

Investigation of facial recognition memory and happy and sad facial expression perception: an fMRI study

Mary L. Phillips^{a,*}, Edward T. Bullmore^a, Robert Howard^c, Peter W.R. Woodruff^a, Ian C. Wright^a, Steven C.R. Williams^b, Andrew Simmons^b, Christopher Andrew^b, Michael Brammer^a, Anthony S. David^a

^a*Department of Psychological Medicine, Institute of Psychiatry, Denmark Hill, London SE5 8AF, UK*

^b*Department of Clinical Neurosciences, Institute of Psychiatry, De Crespigny Park, London SE5 8AF, UK*

^c*Section of Old Age Psychiatry, The Maudsley Hospital, London SE5 8AZ, UK*

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Abstract

We investigated facial recognition memory (for previously unfamiliar faces) and facial expression perception with functional magnetic resonance imaging (fMRI). Eight healthy, right-handed volunteers participated. For the facial recognition task, subjects made a decision as to the familiarity of each of 50 faces (25 previously viewed; 25 novel). We detected signal increase in the right middle temporal gyrus and left prefrontal cortex during presentation of familiar faces, and in several brain regions, including bilateral posterior cingulate gyri, bilateral insulae and right middle occipital cortex during presentation of unfamiliar faces. Standard facial expressions of emotion were used as stimuli in two further tasks of facial expression perception. In the first task, subjects were presented with alternating happy and neutral faces; in the second task, subjects were presented with alternating sad and neutral faces. During presentation of happy facial expressions, we detected a signal increase predominantly in the left anterior cingulate gyrus, bilateral posterior cingulate gyri, medial frontal cortex and right supramarginal gyrus, brain regions previously implicated in visuospatial and emotion processing tasks. No brain regions showed increased signal intensity during presentation of sad facial expressions. These results provide evidence for a distinction between the neural correlates of facial recognition memory and perception of facial expression but, whilst highlighting the role of limbic structures in perception of happy facial expressions, do not allow the mapping of a distinct neural substrate for perception of sad facial expressions. © 1998 Elsevier Science Ireland Ltd. All rights reserved.

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* Corresponding author. Department of Psychological Medicine, King's College School of Medicine and Dentistry and Institute of Psychiatry, 103, Denmark Hill, London SE5 8AZ, UK. Tel.: +44 171 7405078; fax: +44 171 7405129; e-mail: spmampl@iop.bpmf.ac.uk

1. Introduction

Intact processing of faces is critical in social interaction, in view of the enormous amount of information contained in a face (Sergent, 1988). Such processing can be subdivided into various dissociable categories: for example, the recognition of facial expression and the recognition of facial familiarity.

Whilst the role of the right hemisphere in facial perception has been highlighted by neuropsychological and functional imaging studies (Etcoff, 1984a,b; Sergent, 1988; Sergent et al., 1992; Puce et al., 1995, 1996; Kanwisher et al., 1997), there is evidence for the dissociation of facial recognition memory and facial expression perception in terms of the neural substrate underlying these two tasks (George et al., 1993; Sergent et al., 1994). The exact nature of the neural substrate underlying each task remains, however, unclear. Facial familiarity perception and unfamiliar face matching have been linked to the right hemisphere (Young et al., 1993), and facial recognition memory for previously unfamiliar faces has been associated with left hippocampus activity (Kapur et al., 1995). Facial working memory has been linked with the left hemisphere (McIntosh et al., 1996), bilateral occipital (extrastriate) cortex (Courtney et al., 1996, 1997), and right prefrontal cortex (Haxby et al., 1996), the latter confirming previous studies linking right prefrontal cortex with episodic memory retrieval (Tulving et al., 1994a,b; Shallice et al., 1994; Moscovitch et al., 1995; Fletcher et al., 1995; Buckner et al., 1996).

There has been much recent interest in the role of the amygdala in perception of fearful facial expressions (Adolphs et al., 1994, 1995; Young et al., 1995; Morris et al., 1996; Breiter et al., 1996; Whalen et al., 1998). Studies of perception of facial expression per se, however, have yielded conflicting results. Lesion studies have implicated both the left hemisphere (Young et al., 1993) and the right hemisphere (Adolphs et al., 1996) in the task, with the latter study demonstrating the role of the right hemisphere in per-

ception of negative emotions, in particular sadness and fear. Functional imaging studies have implicated the right hemisphere (Gur et al., 1994; George et al., 1996), bilateral cingulate cortex (Sergent et al., 1994), and right anterior cingulate and bilateral inferior frontal cortex (George et al., 1993) in recognition of positive and negative facial expressions. Furthermore, bilateral limbic and paralimbic structures have been implicated in induction of sad emotion, with widespread decreases of cortical blood flow during induction of happy emotion (George et al., 1995). More recent studies have demonstrated activation in the amygdala in response to unpleasant emotional stimuli (Lane et al., 1997), and during induction of both happy and sad emotions (Schneider et al., 1997).

The nature of the neural substrate underlying happy and sad facial expression perception, and the distinction between this and the neural substrate for facial recognition memory thus remains unclear. In the current study, we used functional magnetic resonance imaging (fMRI) to investigate brain function during the two tasks of facial recognition memory (for previously unfamiliar faces) and facial expression perception, and to investigate more closely the neural correlates of perception of happy and sad facial expression. On the basis of the literature reviewed above, it was hypothesized that:

1. Facial recognition memory and facial expression perception would activate different brain regions;
2. facial recognition memory would activate left hippocampus, in addition to right prefrontal cortex and bilateral occipital cortex;
3. perception of sad facial expression would specifically activate bilateral limbic structures, right hemisphere more than the left.
4. Finally, the existing literature does not permit a clear prediction for the neural substrate underlying perception of happy facial expressions. In light of earlier research (George et al., 1995), we hypothesised that the pattern of activation would be distinct from that for sad facial expression perception.

2. Method

2.1. Subjects

Eight healthy volunteers (seven male, one female) with normal, uncorrected visual acuity and a mean age of 32 years (range 26–39) were recruited. All subjects were right-handed (Annett, 1970). Informed consent for participation in the study was obtained from subjects after the nature of the experimental procedures had been explained.

2.2. Stimuli

These comprised:

1. Facial stimuli from the Recognition Memory Test (RMT) (Warrington, 1984), which are monochrome photographs of male faces.
2. Facial stimuli depicting affectively or emotionally different expressions from the series of Ekman and Friesen (1976).

Stimuli were presented on a screen 3.5 m away from the subject lying in the MR scanner. The stimuli subtended approx. 10° horizontally and 8° vertically.

2.3. Activation paradigms

In the facial recognition memory task and both facial expression perception tasks, we used a blocked periodic design in which two blocks of contrasting facial stimuli (A and B) were each presented for 30 s. The cycle of alternation between conditions A and B was repeated five times in the course of 5 min.

Brain activation reported in this article refers to periodic BOLD (blood oxygenation level determination; Ogawa et al., 1990) signal changes at the frequency of AB alternation. Two subtypes of activation are distinguished by the phase of BOLD signal change: (1) an A phase response, with maximal signal during the A condition; and (2) a B phase response, with maximal signal during the B condition.

2.4. Facial recognition memory

Before entering the scanner, each subject was shown 25 stimuli from the RMT, with each stimulus presented for 3 s. Subjects were instructed to look at the faces carefully and say whether they appeared pleasant or not. No memory instructions were given, as in the standard RMT.

Each subject entered the scanner 10 min later. During condition A, subjects saw five ‘familiar’ faces, i.e. RMT stimuli they had been shown prior to scanning; during condition B, subjects saw five ‘unfamiliar’ faces, i.e. RMT stimuli they had not previously been shown. Each stimulus was presented for 6 s. Subjects were asked to indicate by pressing one of two buttons whether each stimulus appeared familiar or unfamiliar. Accuracy of facial recognition was recorded.

2.5. Facial expression perception

This comprised two separate 5-min tasks: the perception of happy and sad facial expressions. Thirty minutes before entering the scanner, each subject was presented with five neutral faces from the Ekman–Friesen series, each for 3 s. Pilot work had shown that this was necessary in order to facilitate later distinction between happy or sad faces and the neutral ‘baseline’.

In the task contrasting happy and neutral facial expressions, during condition A subjects were shown a happy face from the Ekman–Friesen series for 30 s; during condition B, subjects were shown a neutral face for 30 s. This duration of stimulus presentation was of the same order as that used by George et al. (1995), in which subjects were presented with happy, sad or neutral faces for 45 s each in order to facilitate induction of the emotion. In the current study, each subject therefore viewed five neutral and five happy facial expressions from five different individuals. In the task contrasting sad and neutral facial expressions, subjects viewed a sad face for 30 s during condition A and a neutral face for 30 s during condition B. In both tasks, subjects were instructed to identify the expression of each stimu-

lus by empathising with the emotional state depicted (to control for automatic emotion induction by the non-neutral faces), and were asked to indicate their decision (neutral vs. emotional: happy/sad) about each stimulus by pressing one of two buttons. Accuracy of facial expression perception was recorded.

2.6. Image acquisition

Gradient echo echoplanar imaging (EPI) data were acquired on a GE Signa 1.5 T system (General Electric, Milwaukee WI, USA) retrofitted with Advanced NMR hardware (ANMR, Woburn MA, USA) at the Maudsley Hospital, London. A quadrature birdcage headcoil was used for RF transmission and reception. One hundred T_2^* -weighted images depicting BOLD contrast (Ogawa et al., 1990) were acquired over 5 min (for each task) at each of 14 near-axial non-contiguous 5-mm thick planes parallel to the inter-commissural (AC-PC) line: TE 40 ms, TR 3 s, in-plane resolution 5 mm, interslice gap 0.5 mm. This EPI dataset provided complete coverage of the temporal lobes (including hippocampus and amygdala) and almost complete coverage of frontal, occipital and parietal lobes. In the same scanning session an inversion recovery EPI dataset was acquired at 43 near-axial 3-mm thick planes parallel to the AC-PC line: TE 80 ms, TI 180 ms, TR 16 s, in-plane resolution 1.5 mm, interslice gap 0.3 mm, number of signal averages = 8. This higher resolution EPI dataset provided whole brain coverage and was later used to register the fMRI datasets acquired from each individual in the standard stereotactic space of Talairach and Tournoux (1988) and Brammer et al. (1997).

2.7. Motion correction

Effects of slight subject motion during image acquisition were corrected in each individual's fMRI dataset by realignment (tricubic spline interpolation) and regression of realigned fMRI time series on a second order polynomial function of lagged and concomitant positional displacement of the subject's head (Brammer et al., 1997; Bullmore et al., 1998).

2.8. Generic brain activation mapping

Periodic change in T_2^* -weighted signal intensity at the (fundamental) experimentally determined frequency of alternation between A and B conditions (i.e. 1/60 Hz in all three tasks) was estimated by pseudogeneralised least squares (PGLS) fit of a sinusoidal regression model to the movement-corrected time series observed at each voxel. PGLS fitting involved modelling the residuals of an ordinary least squares (OLS) fit of the sinusoidal regression model by a first order autoregressive (AR1) process (Bloomfield, 1991; Jones, 1993); transforming the terms of the regression model by the estimated AR (1) coefficient; and refitting the transformed model by OLS. This model included sine and cosine waves at the fundamental AB frequency of the experimental input function, parameterised by coefficients $\{\gamma, \delta\}$. The power of periodic response to the input function was estimated by $(\gamma^2 + \delta^2)$; and this fundamental power divided by its standard error yielded a standardised test statistic, the fundamental power quotient (FPQ), at each voxel (Bullmore et al., 1996a). Parametric maps representing FPQ observed at each intracerebral voxel were constructed. In order to sample the distribution of FPQ under the null hypothesis that observed values of FPQ were not determined by experimental design (with few assumptions), the 99 images observed in each anatomical plane were randomly permuted and FPQ was estimated exactly as above in each permuted time series. This process was repeated 10 times, resulting in 10 randomised parametric maps of FPQ at each plane for each subject (Edgington, 1980).

Observed and randomised FPQ maps were transformed into the standard space of Talairach and Tournoux (1988), and smoothed by a two-dimensional Gaussian filter with full-width half-maximum = 11 mm. This size of filter was chosen to accommodate well-documented individual variability in anatomical location of face processing cortical centres (Clark et al., 1996). The median observed FPQ at each intracerebral voxel in standard space was then tested against a critical value of the randomisation distribution for median FPQ ascertained from the randomised FPQ maps. For

a one-tailed test of size α , the critical value is the $100 \times (1 - \alpha)$ th percentile value of the randomisation distribution. Voxels for which the observed median FPQ exceeded this critical value were considered to be activated with voxel-wise probability of Type I error ($\alpha \leq 0.004$).

The timing of the signal increase relative to the input function is indicated by γ (Bullmore et al., 1996b). If $\gamma > 0$, the modelled response to the experimental function will be relatively increased during the first (A) condition, whereas if $\gamma < 0$, the modelled response will be relatively increased during the second (B) condition. In the context of the tasks in this study, therefore, positive values of median γ indicated maximal signal intensity during presentation of familiar faces, happy or sad facial expressions; and negative values of median γ indicated maximal signal intensity during presentation of unfamiliar faces and neutral expressions.

Activated voxels with signal maximum during condition A were coloured red; activated voxels with signal maximum during condition B were coloured blue. Activated voxels were displayed against the greyscale background of the template image used for spatial normalisation to form a generic brain activation map (GBAM) (Brammer et al., 1997).

3. Results

3.1. Performance

Subjects were able to distinguish familiar from unfamiliar faces with a mean accuracy of 61% (S.D. = 10.03%). [One subject performed at chance level (50%); the other seven performed better than chance.] Subjects were able to distinguish happy from neutral faces with a mean accuracy of 74% (S.D. = 20.0%), and sad from neutral faces with a mean accuracy of 91% (S.D. = 14.6%).

3.2. Generic brain activation maps

3.2.1. Facial recognition memory task

The main regional foci of generic activation in this task included the right middle temporal gyrus [Brodmann area (BA) 21], bilateral posterior cin-

gulate gyri (BA 30/31), right supramarginal gyrus (BA 40), right middle occipital cortex, left postcentral gyrus (BA 3), right premotor cortex (BA 6), bilateral insulae, left medial prefrontal cortex (BA 9) and left dorsolateral prefrontal cortex (BA 45). Phase analysis revealed that the signal increases in the right middle temporal gyrus, left postcentral gyrus, left medial prefrontal cortex and left dorsolateral prefrontal cortex occurred during presentation of familiar faces; whereas the signal increases in bilateral posterior cingulate gyri, right supramarginal gyrus, right middle occipital cortex, bilateral insulae and right premotor cortex occurred during presentation of unfamiliar faces (Fig. 1A and Table 1).

3.2.2. Happy facial expression perception task

The main regional foci of generic activation in this task included left anterior cingulate gyrus (BA 24), bilateral medial frontal cortex, bilateral posterior cingulate gyri (BA 23/30/31), left supramarginal gyrus (BA 40), right putamen, left caudate nucleus and right dorsolateral prefrontal cortex (BA 46). Phase analysis revealed that the signal increase in all the above brain regions other than the left caudate nucleus was during presentation of happy rather than neutral facial expressions (Fig. 1B and Table 2A).

An example of a fitted time series obtained in this task is demonstrated for the signal increase in the bilateral posterior cingulate gyri (Fig. 2A).

3.2.3. Sad facial expression perception task

The main regional foci of generic activation in this task included the left supramarginal gyrus (BA 40), right dorsolateral prefrontal cortex (BA 45) and left middle occipital cortex (BA 18). Phase analysis revealed that the signal increase in all of these brain regions occurred during presentation of neutral rather than sad facial expressions (Fig. 1C and Table 2B).

An example of a fitted time series obtained in this task is demonstrated for the signal increase in the supramarginal gyrus (Fig. 2B).

4. Discussion

The aim of this study was to identify brain

Table 1
Familiar vs. unfamiliar faces: generically activated brain regions

Region (approximate Brodmann area)	Side	x^a	y^a	z^a	No. of voxels	P^b	Condition of signal increase ^c
Middle temporal gyrus (21)	R	58	-31	4	12	0.00001	Familiar
Posterior cingulate gyrus (30/31)	L	-6	-58	15	8	0.00001	Unfamiliar
	R	14	-50	15	2	0.00002	
Postcentral gyrus (3)	L	-49	-19	26	8	0.00003	Familiar
Supramarginal gyrus (40)	R	32	-28	31	6	0.00004	Unfamiliar
Middle occipital (extrastriate) cortex (18)	R	12	-78	-2	6	0.00002	Unfamiliar
Premotor cortex (6)	R	35	0	26	3	0.0003	Unfamiliar
Insula	L	-29	-3	20	3	0.00002	Unfamiliar
	R	35	0	20	3	0.0005	
Dorsolateral prefrontal cortex (45)	L	-32	31	15	2	0.0005	Familiar
Medial prefrontal cortex (9)	L	-6	50	15	2	0.00003	Familiar

^aTalairach co-ordinates refer to the voxel with the maximum fundamental power quotient (FPQ) in each regional cluster.

^bAll such voxels were identified by a one-tailed test of the null hypothesis that median FPQ is not determined by experimental design. The probability threshold for activation was $P \leq 0.004$.

^cSignal increase was detected either during presentation of familiar or unfamiliar faces.

regions specifically involved in facial recognition memory and (happy or sad) facial expression perception. We did not set out to examine the functional anatomy of facial processing per se, which would have required contrasting faces with, for example, other visual objects or scrambled faces (see Puce et al., 1995, 1996; Kanwisher et al., 1997). We have demonstrated different patterns of generic brain activation in response to these two main tasks, in support of our first hypothesis that these two components of facial processing may have dissociable neural substrates.

4.1. Facial recognition memory

A signal increase was demonstrated in the right middle temporal gyrus during presentation of familiar faces, suggesting that this structure may have a role in the detection of familiar faces in

addition to primary facial processing (Puce et al., 1996; Kanwisher et al., 1997). Although the left hippocampus has been linked with facial recognition memory (Kapur et al., 1995), we did not detect any signal increase in this structure in the current study. In addition, we predicted in our second hypothesis a signal increase in the right dorsolateral prefrontal cortex, based on previous studies of facial matching and recognition (Haxby et al., 1994, 1996). Contrary to this, we demonstrated a small signal increase in *left* medial and dorsolateral prefrontal cortex during presentation of familiar faces. The left prefrontal cortex has been implicated in encoding rather than retrieval of facial stimuli (Tulving et al., 1994a,b). A signal increase in this region during presentation of familiar faces may have reflected the relative difficulty subjects had in distinguishing between familiar and unfamiliar faces in the task.

We detected a signal increase in bilateral posterior cingulate gyri, right middle occipital (extrastriate) cortex and right supramarginal gyrus during presentation of unfamiliar faces. Previous studies have implicated bilateral extrastriate cortex in facial working memory (Courtney et al., 1996, 1997), posterior cingulate gyrus (Swartz et al., 1994) in visual memory, and bilateral supramarginal gyri in visuospatial processing per se (Smith et al., 1996).

An unexpected finding was the demonstration

of signal increase in bilateral insulae during presentation of unfamiliar faces. Previous studies have indicated that the right insula in particular is activated during the execution of voluntary saccadic eye movements (e.g. Anderson et al., 1994). The insula has also been shown to have a role in several sensory systems, including, for example, pain perception (Casey et al., 1994; Derbyshire et al., 1994), as well as face-specific processes, such as speech reading of moving facial gestures (Calvert et al., 1997), and the perception of cer-

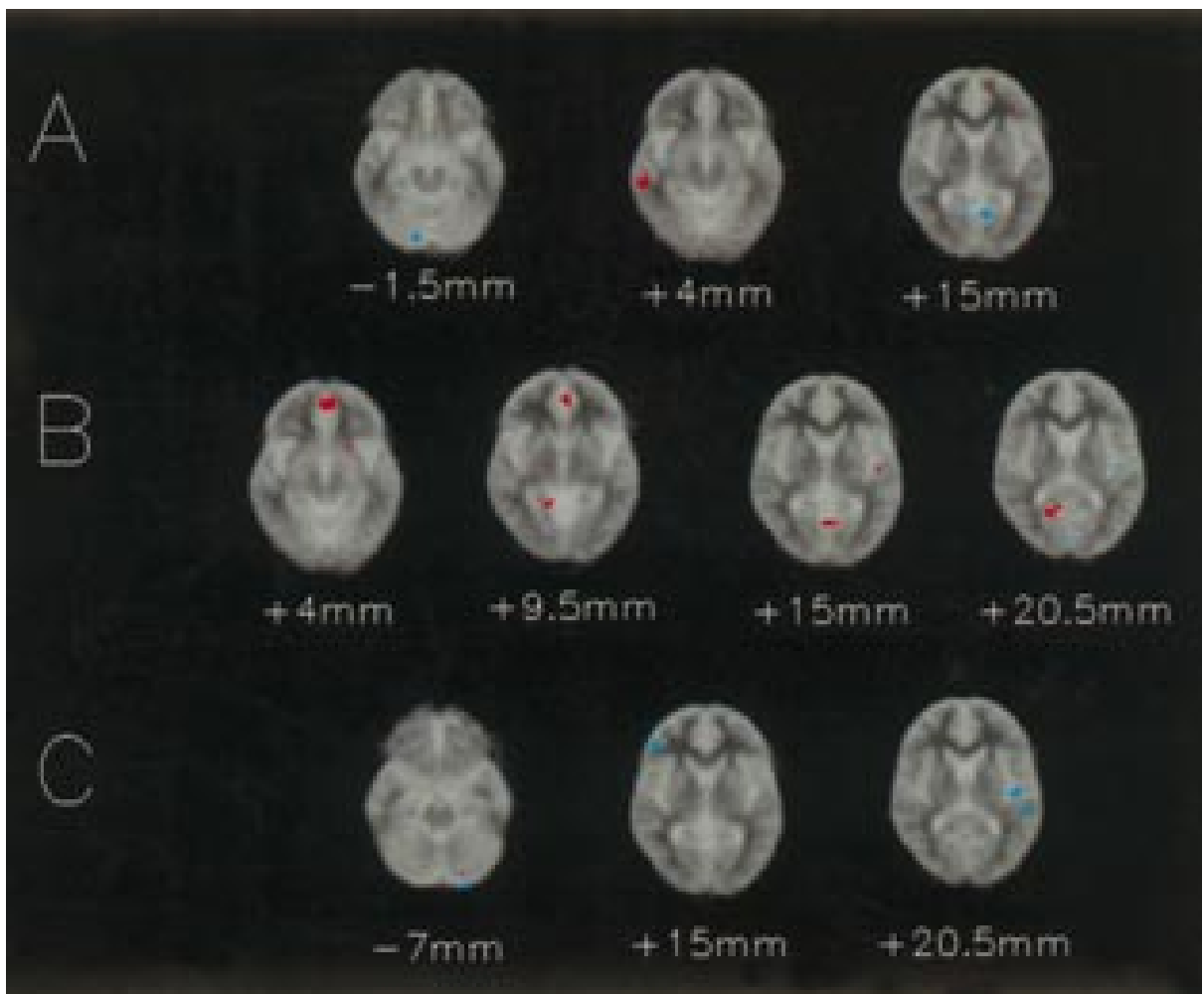


Fig. 1. Brain activations during (a) the facial recognition task, (b) the happy expression perception task and (c) the sad facial expression perception task. [Legend continues on following page.]

tain facial expressions (Phillips et al., 1997). It remains unclear as to the role of the insula in the current study.

4.2. Emotional versus neutral facial expressions

We demonstrated anatomically different patterns of signal increase for perception of happy and sad facial expressions, supporting our fourth hypothesis.

We detected a signal increase in the anterior and posterior cingulate gyri and medial frontal cortex during presentation of happy facial expressions. Earlier studies have implicated the cingulate cortex (Sergent et al., 1994) and anterior cingulate gyrus (George et al., 1993) in the recognition of facial expressions. More recent studies have demonstrated posterior cingulate activation in response to happy facial expressions (Kilts et al., 1996), and anterior cingulate activation in response to novel stimuli (Berns et al., 1997). The role of the medial frontal cortex, and in particular the orbitofrontal cortex, in emotional behaviour

has been highlighted in earlier studies (Rolls, 1990). Our results may therefore reflect the roles of these brain regions in processing of emotional stimuli per se rather than perception of happy facial expressions.

There was an additional signal increase in the left supramarginal gyrus during presentation of happy facial expressions. A previous study has highlighted the role of this structure in the assistance of right-sided regions in demanding visuo-spatial tasks (Smith et al., 1996).

Although we were able to demonstrate a signal increase during presentation of happy faces in several brain regions, it was striking, and in conflict with our third hypothesis, that no brain region showed any detectable signal increase during presentation of the sad faces. This is in contrast to studies of perception of other negative emotional stimuli, including fearful facial expressions, in which the amygdala has been demonstrated to have a role (Adolphs et al., 1994, 1995; Young et al., 1995; Morris et al., 1996; Breiter et al., 1996; Whalen et al., 1998), and facial expressions of

Fig. 1. [Continued] (a) top: Generic brain activations in eight right-handed normal subjects during the facial recognition memory task. The grey-scale template was calculated by voxel-by-voxel averaging of the individual EPI images of all subjects, following transformation into Talairach space. Three transverse sections are shown at 1.5 mm below (left), 4 mm above (middle), and 15 mm above (right) the AC-PC line. The right side of the brain is shown on the left of each section; the left side on the right. Voxels have a probability of false activation ≤ 0.004 . Activated voxels with signal maximum during presentation of the familiar faces are coloured red, and are demonstrated in the right middle temporal gyrus (Talairach co-ordinates: $x = 58, y = -31, z = 4$; BA 21), left dorsolateral prefrontal cortex (Talairach co-ordinates: $x = -32, y = 31, z = 15$; BA 45), and left medial prefrontal cortex (Talairach co-ordinates: $x = -6, y = 50, z = 15$; BA 9). Activated voxels with a signal maximum during presentation of unfamiliar faces are coloured blue, and are demonstrated in the right middle occipital cortex (Talairach co-ordinates: $x = 12, y = -78, z = -1.5$; BA 18) and bilateral posterior cingulate gyri (Talairach co-ordinates: $x = -6, y = -58, z = 15$; BA 31; and $x = 14, y = -50, z = 15$; BA 30). (b) middle: Generic brain activations in eight right-handed subjects during the happy facial expression perception task. The grey-scale template is as in Fig. 1A. Four transverse sections are shown at 4 mm above (left), 9.5 mm above (middle), 15 mm above (middle) and 20.5 mm above (right) the AC-PC line. The right side of the brain is shown on the left of each section; the left side on the right. Voxels have a probability of false activation ≤ 0.004 . Activated voxels with signal maximum during presentation of faces with a happy expression are coloured red, and are demonstrated in the left anterior cingulate gyrus (Talairach co-ordinates: $x = -3, y = 44, z = 4$; BA 24), bilateral medial frontal cortex (Talairach co-ordinates: $x = 0, y = 39, z = 9.5$; BA 32), right putamen (Talairach co-ordinates: $x = 23, y = -14, z = 9.5$), left supramarginal gyrus (Talairach co-ordinates: $x = -43, y = -14, z = 15$; BA 40) and bilateral posterior cingulate gyri (Talairach co-ordinates: $x = 14, y = -56, z = 20.5$; BA 30; and $x = -14, y = -56, z = 15$; BA 31). Activated voxels with signal maximum during presentation of faces with a neutral expression are coloured blue, and are demonstrated in the left caudate nucleus (Talairach co-ordinates: $x = -20, y = -11, z = 20.5$). (c) bottom: Generic brain activations in seven right-handed subjects during the sad facial expression perception task. The grey-scale template is as in Fig. 1A. Three transverse sections are shown at 4 mm above (left), 15 mm above (middle), and 20.5 mm above (right) the AC-PC line. The right side of the brain is shown on the left of each section; the left side on the right. Voxels have a probability of false activation ≤ 0.004 . Activated voxels with signal maximum during presentation of faces with a neutral expression are coloured blue, and are demonstrated in the left middle occipital cortex (Talairach co-ordinates: $x = -20, y = -89, z = -7$ and $x = -12, y = -75, z = -7$; BA 18), right dorsolateral prefrontal cortex (Talairach co-ordinates: $x = 46, y = 31, z = 15$; BA 45) and left supramarginal gyrus (Talairach co-ordinates: $x = -40, y = -17, z = 20.5$ and $x = -49, y = -33, z = 20.5$; BA 40).

Table 2
Happy vs. neutral facial expressions: generically activated brain regions

Region (approximate Brodmann area)	Side	x^a	y^a	z^a	No. of voxels	P^b	Condition of signal increase ^c
Anterior cingulate gyrus (24)	L	-3	44	4	14	0.00001	Happy
Posterior cingulate gyrus (23/30/31)	R	14	-56	20	13	0.00001	Happy
	L	3	-61	15	11	0.00001	
Supramarginal gyrus (40)	L	-14	-56	15	4	0.0001	
	L	-43	-14	15	9	0.00001	Happy
	L	-40	-17	20	4	0.0004	
Medial frontal cortex (32)	R/L	0	39	9	7	0.00001	Happy
Putamen	R	23	-14	9	6	0.00005	Happy
	R	26	-19	9	3	0.0004	
Caudate nucleus	L	-20	-11	20	4	0.0003	Neutral
<i>B: Sad vs. neutral facial expressions: generically activated brain regions</i>							
Supramarginal gyrus (40)	L	-40	-17	20	8	0.0001	Neutral
	L	-49	-33	20	4	0.00006	
Dorsolateral prefrontal cortex (45)	R	46	31	15	7	0.00007	Neutral
Middle occipital cortex (18)	L	-20	-89	-7	5	0.0001	Neutral
	L	-12	-75	-7	2	0.0004	
	L	-20	-78	-7	2	0.0004	
	L	-9	-83	4	2	0.0004	

^aTalairach co-ordinates refer to the voxel with the maximum FPQ (fundamental power quotient) in each regional cluster.

^bAll such voxels were identified by a one-tailed test of the null hypothesis that median FPQ is not determined by experimental design. The probability threshold for activation was $P \leq 0.004$.

^cSignal increase was detected either during presentation of sad or neutral facial expressions.

disgust, in which the anterior insula is central (Phillips et al., 1997). This discrepancy may reflect the relatively complex or evolved nature of sadness as an emotion (Power and Dalgleish, 1997). Further studies with more frequent stimulus presentation and different categories of facial expression will clarify this issue.

4.3. Methodological considerations

For both tasks investigating facial expression perception, subjects were presented with specimen neutral faces prior to scanning. The neutral facial stimuli might therefore have appeared more familiar to subjects during the task than the happy or sad facial stimuli. Although this would not have affected the judgement of facial expression,

in view of previous findings indicating that facial expression decisions are unaffected by the familiarity of the face (Ellis et al., 1990), there may have been a recognition effect. In the task contrasting sad and neutral facial expressions, for example, a signal increase was demonstrated during presentation of the neutral faces in structures implicated in performance of memory tasks: right dorsolateral prefrontal cortex (Haxby et al., 1994, 1996); and left middle occipital cortex (Courtney et al., 1996, 1997). In future studies of facial expression perception, it may be desirable to allow subjects to view all stimuli prior to scanning (rather than neutral faces alone) in order to control more adequately for this potential confound.

Another consideration was the relatively long duration of presentation of faces in the expres-

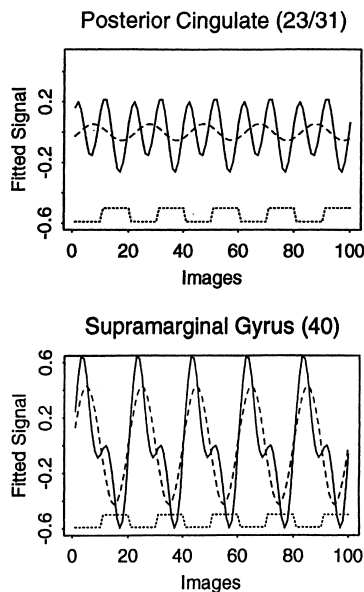


Fig. 2. The median values for the standardised amplitudes of sine and cosine waves at both fundamental and first harmonic frequencies were computed for each generically activated brain region. Multiplied by the appropriate columns of the design matrix, these parameters defined a fitted time series for each activated brain region (see Section 2). (a): The fitted time series demonstrates the patterns of signal intensity change at the fundamental frequency (broken line) and additional first harmonic modulation (solid line) in the bilateral posterior cingulate gyri (BA 23, 30 and 31) in the happy facial expression perception task. (b): The fitted time series demonstrates the patterns of signal intensity change at the fundamental frequency (broken line) and additional first harmonic modulation (solid line) in the left supramarginal gyrus (BA 40) in the sad facial expression perception task.

sion tasks. Although this was chosen to encourage a sustained emotional response, and in order to be consistent with an earlier study in which similar facial expressions were employed (George et al., 1995), the restricted number of stimuli may have led to a reduction in apparent activation (compared with Sergent et al., 1994).

In summary, the current study has provided evidence for the involvement of distinct anatomical substrates for facial recognition memory and facial expression perception. A striking finding was the absence of activation in any brain region associated specifically with presentation of sad

facial expression. Future studies employing fMRI, and stimuli depicting a range of other facial expressions (anger and disgust, for example), will clarify the nature of the neural substrates for perception of distinct facial expressions, in addition to clarifying the nature of structures underlying facial perception in general.

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