**PERGAMON**

# Reading the mind from eye gaze

Andrew J. Calder [a,*], Andrew D. Lawrence [a], Jill Keane [a], Sophie K. Scott [b],
Adrian M. Owen [a], Ingrid Christoffels [c], Andrew W. Young [d]

[a] *MRC Cognition and Brain Sciences Unit, 15 Chaucer Road, Cambridge CB2 2EF, UK*
[b] *Department of Psychology, University College London, Gower Street, London WC1E 6BT, UK*
[c] *Department of Psychology, University of Amsterdam, Roetersstraat 15, 1018 WB, Netherlands*
[d] *Department of Psychology, University of York, Heslington, York YO1 5DD, UK*

## Abstract

Baron-Cohen [Mindblindness: an essay on autism and theory of mind. Cambridge, MA: MIT Press, 1997] has suggested that the interpretation of gaze plays an important role in a normal functioning theory of mind (ToM) system. Consistent with this suggestion, functional imaging research has shown that both ToM tasks and eye gaze processing engage a similar region of the posterior superior temporal sulcus (STS). However, a second brain region associated with ToM, the medial prefrontal (MPF) cortex, has not been identified by previous eye gaze studies. We discuss the methodological issues that may account for the absence of MPF activation in these experiments and present a PET study that controls for these factors. Our experiment included three conditions in which the proportions of faces gazing at, and away from, the participant, were as follows: 100% direct [0% averted], 50% direct—50% averted, and 100% horizontally averted [0% direct]. Two control conditions were also included in which the faces' gaze were averted down, or their eyes were closed. Contrasts comparing the gaze conditions with each of the control conditions revealed medial frontal involvement. Parametric analyses showed a significant linear relationship between increasing proportions of horizontally averted gaze and increased rCBF in the MPF cortex. The opposite parametric analysis (increasing proportions of direct gaze) was associated with increased rCBF in a number of areas including the superior and medial temporal gyri. Additional subtraction contrasts largely confirmed these patterns. Our results demonstrate a considerable degree of overlap between the medial frontal areas involved in eye gaze processing and theory of mind tasks. © 2002 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

A recent functional imaging study by Hoffman and Haxby [19] has shown that matching faces for their direction of gaze engages different brain areas to matching the same faces for their identity. The gaze task was associated with a significantly larger signal in the left posterior superior temporal sulcus (STS) and intraparietal sulcus, whereas the facial identity task produced significantly larger bilateral signals in the fusiform gyri and inferior occipital gyri. The same study also found that averted gaze was associated with a higher left STS signal than direct gaze.

The above results replicate and extend the findings of two earlier neuroimaging studies. The first showed that viewing faces with direct and averted gaze produced an increase in the regional cerebral blood flow (rCBF) of areas adjacent to the posterior STS when compared with viewing faces with downward gaze [31]. In contrast to Hoffman and Haxby, however, Wicker et al. [31] found no reliable difference between their averted and direct gaze conditions. The second study showed posterior STS involvement when participants were shown a dynamic facial stimulus switching between averted and direct gaze [30], relative to when they were shown a static facial image looking directly at them. Interestingly, the results of none of these three studies bear much resemblance to an investigation of eye gaze processing by Kawashima et al. [22] that found no evidence of STS involvement. Instead, both direct and averted gaze conditions in the Kawashima et al. study produced amygdala activation, with the direct gaze condition showing significantly greater right amygdala activation than the averted gaze condition: Kawashima et al. attributed the amygdala involvement to the emotional component of processing another person's gaze.

More recent research has examined the neural correlates of eye gaze in more detail. George et al. [15] showed that relative to averted gaze, direct gaze produced more metabolic

* Corresponding author. Tel.: +44-1223-355-294x750;
fax: +44-1223-359-062.
*E-mail address:* andy.calder@mrc-cbu.cam.ac.uk (A.J. Calder).

activity in an area of the fusiform gyrus that has consistently been shown to respond to facial images. The authors suggested that this finding follows because (i) previous research has shown that attending to facial images in a display enhances the signal in the fusiform face area, and (ii) direct gaze can convey a number of meanings (e.g. threat, sexual attraction, interest, etc.), and hence it is important to pay careful attention to other aspects of the face (e.g. identity, facial expression, sex) in order to attribute the correct meaning.

Finally, Kampe et al. [21] demonstrated that certain neural correlates of gaze interact with the attractiveness of the face. They showed that the signal in an area identified as the ventral striatum increased with increasing facial attractiveness for faces displaying direct gaze, and decreased with increasing facial attractiveness for faces displaying averted gaze. The authors suggested that the ventral striatal signal reflected the reward value of making eye contact with an attractive individual.

## 2. The role of STS in the attribution of mental states to others

Wicker et al. [31] suggested that the STS activation they observed was related to the perception of both averted and direct gaze, whereas Puce et al. [30] concluded that this area was involved in processing the direction signalled by gaze. Hoffman and Haxby [19] on the other hand have suggested that this area of STS has a more general role in the perception of changeable aspects of faces (e.g. gaze, expression, lip speech, etc.) (see also [17]).

All of these suggestions are plausible interpretations of the data. However, it is important to remember that gaze not only acts as an indicator of where another person is looking, it also indicates that something (or someone) at this location has captured the person's (gazer's) attention. In addition, it implies that the person may have some intention or goal towards this particular object. In other words, gaze engages the mechanisms involved in the attribution of intentions and goals to others, a mechanism that is generally known as theory of mind (ToM). Moreover, Perrett and co-workers have shown that detection of an external agent's direction of attention, and the attribution of intentions to the agent may be served by separate neural mechanisms. In a series of cell recording studies these researchers have demonstrated that certain cells in the macaque STS are sensitive to the direction of gaze and body posture of external agents (i.e. cues to an individual's direction of attention) [29], while others are sensitive to the limb movement of external agents. Of most interest, however, is the observation that the responses of a subset of limb movement cells are modulated by the agent's direction of attention [20]. Jellema et al. [20] suggest that this combined analysis of direction of attention and body movements underlies the detection of intentional actions (see also [9,28]).

With regard to the likely neural correlates of ToM, neuroimaging research has shown that areas of the medial prefrontal (MPF) cortex, in particular Brodmann's areas 8 and 9 (BA 8/BA 9), are plausible neural candidates [6,10,13,14]. In a recent paper, Castelli et al. [7] listed a number of neuroimaging studies that found MPF cortex activation for tasks that involved the attribution of beliefs and intentions to others (ToM tasks); in addition, Castelli et al. also listed a number of studies that found similar MPF involvement when participants monitored their own mental states. It is of interest that all of the studies that used ToM tasks found significant signals in a similar brain area to the region of posterior superior temporal cortex identified by the gaze studies discussed above. In contrast, just one of the five studies involving the monitoring of one's own mental states engaged this region. The study in question [26] involved the participants hearing another person's voice in place of their own while they read aloud sentences; hence, like the more classic ToM tasks, it also involved monitoring the behaviour of an external agent.

To illustrate the degree of overlap between the posterior temporal regions identified by ToM and gaze studies, Fig. 1 shows the points of maximal activation of voxel clusters found in these two sets of studies. It is clear that the region of posterior temporal cortex (i.e. STS) that Haxby et al. [17] associated with the visual analysis of changeable aspects of the face (i.e. gaze, emotional expressions, mouth movements, etc.), is very similar to the regions engaged by ToM tasks. Moreover, it is worth noting that none of the ToM studies included gaze or face processing tasks.

One possibility, then, is that the posterior temporal region identified by the gaze experiments forms part of a more general post-perceptual system involved in processing the actions of external agents. For example, Frith and Frith [13], have proposed that this area is involved in detecting the behaviour of agents, and analysing the goals and outcomes of this behaviour (see also [1,14]). This concurs with Baron-Cohen's [4] proposal that the interpretation of gaze plays a fundamental role in reading other people's thoughts and intentions. In addition, it is consistent with Hikosaka's [18] work showing that the posterior STS in the macaque brain constitutes a polysensory area involved in the direction of global attention to sensory cues from multiple modalities.

However, if gaze does play such a critical role in reading other people's mental states, then it is surprising that the aforementioned gaze studies did not also implicate other brain areas associated with ToM tasks. One area in particular is the MPF cortex (BA 8/9); an area linked to posterior STS by direct connections [3]. Frith and Frith [13] have proposed that, together with the anterior cingulate, the MPF cortex represents mental states of the self; states which are attributed to others in the process of inferring another person's thoughts and intentions. However, these MPF areas would only be found for processing gaze if the control condition(s) did not also engage these areas to a similar extent. In relation to this issue it may be relevant
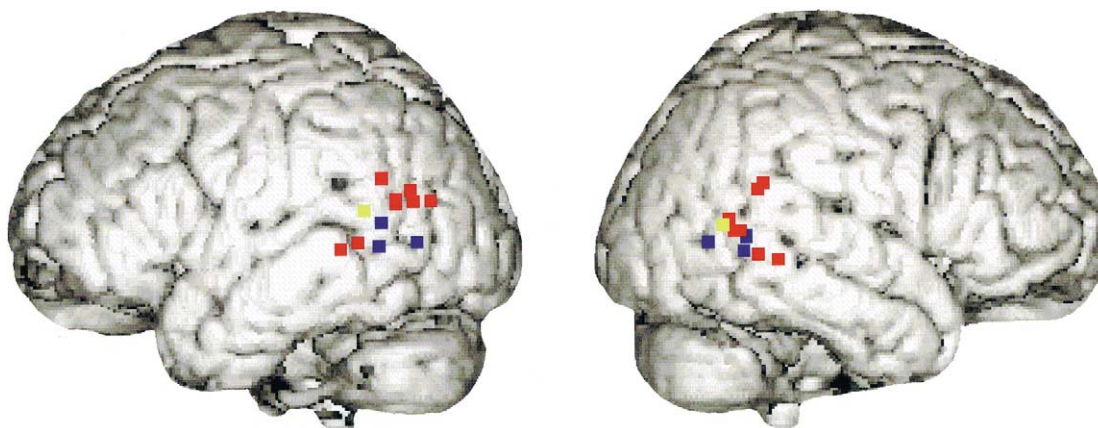
Fig. 1. The maximal points of activation of voxel clusters in the temporal lobe for a series of functional imaging studies investigating the attribution of intentions and thoughts to another (red) and to oneself (yellow). Similar maxima are also shown for two recent studies of gaze processing (blue) conducted by Hoffman and Haxby [19] and Wicker et al. [31]. The stereotactic coordinates are illustrated on the average brain template from the MNI. Consequently, coordinates that were originally reported in Talairach space were converted to MNI space using the procedure described in ref. [5].

that three of the gaze studies discussed used a passive viewing procedure ([9,19,30,31] experiment 2), one, a cognitively undemanding task ([19] experiment 1), and another a passive baseline condition (blank screen) [15]. These observations may be important because McGuire et al. [25] have demonstrated that spontaneous thoughts (i.e. verbal or visual self-generated thoughts or daydreams) engage the medial (BA 8) and orbito-medial (BA 10) regions of frontal cortex, but not the STS or adjacent regions (see also a recent review by Gusnard and Raichle [16]). Thus, given that the participants' attention was not always fully engaged by the experimental tasks in these gaze studies it is not improbable that spontaneous thoughts could have occurred.

The Kawashima et al. [22] study did not involve passive viewing, however, each experimental condition contained highly social facial signals (i.e. looking the participant up and down [direct gaze], looking a person to the left of the participant up and down [averted gaze], and looking away from the participant and winking [baseline]), hence, this alone could explain the absence of signals in areas previously associated with ToM tasks. By controlling for the experimental design factors discussed above, our study aimed to address whether the MPF areas, previously associated with ToM tasks, are involved in processing another person's gaze.

We were aware that the absence of MPF activation in previous gaze studies could also be due to a second factor—the question of whether the attribution of mental states to others is an automatic process (i.e. it does not require deliberate mental effort on the individual's part). In other words, it is possible that MPF involvement was not observed in the gaze studies discussed because the participants were not performing an explicit 'mind reading' task.

The question of whether the attribution of mental states to others is automatic is interesting, but as far as we are aware, it has not been addressed by ToM studies. It is relevant, however, that recent research has shown that participants

make reflexive shifts in attention towards the direction signalled by another person's gaze [8,11,24]. Given these findings, we decided to investigate whether the MPF areas are engaged when participants are not asked to make any explicit decision about a person's thoughts and intentions from their gaze. The (implicit) task selected involved participants deciding whether each face's eyebrows were thick or thin. This task had the advantage of focussing the participants' attention on the eye region, and could be applied to every condition of the experiment.

In summary, the goals of our study were (i) to test the hypothesis that processing another person's gaze engages the brain areas involved in reading other people's mental states, (ii) to test whether these areas are engaged even if the participants are not explicitly instructed to attend to the faces' gaze, and (iii) to investigate whether direct and averted gaze are associated with different neural correlates, as previous studies have suggested.

## 3. Method

### 3.1. Participants

Nine female members of the MRC Cognition and Brain Sciences Unit participant panel (mean age = 58.3, S.D. = 2.9) participated in the experiment for payment. All participants were post-menopausal, right-handed, and had normal or corrected-to-normal vision. All had given written informed consent to participate in the study. Ethical approval for the study was obtained from the Cambridge Local Research Ethics Committee.

### 3.2. Materials

The stimulus materials consisted of colour photographs of 16 young models (eight men and eight women). Each

model was positioned directly in front of a camera, with their head orientated 10° to the left of the central (0°) camera position. Photographs were then taken with the participants looking directly at the camera (direct gaze, 0°), 15° to the left of the camera (averted gaze), down at the floor (down), and with their eyes closed (closed). For the direct and averted gaze conditions the participants were instructed to look straight ahead (i.e. not up or down), as if they were looking into the eyes of a person of identical height to themselves. An equivalent sequence of images was also taken with the participants' heads orientated 10° to the right, (i.e. direct gaze, gaze averted 15° to the right, gaze directed downwards, and eyes closed).

The participants' task was to decide whether each face had thick or thin eyebrows. Models that did not fit obviously into either set had their photographs adjusted by a qualified computer-graphics artist so that there were equal numbers (8) of male and female models with thick and thin eyebrows. All faces were standardised for their eye position and inter-ocular distance, and the background of each picture was excluded with an oval mask (see Fig. 2).

### 3.3. Design and procedure

There were three experimental conditions (100% direct, 50% direct—50% horizontally averted, and 100% horizontally averted) and two baseline conditions (eyes closed and eyes down). As with the horizontally averted condition, the eyes down condition showed someone looking away from the camera. Nonetheless, we opted to use this as a baseline because it had been used successfully in a previous PET study of eye gaze by Wicker et al. [31]. In addition, in line with the stimuli used by Wicker et al. [31] the models' gaze in our eyes down condition was difficult to discern because

looking down towards the floor makes the eyes barely visible (see Fig. 2).

All conditions were blocked with each block containing 32 trials of the same format; the trial format for each block is described below. Each participant completed the same twelve blocks of trials but in different pseudo-random order; the number of blocks assigned to each condition is shown in brackets below.

### 3.4. Experimental conditions

1. *100% direct [0% horizontally averted] (3 blocks)*: Each trial consisted of a face gazing directly at the camera.
2. *50% direct—50% horizontally averted (2 blocks)*: Half of the trials consisted of faces gazing directly at the camera, the other half contained faces gazing away from the camera.
3. *100% horizontally averted (0% direct) (3 blocks)*: Each trial consisted of a face gazing away from the camera.

### 3.5. Baseline conditions

1. *Eyes down (2 blocks)*: Each trial consisted of a face gazing down towards the floor.
2. *Eyes closed (2 blocks)*: Each trial consisted of a face with the eyes closed.

Each block contained two pictures of the same 16 models in random order; in one their head was angled 10° to the left of the central camera, and in other 10° to right; a total of 32 trials. The models' gaze in each block varied according to the block design listed above. Blocks were preceded by eight practice trials whose format was consistent with the experimental condition. Each trial consisted of a 2250 ms
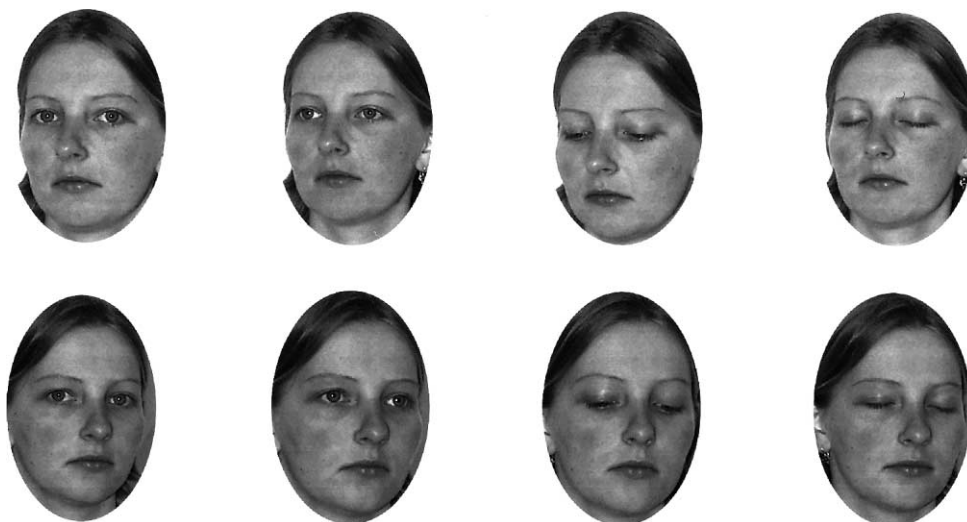


Fig. 2. Examples of the facial stimuli posed by one female model. For the upper row the model's head is oriented 10° to the left, in the lower row, 10° to the right. From left to right the model's gaze is oriented (i) towards the camera, (ii) 15° away from camera, (iii) down, and (iv) in the final column the model's eyes are closed. The model shown was from the "thin eyebrows" group.

presentation of a stimulus face; the inter-trial interval was 1000 ms. The participants' task was to press one of two keys (with the first or index finger of their right hand) to indicate whether each face had thick or thin eyebrows.

## 3.6. PET data acquisition

All scans were performed at the Wolfson Brain Imaging Centre (WBIC), Cambridge, on a GE Advance PET scanner (General Electric Medical Systems, Milwaukee, WI) with an axial field-of-view of 15.3 cm, allowing for whole-brain coverage. Each participant received a 20 s intravenous bolus $H_2[15]O$ infusion of 300 MBq activity, via a forearm cannula at a flow rate of $10 \, ml \, min^{-1}$, prior to each of 12 emission scans, for a total radiation exposure of 4.2 mSv. With this method, each scan provides an image of regional cerebral blood flow (rCBF) integrated over a period of 90 s from the time at which the tracer first enters cerebral circulation. Following an initial transmission scan, emission data were acquired with the septa retracted (3D mode) and reconstructed using the PROMIS algorithm [23], with an unapodised Colsher filter. Corrections were applied for random, scatter, attenuation, and dead time. Reconstructed voxel sizes were 2.34 mm × 2.34 mm × 4.25 mm.

## 3.7. Data pre-processing

The functional images were realigned using the algorithms provided in the Statistical Parametric Mapping software (SPM99, [12]). Translation and rotation corrections did not exceed 5 mm and 3°, respectively, for any participant. Two participants made unacceptably large movements in the scanner, and were excluded from further analysis. The following analyses are therefore based on the results of seven participants.

The mean image created by the realignment procedure was used to determine the parameters for transforming the images onto the Montreal Neurological Institute (MNI) mean brain. The normalization parameters were then applied to the functional images [2]. After normalisation, the voxels were isotropic at $2 \, mm^3$. Scans were normalised for global CBF value and then each image was smoothed with a 16 mm full width at half-maximum (FWHM) Gaussian filter.

## 4. Results

### 4.1. Behavioural data

Participants' mean RTs and percent errors for the five conditions (100% direct, 50% direct—50% horizontally averted, 100% horizontally averted, down, and closed) are summarised in Table 1. Errors were low indicating that participants were concentrating on the task. RTs and error scores (arcsin transformed) were each submitted to separate repeated measures ANOVAs examining the five conditions. Both produced significant effects of condition: RTs, $F(4.24) = 3.56$, $P < 0.02$; errors $F(4.24) = 2.87$, $P < 0.05$. Newman-Keuls tests ($P < 0.05$) indicated that this was due to participants making more errors, and taking longer to respond, in the 100% horizontally averted condition compared with the eyes down condition; no other comparisons reached statistical significance.

### 4.2. Neuroimaging data

#### 4.2.1. Statistical analysis

Conditions and covariates for each participant were specified in the appropriate design matrix; this also included global activity and scan order as confounding covariates, and can therefore be considered an analysis of covariance (ANCOVA). Effects at each voxel were estimated according to the general linear model (GLM) and regionally specific effects were compared using parametric analyses [12]. The resulting set of voxel values for each contrast constituted a statistical parametric map of the *t*-statistic (SPM{*t*}). The significance of a given *t*-statistic was assessed by application of an intensity threshold to the SPM images, based on 3D Gaussian random field theory [33]. For changes in rCBF of brain areas predicted by previous gaze research or ToM studies (i.e. the medial frontal cortex, STS, and fusiform gyrus), an intensity threshold (uncorrected for multiple comparisons) of $P \leq 0.001$ was applied; other areas that achieved this level of significance are also shown for the reader's information. In addition, in line with our a priori hypothesis, significance thresholds for medial prefrontal cortex activations were adjusted, using a region-of-interest (ROI). We defined the ROI by taking a sphere of 16 mm

Table 1
Participants' mean correct RTs and mean percent errors with S.D.s for the five experimental conditions (100% direct, 50% direct—50% averted, and 100% averted, eyes down, and eyes closed)

|  | 100% direct | 50% direct—50% averted | 100% averted | Eyes down | Eyes closed |
|---|---|---|---|---|---|
| *RTs* | | | | | |
| Mean | 817 | 825 | 837 | 777 | 789 |
| S.D. | 90 | 90 | 67 | 48 | 87 |
| *Percent errors* | | | | | |
| Mean | 4.69 | 4.02 | 5.21 | 2.23 | 3.35 |
| S.D. | 4.69 | 2.97 | 3.85 | 1.99 | 2.46 |

radius centred on the median $x$, $y$, $z$ MNI coordinates of the right medial PFC points displayed in Fig. 3. This ROI had coordinates 4, 42, 36. Brain regions were identified by converting the MNI coordinates to Talairach space [5].

### 4.3. Brain areas engaged by processing gaze

To determine the brain areas engaged by processing gaze we conducted two contrasts. For the first, we subtracted the changes in rCBF produced by the eyes down baseline condition (down) from changes produced by all three experimental conditions (i.e. [100% direct, 50% direct—50% horizontally averted, & 100% horizontally averted] minus eyes down). The results showed a significant increase in rCBF in the MPF cortex (BA 8) ($x = 14$, $y = 26$, $z = 36$; $t = 3.72$ $P < 0.001$, uncorrected; $P < 0.05$ corrected for MPF ROI). For the second contrast the change in rCBF produced by the eyes closed baseline condition (closed) was subtracted from that produced by all three experimental conditions (i.e. [100% direct, 50% direct—50% horizontally averted, & 100% horizontally averted] minus closed). The results produced a borderline increase of rCBF in a more ventro-anterior section of the medial frontal cortex (BA 10) ($x = -8$, $y = 56$, $z = 2$; $t = 3.18$, $P = 0.0011$, uncorrected).

Our results indicate that medial frontal regions, associated with ToM tasks, are engaged more by faces displaying direct and horizontally averted gaze, than faces in which the gaze is directed downwards, or the eyes are closed. Having established this we went on to analyse whether direct and horizontally averted gaze were associated with particular neural profiles.

### 4.4. Brain areas engaged by direct and horizontally averted gaze

#### 4.4.1. Parametric analysis

The neural correlates of horizontally averted and direct gaze were examined with parametric analyses (linear correlations) of the three experimental conditions (100% direct, 50% direct—50% horizontally averted, 100% horizontally averted). As illustrated in Table 2, these analyses showed that two predicted areas produced a significant increase in rCBF as the proportion of faces with horizontally averted gaze increased—these were, the MPF cortex (BA 8/9), and middle temporal gyrus (BA 21) (one of the two gyri that form the banks of the STS). As the proportion of faces with direct gaze increased, significant increases in rCBF were seen in a number of different areas. These included the right middle temporal gyrus (BA 21) and superior temporal gyrus (BA 22); although both temporal lobe signals were more anterior to the middle temporal gyrus signal observed for horizontally averted gaze.

### 4.5. Subtraction contrasts

The brain areas engaged by the horizontally averted and direct gaze conditions were also investigated using three subtraction contrasts. First, the change in rCBF produced by the direct condition was subtracted from that produced by the horizontally averted condition (averted minus direct), and vice versa (direct minus averted). Next, the rCBF change for the eyes down baseline was subtracted from that for each of the direct and horizontally averted gaze conditions (direct minus down and averted minus down). Finally, the rCBF change produced by the eyes closed baseline condition was

Table 2

Coordinates of the maximally activated voxels and associated $t$-statistics for parametric analyses (linear correlations) identifying the regions selectively activated with increasing proportions of averted gaze (i.e. 100% direct, 50% direct—50% averted, and 100% averted), and increasing proportions of direct gaze (i.e. 100% averted, 50% direct—50% averted, and 100% direct)

| Area of activation (BA) | MNI stereotactic coordinates | | | | |
|---|---|---|---|---|---|
| | Side | $x$ | $y$ | $z$ | $t$-Statistics |
| *Increasing proportions of averted gaze* | | | | | |
| Medial frontal gyrus (8/9) | R | 2 | 44 | 36 | 4.44* |
| Middle frontal gyrus (10/11) (orbitofrontal) | L | −26 | 44 | −8 | 4.03 |
| Middle temporal gyrus (21) | L | −66 | −42 | −12 | 3.54 |
| | L | −54 | −20 | −8 | 3.39 |
| Inferior frontal gyrus (44/9) | R | 52 | 16 | 44 | 3.38 |
| *Increasing proportions of direct gaze* | | | | | |
| Insular cortex | R | 34 | −26 | 22 | 4.01 |
| Thalamus | L | −12 | −16 | −4 | 3.95 |
| Uncus (20/28) | R | 24 | −12 | −32 | 3.60 |
| Middle temporal gyrus (21) | R | 60 | −2 | −14 | 3.59 |
| Superior temporal gyrus (22) | R | 62 | −10 | 8 | 3.31 |
| Postcentral gyrus (somatosensory cortex) (1) | R | 54 | −26 | 52 | 3.31 |

Activations in all regions are significant at $P < 0.001$ (uncorrected). The symbol (∗) indicates the significance threshold of the MPF activation adjusted for MPF region of interest (ROI).

* $P < 0.003$, corrected for ROI.

Table 3
Coordinates of the maximally activated voxels and associated *t*-statistics for contrasts comparing each of the 100% direct and 100% averted gaze conditions with one another and each of the two baseline conditions (eyes down and eyes closed)[a]

| Area of activation (BA) | MNI stereotactic coordinates | | | | |
|---|---|---|---|---|---|
| | Side | *x* | *y* | *z* | *t*-Statistics |
| *Averted gaze* | | | | | |
| Averted minus direct | | | | | |
| Medial frontal gyrus (8/9) | R | 2 | 42 | 36 | 4.87* |
| Middle frontal gyrus (10) | L | −28 | 44 | −6 | 4.16 |
| Averted minus closed | | | | | |
| Medial frontal gyrus (8/9) | R | 2 | 42 | 34 | 4.18** |
| Middle frontal gyrus (10) | L | −30 | 56 | −4 | 3.74 |
| Averted minus down | | | | | |
| Medial frontal gyrus/anterior cingulate gyrus (8/32) | R | 12 | 26 | 36 | 3.62*** |
| Middle frontal gyrus (6) | R | 52 | 10 | 38 | 3.52 |
| Temporal/parietal junction (40) | L | −64 | −54 | 24 | 3.38 |
| Middle frontal gyrus (6/8) | L | −44 | 12 | 50 | 3.23 |
| *Direct gaze* | | | | | |
| Direct minus averted | | | | | |
| Superior temporal gyrus (22) | R | 60 | −6 | 6 | 3.65 |
| Middle temporal gyrus (21) | R | 58 | −2 | −14 | 3.52 |
| Uncus (20/28) | R | 26 | −12 | −32 | 3.25 |
| Fusiform gyrus | R | 32 | −74 | −8 | 3.15 |
| Postcentral gyrus (somatosensory cortex) (1) | R | 52 | −28 | 52 | 3.14 |
| Direct minus closed | | | | | |
| Substantia nigra | L | −14 | −20 | −8 | 3.20 |
| Medial frontal gyrus (10) | L | −10 | 58 | 0 | 3.10 |
| Direct minus down | | | | | |
| Anterior cingulate gyrus (32)/medial frontal gyrus (9) | R | 14 | 26 | 36 | 3.56**** |
| Thalamus | L | −12 | −16 | 6 | 3.37 |
| | R | 12 | −8 | 10 | 3.16 |
| Postcentral gyrus (somatosensory cortex) (3) | L | −20 | −34 | 70 | 3.20 |
| Middle frontal gyrus (6) | R | 30 | −4 | 46 | 3.19 |

[a] Activations in all regions are significant at $P < 0.001$ (uncorrected). The symbols (∗) indicates the significance thresholds adjusted for MPF cortex region of interest (ROI).

* $P < 0.001$, corrected for ROI.

** $P < 0.006$, corrected for ROI.

*** $P < 0.03$, corrected for ROI.

**** $P < 0.077$, corrected for ROI.

subtracted from the change for each of the direct and horizontally averted gaze conditions (direct minus closed and averted minus closed). The results of these six contrasts are summarised in Table 3. As expected, the horizontally averted minus direct contrast replicated the MPF cortex (BA 8/9) signal seen for the parametric analysis of increasing proportions of horizontally averted gaze; a similar pattern was also seen for the horizontally averted minus closed contrast. The horizontally averted minus down contrast engaged a region of MPF cortex bordering on the anterior cingulate (BA 8/32). This same contrast also showed an increase in rCBF in the temporal/parietal junction (BA 40), an area that has been previously associated with ToM tasks [10,14].

The three contrasts examining the direct gaze condition produced less consistent effects. The direct minus horizontally averted contrast replicated the STG, and MTG signals

observed for the parametric analysis of increasing proportions of direct gaze stimuli. In addition, consistent with George et al. [15], the direct minus averted contrast showed increased rCBF in the fusiform gyrus. The direct minus closed contrast showed rCBF changes in the MPF gyrus (BA 10), while the direct minus down contrast produced significant changes in the MPF cortex/anterior cingulate (BA 8/32). It is worth noting that the direct minus down contrast also produced an increased signal in the right and left thalamus. Moreover, the point of maximal activation of the right thalamus signal was identical to the point identified as the right ventral striatum in the gaze study by Kampe et al. [21]. This point, however, appears to be within the region of the thalamus, as described by the Talairach atlas, and may relate to the increased arousal associated with direct gaze as indexed by increased galvanic skin response [27]. A similar

region of the left thalamus was also identified by the parametric analysis of increasing proportions of direct gaze.

## 5. Discussion

Our results demonstrate that an area of medial frontal cortex (BA 8/9), previously associated with the ToM tasks, is indeed engaged by processing another person's gaze. This concurs with the idea that gaze plays a central role in social communication, and hence, the attribution of mental states to others (i.e. ToM) [4]. From an evolutionary perspective this would seem to make good sense, in that survival depends on maintaining a constant degree of vigilance and an ability to second guess another individual's mind state. Consistent with our findings, a recent independent functional imaging study by Wicker et al. [32] has also found MPF involvement for an eye gaze task.

Our study found some evidence to suggest that direct and horizontally averted gaze were associated with different neural profiles. In particular, the parametric analysis showed that horizontally averted gaze was associated more with the MPF cortex, whereas direct gaze engaged a number of areas, including the right middle and superior temporal gyri. In addition, we have replicated George et al.'s [15] finding that direct gaze produces more fusiform gyrus involvement than averted gaze, and Kampe et al.'s [21] observation that direct gaze causes an increased sub-cortical signal relative to averted gaze.

It is important to emphasise that the participants in our study were not instructed to make an explicit judgement about the intentions of the models; they were simply asked to indicate whether each model had thick or thin eyebrows. Hence, it is likely that the observed differences in rCBF reflect an 'implicit' interpretation of the faces' gaze. Of course we cannot rule out the possibility that participants first made an eyebrow decision and then explicitly attended to the models' gaze in order to consider their mental states. However, even if this unlikely strategy was true, our findings are still consistent with the idea that the gaze information was sufficiently important to capture the participants' attention, despite being instructed to concentrate on an unrelated task (i.e. eyebrow thickness). This interpretation is also supported by the results of the behavioural analysis which showed that the RTs and error rates for the 100% horizontally averted gaze condition were significantly greater relative to the eyes down condition; no other results reached statistical significance.

### 5.1. MPF cortex

It is interesting that the MPF cortex was primarily engaged by viewing horizontally averted, rather than direct gaze. The reason for this is not entirely clear. One explanation may be that more computation is involved to work out the goals and intentions of a person with averted gaze relative to a person with direct gaze. This is because for the direct condition the focus of the person's attention is clearly the observer, whereas for averted gaze the focus of attention could be any one of a number of objects or people. Alternatively, it was also the case that for the horizontally averted gaze condition the models' head direction and direction of gaze changed from trial to trial (e.g. from attending to the left on one trial to attending to the right on another). In contrast, while the models' head direction changed similarly for the direct gaze condition, their direction of gaze was constant (i.e. looking at the participant). Similarly, although gaze changed from trial to trial in the 50% horizontally averted—50% direct condition, fewer consecutive trials would have involved as conspicuous a change in the models' direction of attention
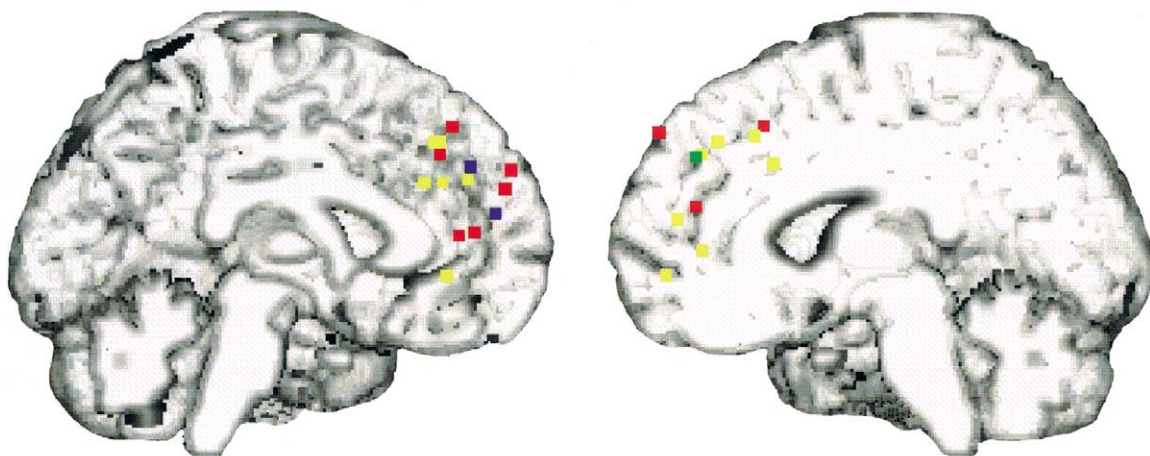


Fig. 3. The maximal points of activation of voxel clusters in the medial frontal cortex for a series of functional imaging studies investigating the attribution of intentions and thoughts to another (red) and to oneself (yellow). Maxima in the same region are also shown for our own study (green), and a recent study of gaze processing by Wicker et al. [32] (blue). The stereotactic coordinates are illustrated on the average brain template from the MNI. Consequently, coordinates that were originally reported in Talairach space were converted to MNI space using the procedure described in ref. [5].

as a left–right shift. It is worth noting, however, that the MPF activation was not exclusively confined to the horizontally averted gaze condition because the direct minus down and direct minus closed contrasts also showed a significant increase in rCBF in similar brain areas (BA 8/32 & BA 10); although the former failed to survive correction for the MPF ROI, and the latter was out with the MPF ROI. Overall, then, our findings are consistent with the idea that both horizontally averted and direct gaze engage the MPF areas, but to greater and lesser extents.

As we discussed, the MPF cortex has previously been associated with ToM tasks and tasks involving the attribution of thoughts and intentions to the self. Fig. 3 shows that there is a good deal of overlap between maxima associated with these tasks and our own study. In addition, the MPF maxima from a recent gaze study by Wicker et al. [32] are also shown.

### 5.2. Superior temporal sulcus (STS)

Earlier we discussed that Hoffman and Haxby [19] have found evidence that the posterior STS is involved in processing gaze, but particularly averted gaze. Our own study found significant signals in more anterior regions of the superior and middle temporal gyri (the gyri that form the banks of the STS), and posterior superior temporal region. However, in line with other functional imaging studies of gaze [22,31] we did not find that the posterior STS was preferentially involved in processing horizontally averted gaze; although a contrast comparing horizontally averted gaze with the eyes down baseline did show increased rCBF in an adjacent region of the temporal-parietal junction. One reason for the inconsistency between Hoffman and Haxby's [19] study and others (including our own) was suggested by George et al. [15]. As was the case in our own study, the head direction and direction of gaze of the facial stimuli used by George et al. were manipulated; moreover, head and gaze direction were not always congruent (e.g. averted head with direct gaze). Consequently, these authors suggested that posterior STS involvement might not be expected in this type of design if the same area of STS was also sensitive to head direction; as has been shown in cell recording studies of non-human primates by Perrett and co-workers [29]. In line with this observation it is of interest that all of the stimuli used by Hoffman and Haxby [19] were full-face images.

To summarise, our results demonstrate that, under the correct testing conditions, brain areas previously associated with ToM tasks (MPF cortex) are engaged by processing another person's gaze; particularly if the person's gaze is averted. These findings concur with Baron-Cohen's [4] proposal that gaze interpretation plays a central role in a normal functioning ToM system. Moreover, the implicit nature of the task used indicates that the attribution of intentions to others may operate in a mandatory fashion. In other words, the presentation of highly social stimulus, such as gaze, is in itself sufficient to engage the mechanisms involved in attributing mental states to others.

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