aggression. *Journal of Neuropsychiatry and Clinical Neurosciences* 1998;10:413–20.
- [18] Lee GP, Reed MF, Meador KJ, Smith JR, Loring DW. Is the amygdala crucial for cross-modal association in humans? *Neuropsychology* 1995;9:236–45.
- [19] Morris JS, Friston KJ, Buchel C, Frith CD, Young AW, Calder AJ, Dolan RJ. A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain* 1998;121:47–57.

- [20] Morris JS, Frith CD, Perrett DI, Rowland D, Young AW, Calder AJ, Dolan RJ. A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature* 1996;383:812–5.
- [21] Phillips ML, Young AW, Senior C, Brammer M, Andrew C, Calder AJ, Bullmore ET, Perrett DI, Rowland D, Williams SCR, Gray JA, David AS. A specific neural substrate for perceiving facial expressions of disgust. *Nature* 1997;389:495–8.
- [22] Tranel D, Hyman BT. Neuropsychological correlates of bilateral amygdala damage. *Archives of Neurology* 1990;47:349–55.
- [23] Weiskrantz L. Behavioral changes associated with ablation of the amygdaloid complex in monkeys. *J Comp Physiol Psychol* 1956;49:381–91.
- [24] Whalen PJ, Rauch SL, Etcoff NL, McInerney SC, Lee MB, Jenike MA. Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience* 1998;18:411–8.
- [25] Young AW, Aggleton JP, Hellowell DJ, Johnson M, Brooks P, Hanley JR. Face processing impairments after amygdalotomy. *Brain* 1995;118:15–24.
- [26] Young AW, Hellowell DJ, Van de Wal C, Johnson M. Facial expression processing after amygdalotomy. *Neuropsychologia* 1996;34:31–9.