THE ROYAL SOCIETY

Neural structures associated with recognition of facial expressions of basic emotions

R. Sprengelmeyer[1]*, M. Rausch[2], U. T. Eysel[2] and H. Przuntek[1]

[1]*Neurologische Klinik im St Josef-Hospital, Ruhr-Universität Bochum, Gudrunstrasse 56, D-44791 Bochum, Germany*
[2]*Abteilung für Neurophysiologie, Medizinische Fakultät, Ruhr-Universität Bochum, Universitätsstraße 150, D-44780 Bochum, Germany*

People with Huntington's disease and people suffering from obsessive–compulsive disorder show severe deficits in recognizing facial expressions of disgust, whereas people with lesions restricted to the amygdala are especially impaired in recognizing facial expressions of fear. This double dissociation implies that recognition of certain basic emotions may be associated with distinct and non-overlapping neural substrates. Some authors, however, emphasize the general importance of the ventral parts of the frontal cortex in emotion recognition, regardless of the emotion being recognized. In this study, we used functional magnetic resonance imaging to locate neural structures that are critical for recognition of facial expressions of basic emotions by investigating cerebral activation of six healthy adults performing a gender discrimination task on images of faces expressing disgust, fear and anger. Activation in response to these faces was compared with that for faces showing neutral expressions. Disgusted facial expressions activated the right putamen and the left insula cortex, whereas enhanced activity in the posterior part of the right gyrus cinguli and the medial temporal gyrus of the left hemisphere was observed during processing of angry faces. Fearful expressions activated the right fusiform gyrus and the left dorsolateral frontal cortex. For all three emotions investigated, we also found activation of the inferior part of the left frontal cortex (Brodmann area 47). These results support the hypotheses derived from neuropsychological findings, that (i) recognition of disgust, fear and anger is based on separate neural systems, and that (ii) the output of these systems converges on frontal regions for further information processing.

Keywords: emotion recognition; disgust; fear; anger; fMRI; frontal cortex

1. INTRODUCTION

Damage to the human amygdala impairs recognition of fearful (and to a lesser extent angry) facial expressions (Adolphs *et al*. 1994; Calder *et al*. 1996; Broks *et al*. 1998), while leaving recognition of other basic emotions relatively unaffected. These neuropsychological results are supported by recent demonstrations of a differential neural response in the human amygdala to facial expressions of fear using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) (Morris *et al*. 1996, 1998; Phillips *et al*. 1997).

Contrasting results come from neuropsychological studies looking in detail at recognition of facial expressions of emotion in Huntington's disease (Sprengelmeyer *et al*. 1996, 1997*a*), Huntington's disease gene carriers (Gray *et al*. 1997) and people suffering from obsessive–compulsive disorder (Sprengelmeyer *et al*. 1997*b*). People from all these clinical groups investigated were selectively impaired in recognizing facial expressions of disgust.

The selective impairment in recognition of disgust demonstrated by these people forms a double dissociation with the specific deficit in fear recognition shown in people with amygdala damage, which strongly supports the conclusion that separable neural systems are involved in the recognition of basic emotions.

A different approach to the neuropsychology of emotions comes from Hornak, Rolls and colleagues (Rolls *et al*. 1994; Hornak *et al*. 1996), who argued that the orbitofrontal cortex is a structure of particular significance in the recognition of facial expressions of emotion. This hypothesis does not posit separate neural systems for each emotion. To support their position, Hornak, Rolls and their colleagues have presented data from people with lesions restricted to the ventral parts of the frontal lobe; they found that people with such lesions were severely impaired in recognizing all facial expressions of emotions, whereas people without damage to these areas (but with lesions to other parts of the brain) were unimpaired on tasks of emotion recognition.

The following fMRI study aims to explore the extent to which recognition of basic emotions is based on the ventral parts of the frontal cortex (as is implicated by the neuropsychological results of Hornak, Rolls and colleagues), or associated with independent and non-overlapping neural structures.

2. METHODS

(a) *Subjects*

Six right-handed healthy volunteers (two male, four female) with no history of neurological or psychiatric illness participated in this study. Mean age was 23.5 years (s.d. 1.3 years) and mean IQ estimate was 118 (s.d. 3.7). No subject was taking regular

*Author for correspondence.

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medication. All subjects gave their informed consent to take part in the study, which was approved by the local ethics committee of the Ruhr-Universität Bochum.

(b) *Experimental design*

The faces of eight individuals (four male, four female), each showing fearful, angry, disgusted and neutral facial expressions, were used in this study. These were taken from a standard set of expressions of emotions (Ekman & Friesen 1976). Each face was presented once for 3 s before the fMRI experiment to familiarize subjects with the experimental stimuli.

The fMRI experiment comprised ten separate blocks for each of the four different facial expressions investigated (fear, anger, disgust and neutral) and all blocks were presented in randomized order. In each block, the eight different faces depicting the same emotion were projected in randomized order, one at a time, for 2.5 s each (with an interstimulus interval of 0.5 s in which the screen was blank) onto a translucent screen at the back of the scanner. This resulted in a block length of 24 s for each emotion. All faces could be viewed easily by the subjects by means of a mirror mounted into the headcoil, subtending visual angles of 15° horizontally and 10° vertically.

Subjects had to make a decision as to the gender of each face presented by pressing one of two buttons either with the thumb of the right or the left hand. This task was balanced across subjects. The gender decision task was chosen to permit a comparison with previous studies that also used this procedure and to allow an identical task and response across all experimental conditions. Subjects were not explicitly informed about the aim of the study. All subjects were paid for participating in the experiment (75 DM).

(c) *Image acquisition and data analysis*

The imaging was done using a 2.0 Tesla system (Tomikon S200, Bruker, Germany) using a standard headcoil. To minimize movement artefacts, the head of the subject was fixed with a vacuum headholder. Images were acquired with a $T2^*$-sensitive GE-EPI sequence (TR = 4 s, TE = 50 ms, matrix = 64 × 64, FOV = 240 mm × 240 mm, slice thickness = 6 mm, interslice distance = 8 mm). We recorded from 16 transaxial slices parallel to the AC–PC line that covered almost the whole brain. T1-weighted anatomical images were acquired with the same slice orientation using a Fast-SE-IR sequence.

Analyses and image manipulations were performed on a SPARC workstation (Sun Computers). For the statistical processing the statistical parametric mapping software (SPM96, Wellcome Department of Cognitive Neurology, London) implemented in Matlab (Mathworks, Sherborn, MA) was used. Before statistical analysis, images were realigned, normalized to the Talairach space, and smoothed with an isotropic three-dimensional Gaussian filter with a full width at half maximum (FWHM) of 9 mm in each direction. The statistical parametric maps (SPMs) were calculated by comparing the neutral faces as the baseline condition with the 'anger', 'fear' and 'disgust' conditions. Because our study was based on specific *a priori* hypotheses, a statistical threshold of $p < 0.01$ (not corrected for multiple comparisons) and a cluster size of more then 1 voxel was applied to identify significant changes of activation. As a last step, the SPMs were projected onto a normalized anatomical scan.

3. RESULTS

Areas demonstrating significant increases in activation during performance in the condition where disgusted faces were shown relative to neutral faces are presented in figure 1*a*. The results of the comparison of the 'disgust' versus 'neutral' condition, cluster size and location of the areas activated given in Talairach & Tournoux coordinates (Talairach & Tournoux 1988), and statistics are summarized in table 1*a*. We found that the basal ganglia (anterior putamen and pallidum) of the right hemisphere as well as left anterior insula were activated when disgusted-looking faces are presented. In the left hemisphere, there was also activation of the inferior parts of the frontal cortex (Brodmann area 47).

Brain areas showing significant activation in the 'fear' compared with the 'neutral' condition are given in table 1*b* and figure 1*b*. There was activation only of the left frontal lobe (Brodmann areas 46 and 47) and the right fusiform gyrus (Brodmann area 37); there was, however, no evidence of activation within the amygdala, which had been expected from the results of other studies (Breiter *et al*. 1996; Morris *et al*. 1996; Phillips *et al*. 1997).

Areas demonstrating significant activation in the 'anger' compared with the 'neutral' condition are presented in figure 1*c* and table 1*c*. There was activation in the left inferior frontal lobe (Brodmann area 47) and in the posterior part of the left temporal lobe (Brodmann area 21). In the right hemisphere, the region activated by angry-looking faces was the posterior part of the gyrus cinguli (Brodmann area 31). Activation of Brodmann area 47 for disgusted-, fearful-, and angry-looking faces compared with neutral facial expressions is shown in figure 2.

4. DISCUSSION

In this study, we tried to locate neural structures that are critical for recognition of facial expressions of basic emotions using fMRI. We were particularly interested in whether recognition of basic emotions is based on the ventral parts of the frontal cortex as proposed by Hornak, Rolls and colleagues (Rolls *et al*. 1994; Hornak *et al*. 1996), or whether it is associated with independent and non-overlapping neural structures as implicated by the double dissociation for recognition of disgust and fear that is found in people suffering from putative frontostriatal diseases (Sprengelmeyer *et al*. 1996, 1997*a*,*b*; Gray *et al*. 1997), and in people with lesions involving the amygdala (Adolphs *et al*. 1994; Calder *et al*. 1996; Young *et al*. 1996; Broks *et al*. 1998).

We found emotion-specific activation of non-overlapping brain areas for each of the three emotions investigated as well as a region (Brodmann area 47) in the left inferior frontal cortex responding equally to disgusted-, fearful-, and angry-looking faces when compared with neutral facial expressions. Before discussing the theoretical implications of activation of Brodmann area 47 in more detail, we will first consider the neural substrates specific to disgust, fear and anger.

We found that seeing facial expressions of disgust is paralleled by activation of the right putamen. The involvement of the basal ganglia in recognizing facial expressions of disgust is well in accordance with our predictions derived from the neuropathology of Huntington's disease and obsessive–compulsive disorder, where sufferers show a striking loss of their ability to

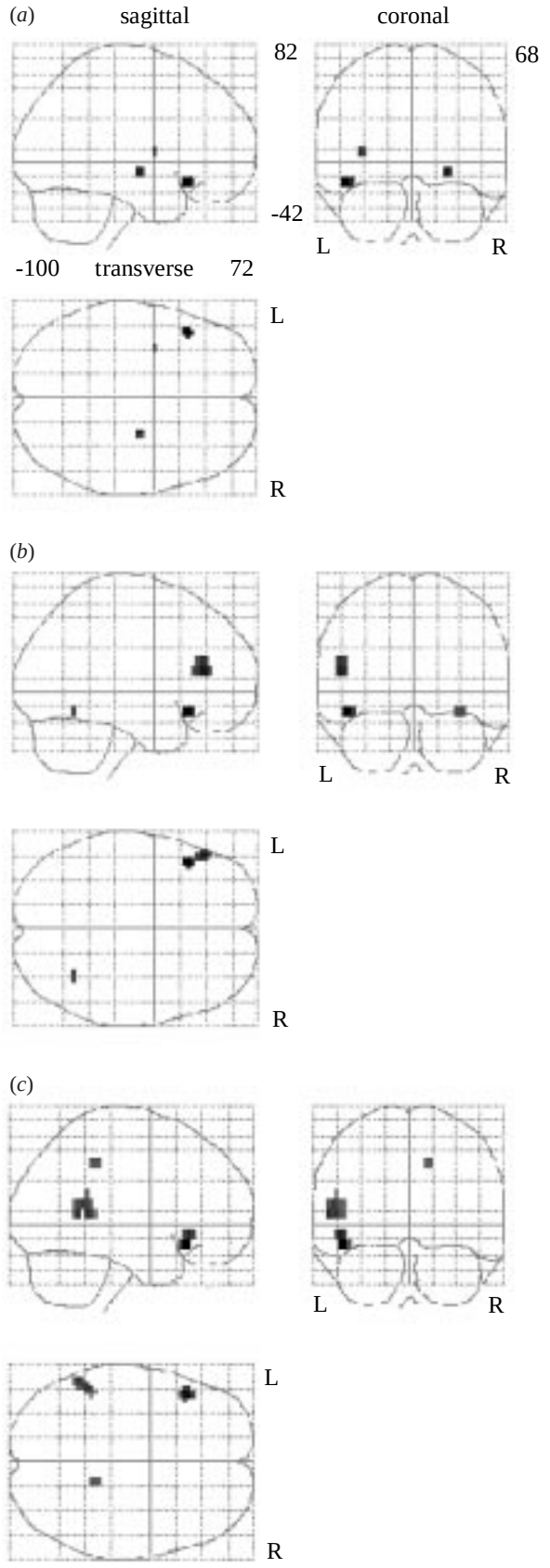

Figure 1. Regions of significant activation for (*a*) faces expressing disgust compared with faces showing neutral expressions, (*b*) faces expressing fear compared with faces showing neutral expressions, and (*c*) faces expressing anger compared with faces showing neutral expressions, shown as through-projections onto representations of standard stereotactic space (Talairach & Tournoux 1988).

recognize disgust from the face. We were also able to show activation of the insula cortex of the left hemisphere, a neural structure that has been identified in primates as the primary gustatory cortex (Rolls 1995). Future studies will need to determine whether activation of the insula cortex in response to expressions of disgust indicates extraction and evaluation of disgust-specific features from the face or a 'state of preparedness' induced by a warning stimulus (the disgusted-looking face) to process taste-related information.

Activation of the basal ganglia and the anterior insula was also found by Phillips *et al.* (1997) using fMRI, who presented computer-manipulated images of faces depicting different degrees of disgust to normal individuals. There is a strong and remarkable overlap between our fMRI results and the results reported by Phillips *et al.* (1997), which are in addition paralleled by previous findings of specific and circumscribed deficits in disgust recognition in Huntington's disease and obsessive–compulsive disorder. The converging evidence from both neuropsychological studies of clinical groups and neuroimaging studies of healthy subjects thus supports the view that a distinct neural network incorporating basal ganglia and insula cortex is involved in the processing of facial expressions of disgust.

Neuropsychological lesions studies (Adolphs *et al.* 1994; Calder *et al.* 1996), and neuroimaging experiments (Breiter *et al.* 1996; Morris *et al.* 1996, 1998; Phillips *et al.* 1997), underline the importance of the amygdala for recognition of fearful facial expressions. Activation of the amygdala was therefore expected in response to expressions of fear. In our study, however, this activation could not be shown. The most likely reason for this seems to be the rapid habituation of the amygdala in response to fearful faces, an effect already reported by Breiter *et al.* (1996). We did, however, find activation of more dorsolateral regions of the left frontal cortex and the right fusiform gyrus. Activation of the latter structure to fearful facial expressions is particularly interesting because Morris *et al.* (1998) supposed a neuromodulatory function (top-down processing) of the amygdala on extrastriate cortical regions. They performed regression analyses on data from a functional imaging (PET) experiment that was focused on the perception of facial expression. They found a specific psychophysiological interaction between the amygdala and the fusiform gyrus in response to fearful-looking faces, in that reduced activation in the amygdala was paralleled by enhanced activation of the fusiform gyrus. Our data—and especially the failure to show the predicted activation of the amygdala—could mirror this neuromodulatory effect.

Although anger has long been seen as an important basic emotion, which has evolved to enhance the survival of the species and to regulate interpersonal behaviour, we are aware of no other functional imaging study that has investigated the neural basis of this particular emotion. In a comparison of angry faces with neutral-looking ones, we found activation of the right gyrus cinguli (Brodmann area 31) and of the posterior parts of the left hemisphere (Brodmann area 21). Involvement of the gyrus cinguli in facial emotion recognition (Sergent *et al.* 1994) and in the emotional experience of anger are well known (Devinsky *et al.* 1995). Hence, these results are consistent with the

Table 1. *Main activated brain regions for (a) faces expressing disgust compared with faces showing neutral expressions, (b) faces expressing fear compared with faces showing neutral expressions, and (c) faces expressing anger compared with faces showing neutral expressions*

('BA' indicates the Brodmann area activated, whereas 'region' refers to the activated structure or gyrus according to the nomenclature of Talairach & Tournoux (1988). The values *x*, *y* and *z* are the Talairach coordinates (Talairach & Tournoux 1988) of the voxel with the maximum *p*-value as determined from the *t*-maps. '*p*' indicates the maximum *p*-value for each activated cluster of voxels.)

BA/region	side	*x*	*y*	*z*	Z	*p*	number of activated voxels
(*a*) Disgust versus neutral							
g. frontalis inf. 47	left	−45	24	−14	3.19	0.001	6
putamen	right	24	−12	−7	2.93	0.002	4
insula	left	−36	0	7	2.60	0.005	2
(*b*) Fear versus neutral							
g. frontalis inf. 47	left	−48	24	−14	3.13	0.001	6
g. frontalis med. 46	left	−51	33	14	2.89	0.002	16
g. fusiformis 37	right	33	−57	−14	2.42	0.008	3
(*c*) Anger versus neutral							
g. frontalis inf. 47	left	−48	24	−14	3.90	<0.001	14
g. temporalis med. 21	left	−57	−51	7	3.34	<0.001	24
g. cinguli post. 31	right	15	−39	42	2.92	0.002	6

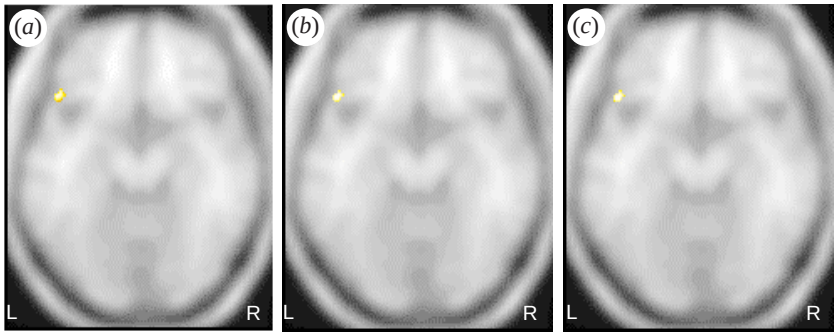

Figure 2. Statistical parametric maps (SPMs) superimposed onto normalized MRI-scans. The SPMs show significant activation of the left inferior frontal cortex (Brodmann area 47) for the following conditions: (*a*) faces expressing disgust compared with faces showing neutral expressions, (*b*) faces expressing fear compared with faces showing neutral expressions, and (*c*) faces expressing anger compared with faces showing neutral expressions. Talairach & Tournoux coordinates, Z-scores and *p*-values are given in table 1.

hypothesis that the activation of the gyrus cinguli is related to recognition of anger from the face.

A contribution of the posterior parts of the left hemisphere to the recognition of facial expressions has been reported by Young *et al*. (1993), who investigated the performance of a group of ex-serviceman suffering from left or right unilateral lesions. They presented two cases with lesions involving left temporoparietal regions and one case with a left occipitoparietal lesion, all showing highly selective deficits on tasks of facial-expression recognition and facial-expression matching. As Young and colleagues did not look at specific emotions, but at facial emotion expressions overall, no statement can be made from their results concerning the extent to which the posterior part of the left hemisphere is involved in processing angry-looking faces. Nevertheless, a role of this region in emotion recognition has been established by a clinical study (Young *et al*. 1993), and our results suggest that this structure might be a potential candidate for mediating anger.

In conclusion, we found emotion-specific activation of non-overlapping brain areas that were responsive selectively to disgusted-, fearful- and angry-looking faces. These results confirm the hypothesis derived from clinical studies (Adolphs *et al*. 1994; Calder *et al*. 1996; Sprengelmeyer *et al*. 1996, 1997*b*), that recognition of different facial expressions is based on separate or at least partly separable neural structures.

We now turn to consider the activation of the left inferior frontal cortex (Brodmann area 47), which was equally responsive to faces depicting disgust, fear and anger when compared with neutral faces. Our results are consistent with previous studies reporting that the orbitofrontal and the inferior part of the frontal cortex are involved in face perception and the recognition of facial expressions. Ó Scalaidhe *et al*. (1997) recently performed a single-cell recording study on macaque monkeys and showed that the inferior frontal cortex contains a circumscribed region with neurons selectively responsive to faces. The face selective cells within this area receive information mainly from the ventral bank of the superior temporal sulcus, a region where cells were found that were selectively responsive to facial expressions of emotions (Hasselmo *et al*. 1989). Morris *et al*. (1998) extended these findings by showing orbitofrontal

activation in response to emotional facial expressions in the human brain. In addition, Hornak, Rolls and colleagues (Rolls *et al*. 1994; Hornak *et al*. 1996), presented data of people with lesions to the ventral parts of the frontal cortex who were impaired in the recognition of facial expressions. Based on clinical results of altered emotional behaviour and experience after frontal-lobe lesions in humans, as well as deficits in learning and behavioural adaptation in brain-lesioned monkeys, a theoretical model has been suggested by Hornak, Rolls and colleagues (Rolls *et al*. 1994; Hornak *et al*. 1996), in which the orbitofrontal cortex is of particular importance for recognizing emotional facial expressions overall; this model does not postulate separate neural systems for each emotion.

Our results, however, reconcile these discrepancies by indicating that recognition of facial expressions can be regarded as a multiple-stage process, in part based on (emotion-specific) separate neural pathways working in parallel, and in part based on neural structures that all emotions investigated have in common (Brodmann area 47). We may now ask about the role of Brodmann area 47 within a system for recognition of emotions. Given that there is a strong posterior–anterior processing axis in the visual system, a plausible answer seems to be that Brodmann area 47 is the common endpoint of the distributed networks involved in emotion recognition, where behavioural integration of information derived from facial expressions might take place. The importance of neighbouring regions in the orbitofrontal cortex for behavioural regulation and behavioural adaptation underline this assumption (Rolls *et al*. 1994).

In summary, the data from this fMRI study provide evidence (conjointly with clinical findings in Huntington's disease, obsessive–compulsive disorder, and people with lesions to the amygdala) that recognition of basic emotions is based on separate neural pathways; it is hypothesized that these pathways project to the inferior frontal cortex.

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