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Rapid Communication

The amygdala processes the emotional significance of facial expressions: an fMRI investigation using the interaction between expression and face direction

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Neuroimaging studies have shown activity in the amygdala in response to facial expressions of emotion, but the specific role of the amygdala remains unknown. We hypothesized that the amygdala is involved in emotional but not basic sensory processing for facial expressions. To test this hypothesis, we manipulated the face directions of emotional expressions in the unilateral visual fields; this manipulation made it possible to alter the emotional significance of the facial expression for the observer without affecting the physical features of the expression. We presented angry/neutral expressions looking toward/away from the subject and depicted brain activity using fMRI. After the image acquisitions, the subject's experience of negative emotion when perceiving each stimulus was also investigated. The left amygdala showed the interaction between emotional expression and face direction, indicating higher activity for angry expressions looking toward the subjects than angry expressions looking away from them. The experienced emotion showed the corresponding interaction. Regression analysis showed a positive relation between the left amygdala activity and experienced emotion. These results suggest that the amygdala is involved in emotional but not visuoperceptual processing for emotional facial expressions, which specifically includes the decoding of emotional significance and elicitation of one's own emotions corresponding to that significance.

Keywords: Amygdala; Emotional facial expressions; Face direction; Experienced emotion; fMRI

Introduction

Facial expressions of emotion are indispensable communicative media for human beings, through which observers can regulate their social behaviors according to the expressers' state of mind. Recent neuroimaging studies, which explored observers' neural activity while viewing emotional facial expressions, consistently indicated the activation of the amygdala. The amygdala is more active in response to emotional expressions than neutral expressions, especially in the case of negative emotions such as fear or anger (Breiter et al., 1996; Critchley et al., 2000; Hariri et al., 2000, 2002; Morris et al., 1996; Phillips et al., 2001; Whalen et al., 1998, 2001). This activation occurs automatically (Critchley et al., 2000; Hariri et al., 2000), even when the subjects have no conscious awareness of faces (Whalen et al., 1998). Despite such incremental evidence for neural activity, little is known with respect to the specific role of the amygdala in facial expression processing.

Evidence from the animal literature provides rich information regarding the function of the amygdala. Electrophysiological studies in monkeys and cats have shown that the amygdala neuron activity for external stimuli reflects the emotional significance of the stimuli regardless of their physical features (Maeda et al., 1993; Ono and Nishijo, 1992). Lesion studies in monkeys and rats indicate that selective damage to the amygdala impairs the triggering of emotional responses for emotionally significant stimuli but does not affect basic sensory processing of the stimuli (Aggleton and Young, 2000). These data suggest that this structure appears to be involved not in basic sensory processing but in emotional processing for external stimuli, which specifically includes the decoding of the emotional significance of the stimulus and the eliciting of emotional reactions corresponding to the significance. In line with this, recent neuroimaging studies revealed that human amygdala activity was associated with the subjective emotion elicited in response to aversive olfactory (Zald and Pardo, 1997) and gustatory (Zald et al., 1998) stimuli and that this activity could not be attributed to basic sensory features.

Based on this evidence, we hypothesized that during the observation of facial expressions of emotion, the activity of the amygdala reflects the emotional significance of stimuli and a perceiver's emotional reactions toward the stimuli, but does not relate to the visual processing of the expressions. To test our hypothesis, we utilized the intriguing property of facial communication that the significance of an emotional message is modulated by the expresser's face/gaze direction, which has been demonstrated in experimental social psychological studies (Ellsworth and Carlsmith, 1968; Kimble and Olszewski, 1980; Kimble et al., 1981). For example, when subjects were asked to express negative feelings strongly or weakly to recipients, they directly

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stared at recipients more when expressing strong feelings than when expressing weak feelings (Kimble et al., 1981). These findings indicate that the direct gaze serves as an intensifier of emotional expression (Ellsworth, 1975). The use of face/gaze direction in emotional interactions is evident even in rats and birds (Chance, 1962), suggesting that this communication mode may be hard-wired in most mammals, including humans, and may have a long evolutionary history. As the face/gaze direction, toward or away from a perceiver, can be manipulated by presenting slightly left- or right-directed faces in unilateral visual fields (see Fig. 1), we can systematically control the emotional significance of facial expressions for a perceiver without altering their visual properties.

We measured brain activity using fMRI during the presentation of facial expressions of either angry or neutral emotion either looking toward or away from subjects in the half visual field (Fig. 1). We chose the emotion of anger because the facial expressions of this emotion were reported to activate the amygdala more strongly than do neutral expressions (Whalen et al., 2001; Wright et al., 2002; Yang et al., 2002), elicit negative emotions (Dimberg, 1988; Hess and Blairy, 2001; Johnsen et al., 1995; Lundqvist and Dimberg, 1995), and interact with gaze direction (Kimble and Olszewski, 1980; Kimble et al., 1981). We presented stimuli in either the left or right visual field, ensuring that the physical features of the faces looking toward and away from the subjects were identical. Subjects were asked to discriminate the gender of the presented faces during image acquisition. To investigate the psychological process for the stimuli, we presented the same stimuli again after the image acquisition, and required the subjects to rate the following two types of measures with regard to the intensity of negative emotion: experienced emotion and recognized emotion of the stimulus faces. The former measure was prepared to measure the subjects' emotion elicited while viewing the expressions. The latter was prepared to measure the subjects' perceptions of the expressions, though this measure would reflect not only visuoperceptual process per se but also other recognition/evaluation processes for the expressions. We specifically predicted that the amygdala activity would show an interaction between facial expression and facial direction, indicating stronger activity for angry expressions looking toward the subjects than angry expressions looking away from them, and that the experienced emotion would also show the corresponding interaction pattern. We also predicted the positive relation between the amygdala activity and experienced emotion.

Material and methods

Subjects

Ten volunteers (five women and five men; mean age 24.4 ± 7.8 years) participated in the experiment. All subjects were right-handed and had normal or corrected-to-normal visual acuity. All subjects gave informed consent to participate in the study, which was conducted in accordance with the institutional ethical provisions and the Declaration of Helsinki.

Experimental design

The experiment involved a within-subject two-factorial design, with expression (angry/neutral) and face direction (toward/away).

Stimuli

The stimuli were chosen from the database set of facial expressions, which contains images of facial expressions posed by more than 50 Japanese models. Color images of full-face neutral expressions and oblique views of angry and neutral expressions of five men and five women were selected. For the expressions shown obliquely, the stimulus persons rotated their faces approximately 15° to their right. For all of these stimuli, the stimulus persons kept their eyes looking in front of them. These faces were cut to roughly oval shapes for the purpose of minimizing extraneous clues (e.g., hair). Mirror images of all the stimuli were also prepared. The stimuli subtended a visual angle of about 12.0° vertical × 8.0° horizontal.

Presentation apparatus

The events were controlled by SuperLab software version 2.0 (Cedrus) implemented on a computer (Inspiron 8000, Dell) running Microsoft Windows. The stimuli were projected from a liquid crystal projector (DLA-G11, Victor Company) to a mirror that was positioned in a scanner in front of the subjects.

Procedure

Each subject completed the experimental scan twice. Each scan lasted 12 min and consisted of twelve 30-s epochs with twelve 30-s rest periods (a fixation point was presented in the center of the

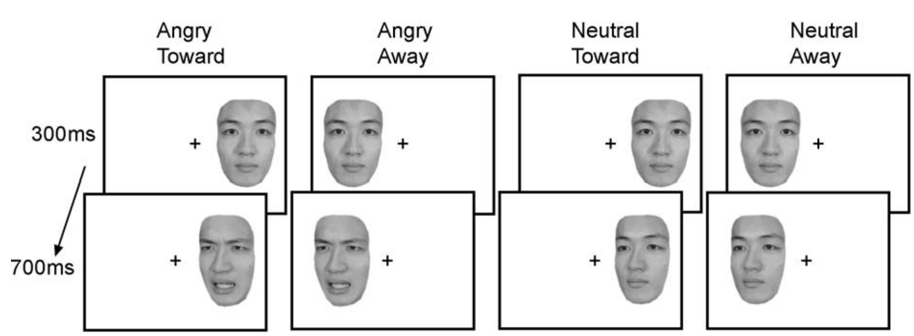

Fig. 1. Illustrations of stimulus presentations. The stimuli were presented in either the left or right visual field. After a full-face neutral expression was presented as the baseline condition of the stimulus person (c.f., Hess et al., 1998), the target oblique facial expression of angry or neutral emotion of the same person looking toward or away from subjects (rotated the face approximately 15°) was presented. The stimulus persons kept their eyes directed in front of them. Note that the physical features of the faces looking toward and away from the subjects were identical.

screen) interleaved. Each of the four stimulus conditions (angry-toward, angry-away, neutral-toward, and neutral-away) was presented in three different epochs within each scan. The order of epochs within each run was pseudo-randomized, and the order of stimuli within each epoch was randomized.

In each epoch, 20 trials (each lasting 1500 ms) were performed. Fig. 1 shows a representative illustration of the sequence of events in a trial. In each trial, after the presentation of a cross as a fixation point, the full-face neutral expression of the stimulus person was first presented for 300 ms in either the left or right visual field (the inside edge was about 9° peripherally from the center). Then, the oblique target facial expression (angry or neutral) of the same person followed for 700 ms in the same location. The first full-face neutral expression was prepared to serve as the baseline of the stimulus person (c.f., Hess et al., 1998). All face images were presented with the edge of the nose between the eyes located in the same eccentric position of each visual field.

The subjects were instructed to maintain the central cross until the oblique face had disappeared and to specify the gender of the presented faces by pressing one of the two buttons with their forefingers after the oblique face had disappeared. This task ensured the subjects' attention to stimuli and also did not require explicit recognition or categorization of emotional expressions. Post hoc debriefing confirmed that the subjects were not aware that investigation of emotional variables was the purpose of the experiment.

After MRI image acquisition, the stimuli were randomly presented to the subjects, and they evaluated each stimulus for the intensity of experienced emotion (i.e., the strength of the emotion that subjects felt when perceiving the stimulus models' expression) and recognized emotion (i.e., the strength of the emotion that subjects recognized from the stimulus models' expression) using a five-point scale of "negativity" ranging from "not at all" to "very strong." We chose this single measure both because this has been found to be a basic component of emotion (Lang et al., 1998) and a previous study that investigated experienced emotion (Wild et al., 2001) and recognized emotion (Russell, 1997) reported the effectiveness of this measure, and because previous psychological studies have shown that angry expressions elicit a complex of diverse negative emotions, including anger, disgust, fear, and repulsion (Hess and Blairy, 2001; Lundqvist and Dimberg, 1995). These two types of evaluation were blocked, and the orders were counterbalanced across subjects.

MRI acquisition

Image scanning was performed on a 1.5-T scanning system (MAGNEX ECLIPSE 1.5T Power Drive 250, Shimadzu Marconi) using a standard radiofrequency head coil for signal transmission and reception. A forehead pad was used to stabilize the head position. The functional images consisted of 52 consecutive slices parallel to the anterior–posterior commissure plane, covering the whole brain. A T2*-weighted gradient echo-planar imaging sequence was used with the following parameters: TR/TE = 6000/60 ms; FA = 90°; matrix size = 64 × 64; voxel size = 3 × 3 × 3 mm. Before the acquisition of functional images, a T2-weighted anatomical image was obtained in the same plane as the functional images using a fast spin echo sequence (TR/TE = 9478/80 ms, FA = 90°; matrix size = 256 × 256; voxel size = 0.75 × 0.75 × 3 mm; number of echoes = 16). For some subjects, additional high-resolution anatomical images were also obtained using a 3D RF-FAST sequence (TR/TE = 12/4.5 ms; FA = 20°; matrix size = 256 × 256; voxel dimension = 1 × 1 × 1 mm) after the functional image acquisition.

Behavioral data analysis

The data for psychological ratings after image acquisition were analyzed with a 2 (expression: angry/neutral) × 2 (face-direction: toward/away) repeated-measures design. To test our specific hypothesis, the interaction between angry vs. neutral expressions and toward vs. away face directions was analyzed. Simple effect analyses were conducted for significant interactions. To compare the results with previous findings, the main effect of expression (angry vs. neutral expression) was analyzed. These analyses were conducted using one-tailed t statistics. The main effect face direction was also analyzed using two-tailed t statistic. Accuracy and reaction time data for the gender classification were analyzed with the same design using two-tailed t statistics. The results were considered statistically significant at $P < 0.05$.

Image analysis

Image and statistical analyses were performed using the statistical parametric mapping package SPM99 (http://www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB (Mathworks Inc.). First, to correct for head movements, functional images of each run were realigned using the first scan as a reference. Data from all 10 subjects showed small motion correction (<2 mm). Then, T2-weighted anatomical images scanned in planes identical to the functional imaging slice were coregistered to the first scan in the functional images. Following this, the coregistered T2-weighted anatomical image was normalized to a standard T2 template image as defined by the Montreal Neurological Institute involving linear and nonlinear three-dimensional transformations. The parameters from this normalization process were then applied to each of the functional image. Finally, these spatial normalized functional images were resampled to a voxel size of 2 × 2 × 2 and smoothed with an isotopic Gaussian kernel (6 mm) to compensate for anatomic variability among subjects.

Significantly activated voxels were searched using random-effects analysis. First, we performed single-subject analysis (Friston et al., 1994; Worsley and Friston, 1995). The task-related neural activities for each condition were modeled with a box-car function convoluted with a canonical hemodynamic response function. A band-pass filter, which was composed of a discrete cosine-basis function with a cut-off period of 480 s for the high-pass filter and a canonical hemodynamic response function for the low pass filter, was applied. Preplanned contrast was thereafter performed for the interactions, which was between angry vs. neutral expressions and toward vs. away directions, based on our a priori hypothesis. When significant regions were detected in this interaction analysis, simple main effect contrasts were performed. To compare the results with previous findings, the main effect of expression (angry vs. neutral expression) was tested. The main effects face direction (toward vs. away; away vs. toward) was also analyzed. Contrast images were generated for each contrast and then entered into a one-sample t test to create a random effect SPM $\{T\}$. For these analyses, significantly activated voxels were identified if they reached the extent threshold of $P < 0.05$ corrected for multiple comparisons, with height threshold of $P < 0.001$ (uncor-

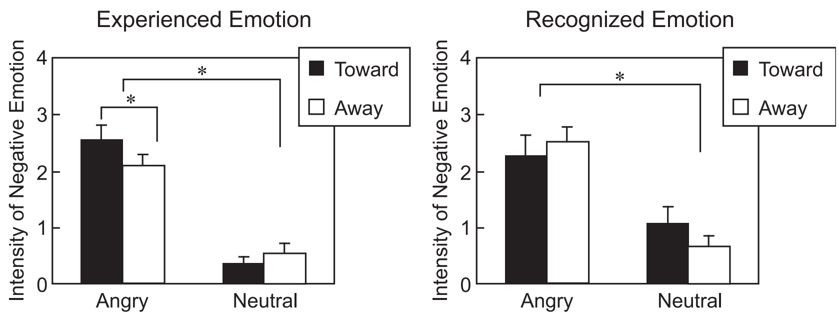

Fig. 2. Mean ratings (±SEM) of experienced emotion (left) and recognized emotion (right).

rected). For the analysis of the amygdala, which was our regions of interest, we used small volume correction (SVC). The regions were defined bilaterally by 6-mm-radius spheres centered on the coordinates (x ±20, y −8, z −16 in the MNI space), which derived from the stereotactic anatomical atlas (Talairach and Tournoux, 1988; c.f., Phillips et al., 2001). Other areas were corrected for the entire brain volume.

For the regression analyses and figures (Figs. 3 and 4), the mean percentage of signal change of the amygdala for each condition of each subject was calculated. Based on the results of the interaction between expression and face direction, the activity of the left amygdala was analyzed. First, the band-pass-filtered raw data were extracted from the 6-mm-radius spherical volume of interest (VOI) on the left amygdala. The center coordinates were the same as that of abovementioned SVC analysis. Then, the percentage of signal change was calculated as the percentage of change from a rest condition as follows: [(mean signal in the specified period − mean signal in a rest condition) / (mean signal in a rest condition)] × 100. The first image for each period was discarded, owing to the time lag in the hemodynamic responses. The data were averaged per subject and condition.

Multiple regression analyses were conducted, with the amygdala activity as the dependent variable and the psychological ratings (experienced emotion/recognized emotion) and dummy variables for subjects as the independent variables. As the two psychological ratings were highly correlated ($r = 0.67$, $P < 0.001$), a separate analysis was conducted for each rating. The coefficients of the psychological measures were evaluated using one-tailed t tests.

Results

Psychological rating

For experienced emotion (Fig. 2, left), the interaction between expression and face direction was significant [$t(9) = 3.02$, $P < 0.01$]. Simple effect analyses indicated that angry expressions directed toward subjects elicited more negative emotional experience than the angry expressions averted from subjects [$t(18) = 3.21$, $P < 0.005$]. The analysis also showed a significant main effect of expression [$t(9) = 7.50$, $P < 0.001$], indicating that angry expressions elicited more negative emotion than neutral expressions did. The main effect of face direction was not significant ($P > 0.1$).

For recognized emotion (Fig. 2, right), the analyses showed that the interaction was not significant ($P > 0.1$). The main effect of expression was significant [$t(9) = 3.44$, $P < 0.01$], indicating that angry expressions were evaluated as more negative than neutral expressions. The main effect of face direction was not significant ($P > 0.1$).

Gender discrimination

Performance of the gender classification task was close to perfect (correct identification rate = 95.2%). There were no

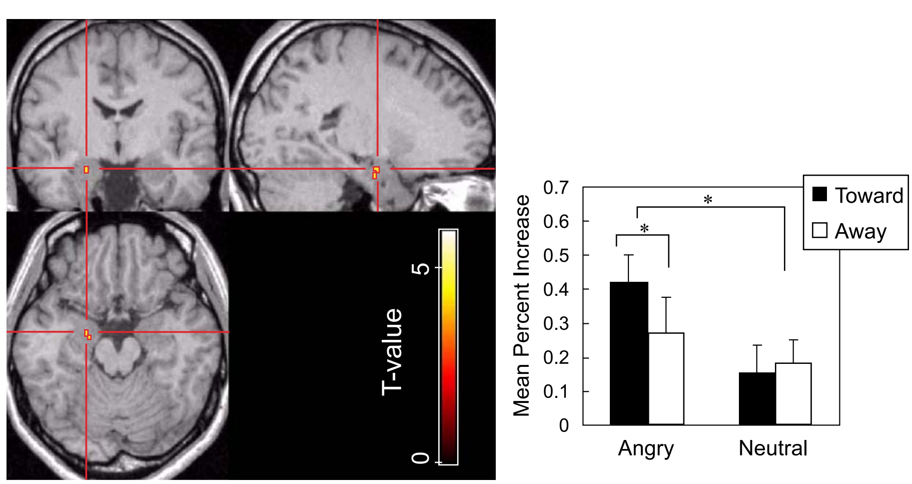

Fig. 3. The statistical parametric map (left) and mean (±SEM) percentage of signal changes (right) showing the left amygdala activity for the interactions between facial expression and facial direction. The area is overlayed on the anatomical MRI of one of the subjects involved in this study.

Table 1
Brain regions showing significant activation

Brain region	BA	Coordinates			T value
		x	y	z	
Interaction					
L. amygdala	–	−22	−9	−16	4.41
Main effect of expression					
L. amygdala	–	−20	−6	−10	4.90
L. middle temporal gyrus	37	−50	−66	7	8.86
R. lateral occipital gyrus	19	40	−80	1	6.85
R. parahippocampal gyrus	26	22	−20	−16	7.79

The activations are shown in the MNI coordinate system.

significant main effects or interactions on the accuracy or reaction time (Ps > 0.1).

Brain activity

A test of the interaction between expression and face direction revealed significant left amygdala activation [x −22, y −9, z −16, T(9) = 4.41; Fig. 3, Table 1]. Simple main effect contrasts confirmed that this activation was higher for angry expressions looking toward subjects than angry expressions looking away from subjects [x −22, y −11, z −16, T(9) = 4.63]. Other significant areas of activation were not detected with our predefined thresholds. There was modest activation in the right amygdala in the interaction and simple main effect contrasts, which failed to reach significance (P < 0.005, uncorrected height threshold), suggesting that the amygdala activation was not clearly lateralized.

The contrast of main effect of expression (angry vs. neutral expression) showed significant activation in the left amygdala [x −20, y −6, z −10, T(9) = 4.90]. This contrast also detected significant activations in some other areas, including the right lateral occipital gyrus, left middle temporal gyrus, and right parahippocampal gyrus (Table 1).

The contrasts of main effects of face direction (toward vs. away; away vs. toward) did not show any significant activation.

Relation between the amygdala activity and psychological rating

Regression analysis with the left amygdala activity as the dependent variable and the experienced emotion as the independent variable (Fig. 4, left) revealed that the coefficient of experienced emotion was positive and significantly different from zero [standardized coefficient = 0.41; t(29) = 2.61, P < 0.01].

Regression analysis with the left amygdala activity as the dependent variable and the recognized emotion as the independent variable (Fig. 4, right) revealed that the coefficient of recognized emotion was not significantly different from zero [standardized coefficient = 0.19; t(29)= 1.15, n.s.].

Discussion

The left amygdala showed not only the main effect of expression, which is consistent with previous imaging studies (Breiter et al., 1996; Critchley et al., 2000; Hariri et al., 2000, 2002; Morris et al., 1996; Phillips et al., 2001; Whalen et al., 1998, 2001; Wright et al., 2002; Yang et al., 2002), but also the interaction between emotional expression and face direction. The simple main effect analysis for the interaction indicated that the amygdala was more active for angry expressions looking toward the perceivers than those looking away from them. The experienced emotion rating for the expressions showed a congruent pattern of interaction. Regression analysis showed a positive relation between the left amygdala activity and experienced emotion. These results cannot be attributed to the difference in the visuoperceptual processing of the expressions because the physical feature of the expressions looking toward the subjects and those looking away from the subjects were identical. The results for recognized emotion, which showed no significant effects of facial direction, support our interpretation that the subjects perceived the same visual images for angry expressions looking toward them and those looking away from them. Overall, these results support our hypothesis that the activity of the amygdala reflects the emotional significance of the emotional facial expressions and the perceiver's emotional reactions toward the expressions, but does not directly relate to the visuoperceptual processing of the expressions.

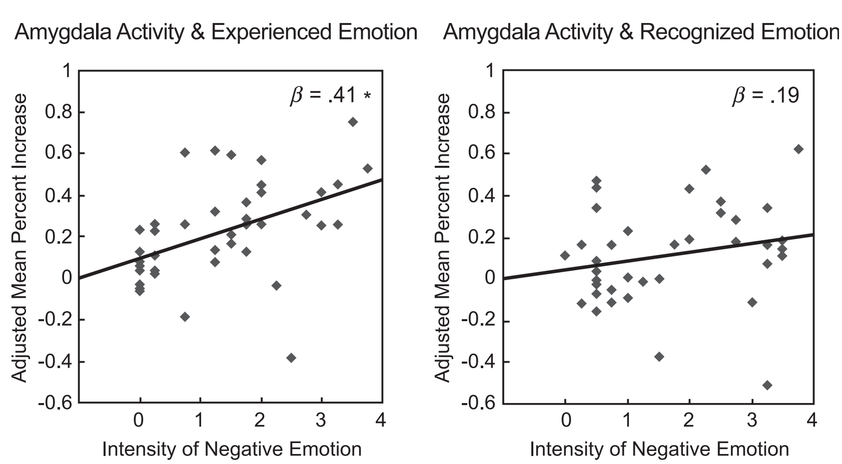

Fig. 4. Scatterplots of the relationship between the adjusted mean percentage of signal changes in the left amygdala activity and the ratings of the experienced (left) or recognized (right) emotion. The regression lines are also plotted. β indicates the standardized coefficient of each psychological rating.

Our finding of the amygdala's involvement in emotional processing is consistent with ample evidence from the animal literature. Electrophysiological studies indicate that the amygdala is involved in the decoding of the emotional significance of external stimuli regardless of the physical features of the stimuli (Maeda et al., 1993; Ono and Nishijo, 1992). Lesion studies in monkeys have shown the importance of the amygdala in the triggering of emotional responses to environmental stimuli (Aggleton and Young, 2000). Recent neuroimaging studies in humans have also suggested that the activity in the amygdala elicited by olfactory and gustatory aversive stimuli is associated with experienced negative emotion but is not attributable to basic sensory features of the stimuli (Zald and Pardo, 1997; Zald et al., 1998). The present study provides the first evidence that this is also the case for the processing of emotional expressions.

Neuroanatomical studies of the primate amygdala support the idea that this structure is involved in emotional processing but not basic sensory processing for facial expressions. As input, the amygdala receives projections from the higher visual areas in the temporal cortex, such as STS (Amaral et al., 1992). Some of these regions contain cell populations that respond selectively to facial expressions of specific emotions (Perrett, 1999), and therefore, the anatomical position of the amygdala is appropriate to receive the processed visual information for facial expressions and analyze their significance for the perceiver. As output, the amygdala projects to many brain regions including the striatum, hypothalamus, and brainstem (Amaral et al., 1992). These regions are important in implementing emotion-specific muscular, autonomic, and behavioral responses (LeDoux, 1996). Psychological studies have indicated that subjective, autonomic, and muscular emotional reactions while observing emotional expressions are intimately related (Dimberg, 1988; Johnsen et al., 1995; Lundqvist and Dimberg, 1995). The anatomical position of the amygdala would be appropriate to implement such widespread emotional reactions.

Our results showing that the activity of the amygdala corresponded with experienced emotion but not with recognized emotion are consistent with the results of a recent neuropsychological study (Adolphs and Tranel, 2000). In that study, a bilateral amygdala damaged patient was shown short clips of movies designed to elicit specific emotions and asked to report her experienced emotional state. The patient reported that she felt neutral emotion when viewing the fearful film. Interestingly, the patient added that she could recognize that most people watching these clips would feel afraid.

Our fMRI results showed that the main effects of expression were in the posterior middle temporal gyrus. Activation of this area in response to emotional facial expressions is consistent with previous neuroimaging (Critchley et al., 2000) and electrophysiological (Ojemann et al., 1992) studies. This region may be homologous to the monkey STS region, which contains expression-selective neurons (c.f., Allison et al., 2000).

Some previous findings are inconsistent with our results. First, some studies (Blair et al., 1999; Sprengelmeyer et al., 1998) have reported no significant activation of the amygdala in response to angry expressions, although other studies (Whalen et al., 2001; Wright et al., 2002; Yang et al., 2002) observed significant amygdala activation, as did our study. This inconsistency may be due to the difficulty in measuring the activity of this structure (c.f., Breiter et al., 1996). In addition, the logic of inductive statistics does not provide a definitive conclusion when the results are not significant. Second, a recent fMRI study (Adams et al., 2003) reported a difference in the pattern of interaction for facial expressions and gaze direction: they found higher amygdala activity in response to angry expressions with averted gaze than to angry expressions with direct gaze. The psychological function of this amygdala activity is unclear since they did not obtain psychological measures. It is possible that the averted gaze in their study expressed stronger negative emotion as compared with direct gaze. Kendon (1967) showed that in diadic conversations, gaze aversion sometimes expresses rejection and withdrawal. Although this function of gaze has not been fully understood, the results of our study and several psychological studies (Ellsworth and Carlsmith, 1968; Kimble and Olszewski, 1980; Kimble et al., 1981) indicate that the direct gaze can intensify the emotional messages to observers in face-to-face interactions. We believe that the assessment of experienced emotion is indispensable for the further investigation of the interaction between emotional expression and gaze direction in amygdala activity. Third, a previous PET study (Kawashima et al., 1999) reported that a neutral face with direct gaze activated the amygdala more than did a face with averted gaze, although other studies (Calder et al., 2002; Hoffman and Haxby, 2000), including ours, did not detect such patterns. In the study by Kawashima et al. (1999), the stimulus depicted a young attractive female and all the subjects were male, which might have heightened the emotional significance of the face with direct gaze as compared to the face with averted gaze. Fourth, a previous fMRI study (Hoffman and Haxby, 2000) showed that the STS was more active in response to averted gaze than in response to direct gaze, whereas another studies (Calder et al., 2002; George et al., 2001) reported no significant STS activation for averted vs. direct gaze. Allison et al. (2000) suggested that averted gaze might activate the STS when it implies motion. Since we presented the full face and oblique stimuli consecutively, by which apparent motion of face direction could be created, both away and toward conditions may have activated the STS in the same way.

One limitation of the present study is that the emotion experienced was assessed by rating after scanning. We adopted this procedure because previous neuroimaging studies have reported that on-line evaluation using verbal labels can reduce the amygdala activity in response to emotional expressions (Critchley et al., 2000; Hariri et al., 2000). Future research incorporating on-line indices of emotional responses, such as physiological measures of autonomic responses, would provide further evidence regarding the elicitation of emotion while viewing stimuli.

In summary, our results revealed that activity in the amygdala showed the interaction between emotional expression and face direction, indicating higher activation for angry expressions looking toward the subject than angry expressions looking away from the subject. This pattern corresponded with the emotion experienced. A positive relation was found between the amygdala activity and experienced emotion. These results could not be attributed to differences in the visuoperceptual processing of the facial expressions. Overall, these results suggest that the amygdala is involved in emotional but not visuoperceptual processing for emotional facial expressions, which specifically includes the decoding of emotional significance and elicitation of one's own emotions corresponding to that significance.

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