NEUROIMAGE 4, 194–200 (1996)
ARTICLE NO. 0070

Neural Activation during Covert Processing of Positive Emotional Facial Expressions

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Received April 30, 1996

Lesion studies indicate distinct neural systems for recognition of facial identity and emotion. Split-brain experiments also suggest that emotional evaluation of a stimulus can occur without conscious identification. The present study tested a hypothesis of a differential neural response, independent of explicit conscious mediation, to emotional compared to nonemotional faces. The experimental paradigm involved holding in mind an image of a face across a 45-s delay while regional cerebral blood flow was measured using positron emission tomography. Prior to the delay, a single face was presented with an explicit instruction to match it to one of two faces, photographed at different angles from the target face, presented at the end of the delay. Repeated blood flow measures were obtained while subjects held happy or neutral faces in mind or during a neutral control fixation condition without initial face presentation. The representation of emotional faces over a delay period, compared to either the nonemotional or the fixation condition, was associated with significant activation in the left ventral prefrontal cortex, the left anterior cingulate cortex, and the right fusiform gyrus. The findings support our hypothesis of a differential neural response to facial emotion, independent of conscious mediation, in regions implicated in the processing of faces and of emotions. © 1996 Academic Press, Inc.

INTRODUCTION

Signaling emotions using the face is a critical channel of social information processing which endows humans with prodigious abilities in perceiving the dispositions and intentions of others, an ability often referred to as social cognition (Brothers, 1990). The perception of facial expression is an early developmental event with infants displaying a capacity for imitative facial expression at 36 h and a capacity for facial gesture at 2 weeks (Meltzoff and Moore, 1977; Sagi and Hoffman, 1976). The early, and invariant, emergence in development of both imitative and expressive facial behavior and the circumscribed repertoire of facial emotions across cultures suggests these capacaties are both innate and hardwired (Ekman, 1992).

Cognitive models of face recognition are derived largely from experiments requiring overt responses. However, there is extensive evidence of covert facial recognition from studies in both normals and prosopagnosics (Bruce and Young, 1986; DeHaan *et al.*, 1987; Bruyer *et al.*, 1983; Rizzo *et al.*, 1987; Tranel and Damasio, 1985; Barrett and Rugg, 1989; Barrett *et al.*, 1988; Uhl *et al.*, 1990). Selective lesions may also result in an inability to recognize facial expressions (Shuttleworth *et al.*, 1982). These observations provide an expanded model of face recognition involving dissociable pathways mediating overt recognition, damaged in prosopagnosia, and covert recognition (Bauer, 1986).

Single cell recordings in the primate indicate that face recognition involves circumscribed brain regions in the inferior temporal cortex (Moran and Desimone, 1985; Perrett *et al.*, 1982; Desimone and Gross, 1979). In humans, lesions of the inferior temporal cortex lead to impairments on tests of face recognition (Meadows, 1974) while in healthy subjects functional imaging studies, across a range of experimental paradigms, have identified a neuronal response to faces in the fusiform gyrus (Haxby *et al.*, 1994; Sergent *et al.*, 1994; Courtney *et al.*, 1996). The neural structures involved in processing emotional salience in faces are less well defined although the ventral and orbital prefrontal cortex are seen as critical to emotional regulation (Damasio and Van Hoesen, 1983; Rolls *et al.*, 1994; Damasio *et al.*, 1990).

Functional imaging studies involving the overt processing of facial emotion have implicated a range of structures including the cingulate cortex, the inferior frontal gyrus, and the right lateral occipital cortex

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(Sergent *et al.*, 1994; George *et al.*, 1993b). The aim in the present study was to identify brain systems involved in the covert processing of facial emotion. In studies of normal subjects involving the induction of both happy and sad moods we have demonstrated activation in the ventral prefrontal cortex suggesting an involvement of this region in the representation of emotional states (Baker *et al.*, 1996). Conversely, an extensive neuropsychological literature implicates the ventral occipital region in the processing of facial identity (Damasio *et al.*, 1982; Meadows, 1974). On this basis we hypothesized activation of the ventral prefrontal cortex in the representation of facial emotion and the medial occipital gyrus in the representation of faces irrespective of emotion.

METHODS

Subjects

Eight normal healthy right-handed male subjects (mean age 23, range 20 to 27 years) were included in the study. Handedness was determined according to the Edinburgh Inventory (Oldfield, 1971). These subjects were free of significant past or concurrent illness. All subjects provided written informed consent for the study which was approved by the local hospital ethics committee and ARSAC (UK).

Psychological Task

To ensure that the processing of emotional faces would be incidental we designed an experimental paradigm that explicitly emphasized a mnemonic requirement. This strategy also minimized any conscious processing such as the linguistic categorization of facial expressions. The task was based upon a delayed matching task in which subjects were instructed to hold in mind, over a 45-s interval, an image of a face in order to match it to a choice of two faces presented at the end of the delay. Each face was presented on a screen 45 cm in front of the subjects for 2 s prior to activation of the scan. During the scan, subjects fixated while consciously holding in mind the target face. At the end of scan acquisition two faces appeared on the screen and subjects were required to point to the target face. Both the distractor and the target faces were photographed at different angles from the target face. The target and distractor faces were matched on variables such as sex, age, and race. The position of the target face was systematically varied. Performance on the task was measured as the percentage of target faces identified correctly.

At the end of the scanning session subjects were debriefed with reference to their spontaneous observations on the study. All subjects reported doing the task by holding a representation of the face in mind over the delay period. Subjects also reported that they found this task difficult and that they tended to lose the image of the face toward the second half of the delay period. None of the subjects were consciously aware that the study embodied a component that involved emotion or emotional expression. The subjects did not report any factor that may have helped their performance across conditions such as facial type. Subjects were subsequently asked to classify the target faces into emotional types and all subjects were reliably able to classify the faces as neutral or happy.

Stimuli were presented in a counterbalanced order. Four of the scans involved the presentation of faces that embodied expressions of happiness while another four scans involved faces that were expressively neutral. In the control condition no faces were presented prior to the scan and subjects fixated at a target point in the center of the screen alone. For the control condition subjects were required at the end of the scanning period to point to the older of two faces that appeared on the screen. The accuracy of delayed facial matching was recorded for the active conditions.

Data Analysis

Scans were obtained using a CTI Model 953B PET Scanner (CTI, Knoxville, TN) with collimating septa retracted. Volunteers received a 20-s intravenous bolus of $H_2{}^{15}O$ at a concentration of 55 MBq ml and a flow rate of 10 ml/min through a forearm cannula. The data were analyzed with statistical parametric mapping (SPM 95 software from the Wellcome Department of Cognitive Neurology, London, UK) implemented in Matlab (Mathworks, Inc., Sherborn, MA). Statistical parametric mapping combines the general linear model (to create the statistical parametric map or SPM) and the theory of Gaussian fields to make statistical inferences about regional effects (Friston *et al.*, 1991, 1994).

The scans from each subject were realigned using the first as a reference. Following realignment all images were spatially normalized, using nonlinear transformation, into a standard space and smoothed (Friston *et al.*, 1995a). As a final preprocessing step, the images were smoothed using an isotropic Gaussian kernel.

The condition, subject, and covariate effects (global blood flow) were estimated according to the general linear model at each voxel (Friston *et al.*, 1995b). To test hypotheses about regionally specific condition effects, the estimates were compared using linear compounds or contrasts. The resulting set of voxel values for each contrast constitutes a statistical parametric map of the t statistic, SPM(t). The SPM(t) were transformed to the unit normal distribution [SPM(z) and thresholded at 3.09 (or $P = 0.001$ uncorrected for multiple comparisons)].

TABLE 1

Coordinates and Significance of Activations for the Comparison of the Combined Faces with the Control Condition (1a) and the Emotional with the Nonemotional Condition (1b)

	x	*y*	*z*	*Z* value
(a) Faces versus control				
Left inferior frontal gyrus	−44	22	−8	3.38
Right inferior frontal gyrus	28	28	−12	3.23
Left anterior cingulate gyrus	−12	26	28	3.21
Right fusiform gyrus	44	−44	−12	3.08
(b) Emotional versus nonemotional				
Left inferior frontal gyrus	−50	26	0	3.50
Left anterior cingulate gyrus	−12	26	28	3.53
Right fusiform gyrus	44	−42	−12	3.26
Thalamus	8	−10	12	3.19

RESULTS

Performance

For all delayed matching conditions performance was at ceiling with no errors recorded for either the emotional or the nonemotional conditions.

Functional Imaging Data

All Faces (Emotional and Nonemotional) versus the Control Condition

The comparison of the combined faces condition with the reference condition was associated with a number of regional activations which survived a preset threshold of significance ($P < 0.001$). The coordinates of the maxima for these foci are detailed in Table 1a and were centered on the left inferior frontal gyrus (BA 47), the left anterior cingulate cortex (BA 32), and the right fusiform gyrus (BA 20).

Emotional Faces versus Nonemotional Faces and Control Condition

A comparison of the emotional with the nonemotional faces conditions was associated with a profile of activation similar to that of the combined faces versus control condition. Significant activations were again observed in the left inferior frontal gyrus (BA 47), the left anterior cingulate cortex (BA 32), and the right fusiform gyrus (BA 20). The coordinates of maximal activation for this comparison are shown in Table 1b and the areas of significant difference are displayed as SPMs in Fig. 1. A comparison of the emotional faces with the fixation control condition was associated with maximal activation in the left inferior prefrontal cortex ($P < 0.0005$), the right inferior prefrontal cortex ($P < 0.001$), the right fusiform gyrus ($P < 0.001$), and the left anterior cingulate cortex ($P < 0.001$).

Nonemotional Faces versus the Control Condition

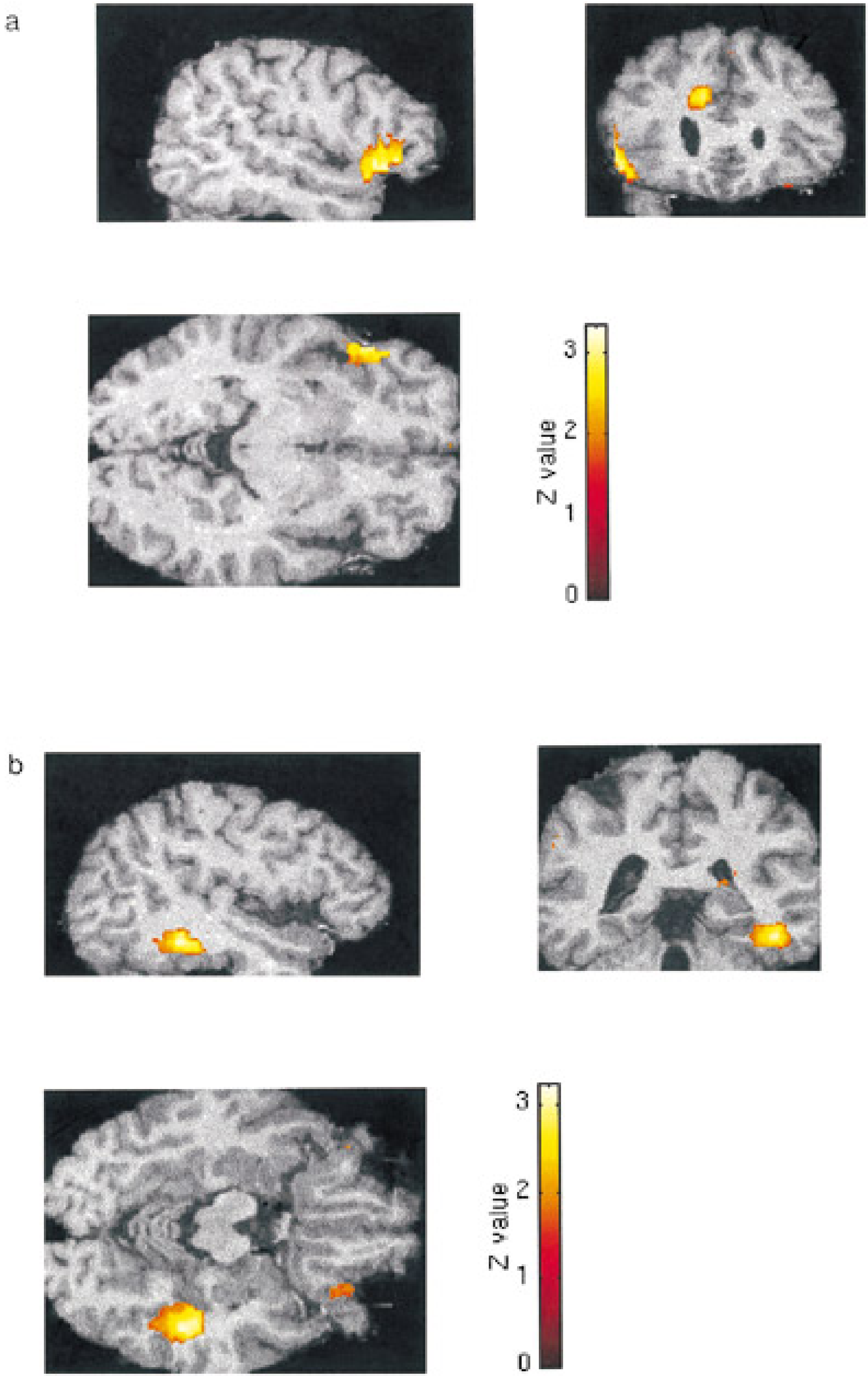
A comparison of the nonemotional faces with the control condition was associated with a single focus of activation ($P < 0.001$) in the left inferior parietal lobule (BA 40). The mean regional cerebral blood flow (rCBF) response at the pixel coordinates of maximal intensity in the left inferior prefrontal cortex, the anterior cingulate cortex, and the right fusiform cortex for each condition is presented in Fig. 2.

DISCUSSION

The human face is a crucial component of social communication particularly in the ability to infer the intentions of others. Psychological models of face recognition postulate dissociable processes related to identity and expression (Bruce and Young, 1986). It has been suggested that "the face stimulus is immediately and obligatorily transformed into the representation of a person (with dispositions and intentions) before having access to consciousness" (Brothers, 1990). The present study suggests that the neural response to emotion in faces is both covert and obligatory. There was no requirement for conscious processing yet there were clear differences in neural activation when representing happy compared to neutral faces. The virtually identical pattern of neuronal response in the combined faces condition compared to that of the emotional faces condition alone implies that emotional salience is an important determinant of the magnitude of the associated neuronal response.

The restriction to one class of emotional expression in the present experiment was determined by two considerations. First, the restriction was a constraint of the delayed matching task methodology. The study design provided a means whereby faces could be presented to subjects without a requirement for them to be explicitly aware of the experimental question. To obtain reasonable statistical power in a task involving the maintenance of a single facial representation over the entire scanning period it was necessary to have multiple repeats of each condition. Second, the choice of happy facial expressions was dictated by empirical evidence of a processing advantage over other forms of facial expression (Kirita and Endo, 1995; Ekman *et al.*, 1982; Kirouac and Dore, 1983). In terms of signal characteris-

FIG. 1. SPM of foci of maximum significance for the comparison of emotional and nonemotional conditions. The foci are shown superimposed on a magnetic resonance structural scan that itself has been transformed to standard stereotactic space. The regions highlighted are (a) the left inferior frontal gyrus, the left anterior cingulate cortex, and (b) the right fusiform gyrus.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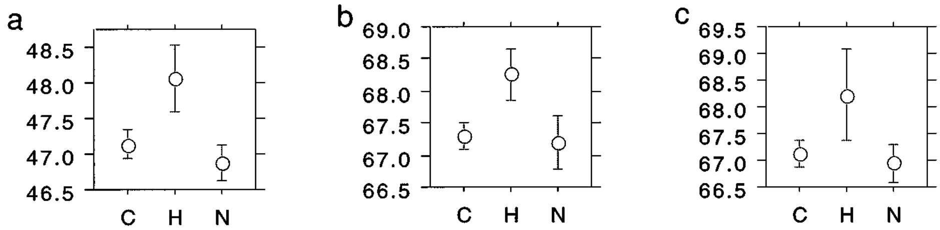

FIG. 2. The mean rCBF responses, at the coordinates of maximal significance in the emotional versus nonemotional condition, are displayed as plots (mean and standard error of the mean) for each condition for (a) the left inferior prefrontal cortex, (b) the left anterior cingulate, and (c) the right fusiform.

tics the smile is the simplest emotional expression but one of the most complex in terms of signal value (Ekman and Friesen, 1982).

The regional activation in the right fusiform gyrus, seen for the combined and emotional faces comparison with the control condition, was not unexpected. An extensive literature implicates the ventral occipitotemporal cortex in the processing of faces in both human and nonhuman primate. Prosopagnosia, a disorder of facial recognition, is seen following bilateral lesions to the ventral temporal cortex (Damasio *et al.*, 1982; Meadows, 1974). Single-cell recordings in a ventral occipital region in the nonhuman primate have identified units specialized for coding faces or features of faces (Perrett *et al.*, 1992, 1982). In humans direct neurophysiological measures, based upon recordings from extracellular electrodes, have described a negative surface potential (N200) evoked by faces, but not other classes of stimuli, centered on the fusiform and inferior temporal gyri while electrical stimulation of the same region producing a temporary inability to name a familiar face (Allison *et al.*, 1994).

Functional imaging data have provided direct *in vivo* evidence for involvement of the ventral temporal cortex in face processing. In a face matching task significant activations in the right fusiform gyrus, virtually identical to the regions activated in the present study, have been reported (Haxby *et al.*, 1994). Similarly, in a face working-memory task, activations in the right fusiform and the inferior frontal cortex and the anterior cingulate gyrus have been observed (Courtney *et al.*, 1996). Whether neutral faces alone were used in the latter study is unclear. In a study requiring the explicit processing of facial identity and emotion, activations were noted in the right fusiform gyrus in the identity condition and in the cingulate in the emotion condition but much more caudal to the focus identified in the present study (Sergent *et al.*, 1994). Our finding of unilateral activation in the right fusiform gyrus, however, is consistent with evidence that impaired facial recognition may also be seen after unilateral right temporal lobe lesions (De Renzi, 1996; Landis *et al.*, 1986).

The evidence from the present study of right fusiform activation in the representation of emotional faces is consistent with evidence of a relative superiority of the right hemisphere in processing facial effect that is independent of its superiority in processing facial identity (Bowers and Heilman, 1985). This suggests an involvement of this region in processes additional to that of identity. Alternatively, the happy expression may be more attentionally engaging. The coactivation of the cingulate cortex would support this notion and also explain the absence of fusiform or cingulate activations in the comparison of nonemotional faces with the control condition. The focus identified in the present study may thus represent a region involved in a number of processes that includes identity and expression. A suggested role in processing the salience of facial representations is strengthened by observations that unilateral lesions of the right temporal cortex, insufficient to impair recognition of identity, may impair recognition of facial expression (Bowers and Heilman, 1984; Rapsak *et al.*, 1993). Whether particular forms of expressive salience are processed is an open question particularly in light of findings regarding selective impairment in fear recognition following bilateral amygdala lesions (Adolphs *et al.*, 1995).

The cingulate cortex was strongly activated in the comparison of emotional and nonemotional faces. In humans the anterior cingulate cortex has heterogenous functions (Devinsky and Luciano, 1993). Its activation in the emotional faces condition may relate to the possibility that emotional faces automatically engage attention. A specific role for the cingulate in emotion is an alternative, though complementary, explanation. Lesions of the cingulate, as well as producing a state of akinetic mutism, lead to states of emotional indifference (Damasio and Van Hoesen, 1983). A specific role in emotion is suggested by findings of a decrease in function in this area during states of clinical depression (Bench *et al.*, 1992). Its role in phonation in primates and degrees of facial expressiveness in humans suggests a specificity in relation to expressive aspects of emotion (Muller-Preuss and Jurgens, 1976; Von Cramon and Jurgens, 1983).

The activation of the ventral prefrontal cortex was a specific prediction of the study. Electrophysiological evidence in the monkey has provided evidence that neurons in the inferior frontal cortex show selective responses to faces (Wilson *et al.*, 1993). Its involvement in emotional processing in humans is supported by observations that lesions involving this region are associated with a failure of the expected augmentation of skin conductance responses to visual stimuli with a high emotional valence (Damasio *et al.*, 1991). The activation of the inferior frontal convexity provides converging evidence of a specific role in emotional processing. Lesions in this region impair the production of emotional, but not nonemotional, facial expressions (Hopf *et al.*, 1992). Activation in a similar region has also been reported in a functional imaging study involving the overt matching of facial expressions (George *et al.*, 1993a). Patients with ventral prefrontal lesions, including unilateral lesions, are impaired in face processing of emotional expression independent of the recognition of identity (Hornak *et al.*, 1995). These findings indicate that the ventral prefrontal activation relates to processing of the emotional salience in facial stimuli. However, a more general role in emotional processing remains a possibility as an identical region is activated by the explicit induction of happy or sad moods in normal subjects (Baker *et al.*, 1996). One important region mediating emotional responses which was not activated in the present study was the amygdala. The empirical evidence indicates that fear, derived from visual perception, is mediated via the amygdala (Adolphs *et al.*, 1995). Thus, the role of the amygdala in emotional processing may be quite specific. The use of a single emotional expression, namely happiness, in the present study leaves open the question of whether a separate neural circuitry might be associated with discrete emotions.

Neuropsychological studies indicate that recognition of facial identity and emotion are dissociable processes (Damasio, 1995; Strauss and Moscovitch, 1981; Bowers and Heilman, 1984). Contrasting views are that these processes are mediated by similar or partially dissociable mechanisms (Hansch and Pirozzolo, 1980; DeKosky *et al.*, 1980). Normal subjects and patients with prosopagnosia produce discriminatory skin conductance responses to familiar faces, suggesting covert or implicit recognition (Tranel *et al.*, 1995). In the present study activation of structures additional to areas implicated in overt facial processing suggests these regions may contribute to processing salience in facial stimuli. A previous functional imaging study of faces has described activation within the inferior prefrontal and anterior cingulate cortex in an overt face matching task (Courtney *et al.*, 1996). However, the facial stimuli used were not neutral and we suggest that the stimuli of emotional expressions are critical determinants of the magnitude and distribution of the neural response to faces.

Our findings have implications for models of face processing. In prosopagnosia, the mechanism of preserved covert discriminatory responses to previously familiar faces is unknown. One possibility is that an intact ventral and medial prefrontal cortex can maintain the emotional response to familiar faces. At a more general level, the findings provide support for a theoretical position of separable, though overlapping, neural systems for the processing of facial identity and emotion. The overlapping components involve the right fusiform gyrus while the separable components involve the ventral prefrontal cortex. Finally, the study provides tentative evidence that the neural response to emotional salience in faces is automatic and independent of conscious processing.

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