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Being the target of another's emotion: a PET study

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Abstract

The eye region and gaze behaviour are known to play a major role in conveying information about direction of attention and emotional dispositions. Positron emission tomography scanning was used to explore the cerebral structures involved while subjects were asked to attribute hostile or friendly intentions to video-taped actors who directed attention towards or away from the subjects. As expected, a number of brain regions known to be involved in emotion processing was found activated when subjects had to attribute an emotion regardless of gaze direction. In addition, results indicate that gaze direction has an impact on the brain regions recruited to interpret emotions. The anterior region of the superior temporal gyrus (STG) was selectively activated during analysis of emotions through eye contact. This result provides neurophysiological evidence for privileged processing when an individual becomes personally involved as the object of another's emotions.

Keywords: Gaze; Intentionality; Eye-contact; Emotion; Theory of mind; Superior temporal gyrus

1. Introduction

Emotions signalled by the face constitute a critical channel of social information processing. Humans are endowed with a prodigious ability in perceiving the dispositions and intentions of others, an ability often referred to as social cognition [11]. In this respect, gaze behaviour and eye contact are a conspicuous aspect of human interaction and the eye region is often used as a cue to predict emotional/mental states of others [3,33].

The salience of the eyes as perceptual features within the face has been well demonstrated psychophysically, neuropsychologically and neurophysiologically both in humans and non-human primates [15,31,40,47]. It is essential to keep in mind several distinctions between different aspects of gaze processing. Indeed, detecting where or what another individual is looking at (and thus directing her/his attention, e.g. Is she/he looking at me?) does not always involve the attribution of mental states to the other. On the other hand, interpreting the social significance of eye gaze once it has been detected (e.g. Why is this person looking at me?) does involve the attribution of mental states to the other, an ability referred to as "theory of mind" [41]. Interestingly, individuals affected by autism seem to be specifically impaired in this ability and often exhibit abnormal gaze behaviour [5].

In this respect, the first aim of this study was to determine whether there is a difference between brain regions involved when individuals experience and judge the emotional nature of a gaze compared to when they experience and judge the focus of a neutral gaze. Second, we hypothesised a difference in the brain regions recruited when subjects experienced and judged an emotional direct gaze versus an emotional averted gaze. Indeed, the processing of emotion may be fundamentally different depending on whether we interpret the emotion as directed at ourselves or directed elsewhere. We therefore, manipulated the direction of gaze of faces displaying hostile or friendly expressions as well as the task given to the subjects. The impact of such expressions was expected to depend on the gaze direction. It is only in the case of eye contact that the subject becomes personally involved as the object of the other's emotion. If this is correct, we might predict such behavioural properties to be underpinned by some specialised neuronal circuitry. Here, we attempt to isolate the brain regions that relate specifically to this personal involvement in emotional perception.

In a previous neuroimaging study, our group has shown that temporal (right superior temporal sulcus, STS) and parietal brain regions are engaged in the perception of eyes, independent of gaze direction [48]. Temporal cortex activation in STS has also been reported during passive viewing of eye and mouth movements [42]. The amygdala, the superior

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temporal gyrus (STG) and the prefrontal cortex appear involved when subjects attribute mental states (e.g. “unconcerned”, “guilt”) to static pictures of the eye region [6]. The brain circuits underlying the processing of static facial expressions of emotions have been the focus of recent neuropsychological and neuroimaging studies. Their results underline the importance of several interconnected brain regions including the ventromedial and dorsolateral prefrontal cortex, the amygdala, and the right temporal, anterior cingulate and insular cortices [1,10,17,36,44].

Here we studied the perception of emotions conveyed by the eye region. We used films instead of static display to enhance realism and because additional cues to interpret emotions may be available from movement. To isolate brain structures involved in emotional processing, we compared two cognitive tasks, one involving interpretation of emotion and a second involving interpretation of the focus of attention.

2. Material and methods

2.1. Subjects

Ten healthy right-handed male volunteers with a mean age of 22.5 (range 20–27), screened for neurological and psychiatric antecedents participated in the experiment. Written consent was obtained after the procedure had been fully explained. The study was approved by the local Ethics Committee (Centre Leon Bérard) and was conducted in accordance with the Declaration of Helsinki. Subjects were not specifically informed about the aim of the study. Subjects were paid for their participation.

2.2. Experimental design

The activation paradigm contrasted emotionally salient and non-emotional conditions of gaze. In the two emotional conditions subjects judged the nature of an emotional gaze while in the non-emotional conditions they judged the focus of a neutral gaze (Fig. 1).

In all activation conditions subjects were presented with video-clips. Each clip was constituted of 23 short video sequences of 3 s showing only the eye region of three male and three female actors (Fig. 1). A blank screen of 1 s was presented between each 3 s, video sequence. For the purpose of the non-emotional tasks three coloured cylinders (right, centre, left) were visible in front of the actor’s eye region and this in all activation conditions.

2.3. Experimental conditions

2.3.1. Direct gaze and emotion: DGE

The actor switches gaze from averted (0.5 s) to eye contact with the camera or to the central cylinder in front of the camera (2 s) and then expresses either an angry or friendly expression (50% friendly, 50% angry expression; 50% eye contact, 50% look at the cylinder). The subjects were asked to judge whether they are looked at in a friendly or hostile way. This condition required subjects to assess emotional attitudes of others towards them during eye contact.

2.3.2. Averted gaze and emotion: AGE

The actor switches gaze from right (0.5 s) to left (2 s) or from left (0.5 s) to right (2 s), focuses either at a lateral cylinder or at a distance equal to that of the camera and then expresses friendly or hostile emotion (50% friendly, 50% angry expression, 50% look at the cylinder, 50% look far away, 50% switch to left, 50% switch to right). The subjects were asked to judge whether the actor looks in a friendly or hostile way. This condition required subjects to assess emotional attitudes of others whose attention is directed away from them.

2.3.3. Direct gaze control: DGC

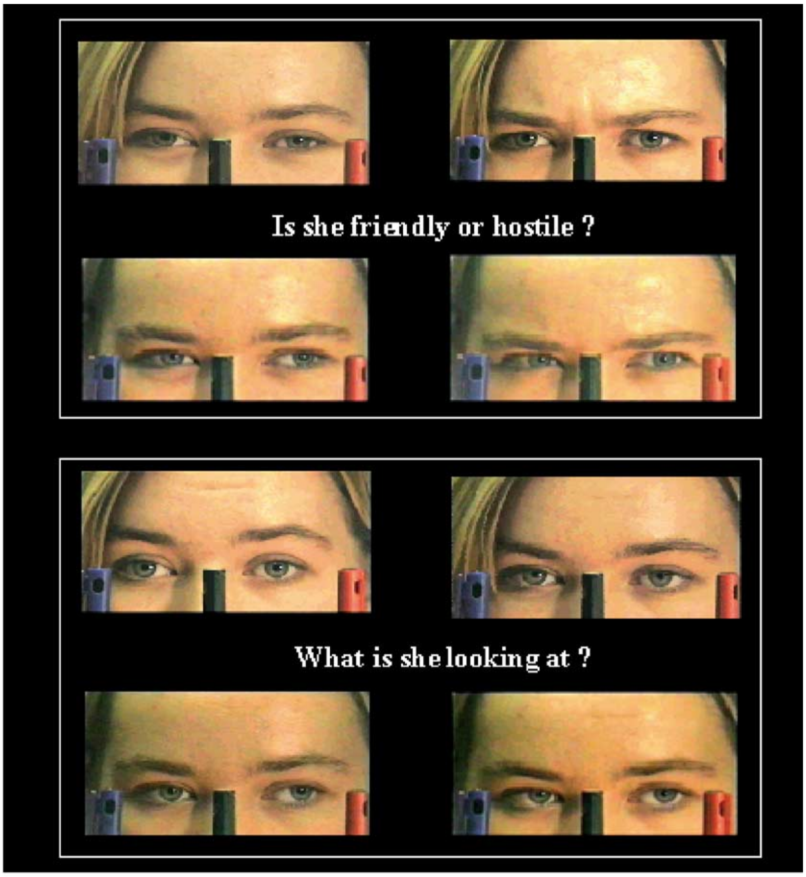
The actor displays a neutral expression and switches gaze from averted (0.5 s) to eye contact with the camera or to a central cylinder in front of the camera for 2 s (50% trials eye contact, 50% look at the cylinder). Provision of an object allowed the eyes of the actor to be directed towards the camera/observer yet clearly converged on a point in between the observer and the actor. Subject were asked to judge whether the actor looks at them or if the actor looks at the cylinders in front of the subject. This condition required subjects to judge the focus of attention of others during a forward-directed gaze.

2.3.4. Averted gaze control: AGC

The actor displays a neutral expression and switches gaze from right (0.5 s) to left (2 s) or left (0.5 s) to right (2 s) and focuses either at a lateral cylinder or behind this cylinder keeping the same line of gaze. Subjects were asked to judge whether the actor looks at a cylinder or adopts a more distant fixation (50% look at the cylinder, 50% look far away, 50% switch to left, 50% switch to right). This condition required subjects to judge the focus of attention of others whose attention is directed away from them.

In each condition, video sequences depicting various stimuli were presented in a random order. Video stimuli were projected on a screen in the back of the scanner using a video projector. Subjects could see the video on reflection in a mirror (15 cm × 9 cm) suspended 10 cm in front of their face and subtending visual angles of 42° horizontally and 32° vertically. The size of the image was matched to the natural size of an eye region at the viewing distance.

All four activation conditions required the subjects to make a forced choice answer about the stimuli by pressing one of two mouse buttons (right index), engaging response selection and motor planning. Thus, none of the brain regions activated in contrasts between conditions should be related to these aspects of the subject’s behaviour.



(A)

	Direct gaze	Averted gaze
Emotion attribution	DGE	AGE
No emotion attribution	DGC	AGC

(B)

Fig. 1. (A) Single frames displaying single shots of the video stimuli presented to the subjects. (B) Four experimental conditions.

2.4. *Pilot study*

Independent of the neuroimaging study, twenty pilot subjects were asked to perform the same tasks as the scanned subjects. Results showed that although it was more difficult to judge fixation distance (mean accuracy ± S.D., DGC: $78 \pm 10\%$; AGC: $72 \pm 11\%$) than emotional content (DGE: $96 \pm 4\%$; AGE: $95 \pm 5\%$), accuracy levels in both tasks were high and above chance level.

2.5. *Eye movements*

Because it was plausible that the amount of eye movements would be different between conditions, four subjects were studied at a later date to assess the amount of eye movements during each condition. The entire imaging protocol was duplicated in the scanner without tracer administration. Video recording of saccades were obtained and assessed manually offline by counting the number of vertical and horizontal saccades.

2.6. *Data acquisition*

PET scans were obtained using a Siemens CTI HR + tomograph, using the water [$H_2{}^{15}O$] bolus technique to measure regional cerebral blood flow (rCBF). Subjects were scanned during each of the four conditions repeated three times (12 scans per subject). PET data acquisition lasted for 60 s. Stimulus presentation began 7 s after bolus injection and covered all the data acquisition time and continued for a few seconds beyond the period of data collection. Scan order was pseudo-randomised across subjects to minimise ordering effects. Subjects were asked to watch the videos and to make a choice after each sequence by pressing one of two mouse buttons following the experimenter's instructions given at the beginning of each session.

2.7. *Data analysis*

Functional imaging data were analysed with statistical parametric mapping (SPM 99) implemented in Matlab®. First, intrasubject registration was performed in order to correct motion between scans within a subject's PET session. For each subject, the imaging time series was realigned using interpolation with an 11 × 11 × 11 kernel [24]. PET image sets for each subject were then spatially normalised into a standard stereotaxic space [43]. To match degree of smoothness and enhance signal relative to noise ratio, PET data have then been 3D smoothed with a Gaussian kernel of 12 mm.

2.8. *Statistical analysis*

Regional cerebral blood flow changes between two different conditions were assessed by conventional subtraction analysis of PET image sets. An ANCOVA model was fitted to the data at each voxel, with a condition effect for each different condition, and global CBF as a confounding covariate [25].

Statistical analysis examined the main effect of perception and attribution of emotion ((DGE + AGE) − (DGC + AGC) in Fig. 1, contrasting emotional judgments with emotional stimuli to non-emotional judgments with neutral faces); the simple effects of perception and attribution of emotion via direct (DGE − DGC) or averted gaze (AGE − AGC); the simple effect of direct gaze on the perception and attribution of emotion (DGE − AGE)[1]; and the interaction between the two factors: emotion/non-emotional judgement and direction of gaze (DGE − DGC) − (AGE − AGC). These statistical contrasts were used to create an SPM$\{t\}$, which was transformed into an SPM$\{Z\}$ and thresholded at $P < 0.001$ non-corrected.

3. Results

3.1. *Task performance and eye movements*

All subjects in the PET scan performed well in the emotional judgement (mean accuracy ± S.D. DGE: 96% ± 5%; AGE: 94% ± 6%) and in the fixation distance judgement (DGC: 75% ± 8%; AGC; 71% ± 6%) tasks. Eye movements recorded in four subjects showed no differences in the amount of saccades between conditions.

3.2. *Functional imaging*

The first aim of the study was to investigate whether there was a difference in activated brain regions when subjects experienced and judged the emotional nature of a gaze (either direct or averted) versus the focus of a neutral gaze (either direct or averted). For this purpose, we examined the main effect of emotion perception and attribution, which contrasts two conditions involving emotional judgments and emotional stimuli with two conditions involving non-emotional judgments and non-emotional stimuli, i.e. (DGE + AGE)−(DGC + AGC). The main effect analysis revealed increased activity in a number of brain areas including dorso-medial prefrontal cortex, bilateral anterior superior temporal gyrus (STGa, Ba 22), temporal pole and adjacent cortices, anterior and posterior cingulate gyrus, right post-central gyrus, medial orbitofrontal cortex and precuneus (Table 1a, Fig. 2).

The second aim of this study was to explore whether there was a possible influence of gaze direction on the activity of structures engaged in emotion processing. Interestingly,

Table 1
Significant brain activations during emotion perception and attribution

Structure	Ba	Coordinates			*Z*-score
		x	*y*	*z*	
(a) Main effect					
Medial dorsofrontal gyrus	9	−4	45	34	5.03
Medial dorsofrontal gyrus	9/10	1	51	18	4.83
Superior temporal gyrus (L)	22	−48	1	−4	4.72
Superior temporal gyrus (R)	22	47	−1	−6	4.29
Temporal pole (R)	21	33	6	−33	4.75
Temporal pole (L)	21	−40	−1	−29	4.23
Precuneus (L)		−4	−48	32	4.44
Medial frontal gyrus	8	−6	28	50	4.22
Post-central gyrus (R)	3	52	−15	39	4.16
Medial orbitofrontal cortex	11	1	34	−18	4.13
Cingulate gyrus	31	3	−27	37	4.06
Anterior cingulate gyrus	24/32	1	37	10	3.81
Transverse temporal gyrus (R)	41	42	−32	10	3.78
(b) Direct gaze context (DGE − DGC)					
Superior temporal gyrus (L)	22	48	4	−6	5.16
Superior temporal gyrus (R)	22	−47	1	−4	4.54
Transverse temporal gyrus (R)	41	41	−36	13	4.02
(c) Averted gaze context (AGE − AGC)					
Insula		45	−5	11	3.98
Insula		−33	−19	9	3.90
Amygdala (R)		24	−5	−26	3.91
(d) Interaction					
Superior temporal gyrus (R)	22	47	6	−5	4.16

Regions of significant cerebral blood flow (rCBF) change associated with emotion perception and attribution. (a) Main effect, (b) and (c) regions in which the effect of emotion is significant depending on the gaze context, and (d) areas significantly activated ($P > 0.001$) in the interaction analysis. The location of maximal *Z*-score were defined according to the brain atlas of Talairach and Tournoux [45], such that *x* is the distance in millimeters to the right (+) or left (−) of the midline, *y* is the distance in millimeters anterior (+) or posterior (−) to the anterior commissure, and z is the distance in millimeters superior (+) or inferior (−) to a horizontal plane through the anterior and posterior commissures. (L) left hemisphere, (R) right hemisphere. Brain regions are identified by name and by putative Brodmann area (Ba) on the basis of the atlas of Duvernoy [21]. L: left hemisphere; R: right hemisphere.

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[1] Prolonged eye contact exists in 100% of trials in conditions DGE and DGC but 0% trials in conditions AGE and AGC.

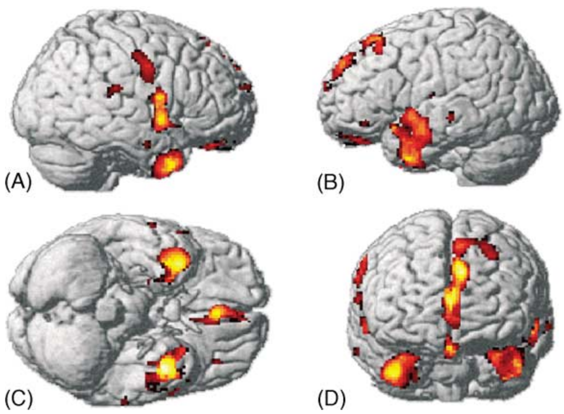

Fig. 2. Areas of activation in the main effects of emotion attribution (DGE + AGE) − (DGC + AGC) in (Fig. 1B). (A) and (B) lateral, (C) ventral and (D) frontal views of maximum-intensity superimposed on a three-dimensional MRI ($P < 0.001$ uncorrected).

examination of the simple effects (DGE − DGC) and (AGE − AGC) revealed that the effect of emotion was significant in the context of direct gaze (i.e. Z-score was above threshold in (DGE − DGC) but not in (AGE − AGC)) bilaterally in anterior superior temporal gyrus (STGa, Ba22) and in the right transverse temporal gyrus (Table 1b). On the other hand, the effect of emotion was significant in the context of averted gaze in the right amygdala, and the insular cortex bilaterally (Table 1c). The examination of the interaction reflects the differential effects of perceiving and attributing an emotion with direct gaze as opposed to averted gaze. This enabled us to investigate the statistically significant effect of direct gaze on the cerebral structures in which activity is correlated to emotion perception and attribution. This interaction analysis showed a unique focus of activity with a location in the anterior right superior temporal gyrus (STGa, Ba 22) similar to the focus found in contrasts (DGE − DGC) (Table 1d, Fig. 3).

Table 2
Brain regions activated during the perception of emotionally salient eyes directed at the subject (contrast DGE − AGE, $P < 0.001$ non-corrected for multiple comparisons)

Structure	Ba	Coordinates			Z-score
		x	y	z	
Direct gaze (DGE − AGE)					
Inferior cerebellum (L)		−17	−63	−51	4.11
Medium occipital gyrus (L)	18	−26	−87	1	4.02
Orbito-frontal cortex (R)	10/11	18	57	−8	4.00
Superior temporal gyrus (R)	22	48	6	−5	3.72

Another way to explore this issue is to examine the effect of gaze direction on the perception and attribution of emotion. Direct comparison of emotion attribution via direct versus averted gaze (DGE − AGE) revealed increased rCBF in the right anterior superior temporal gyrus (STGa), in the right orbito-frontal cortex, in the left occipital gyrus, and in the left cerebellum, (Table 2). This shows that a significant effect of the direction of gaze on emotion attribution is found in the STGa at a location similar to the focus found in (DGE − DGC) and the interaction analysis. All three analyses implicate the STG as a site where direct gaze heightens activity during analysis of others' emotion.

4. Discussion

The main objective of this study was to identify a brain system associated with perception and attribution of emotion displayed in the eye region in the specific context of direct gaze.

Subjects were involved in a task of detection of an emotional expression displayed in the eye region of an actor and were therefore engaged in a task of explicit emotional judgement. The interpretation of socially relevant signals

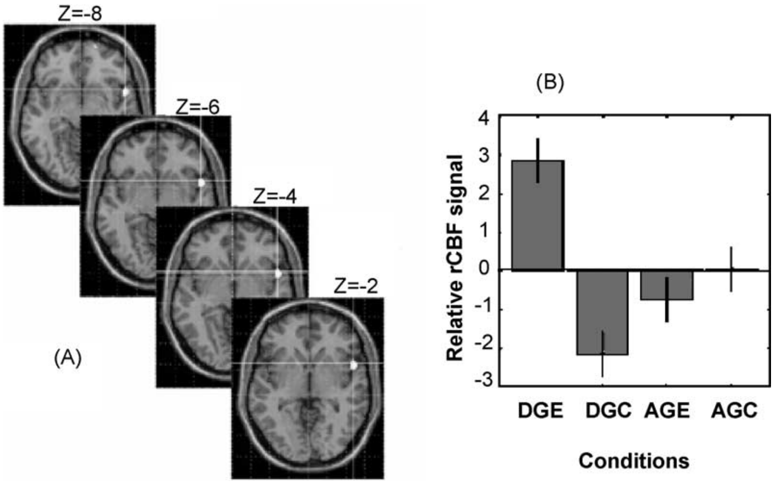

Fig. 3. (A) Significantly increased activity ($P < 0.001$) associated with the interaction between the effects of emotion attribution and direction of gaze. (B) Relative rCBF value in each experimental condition at voxel (47, 6, −5) corresponding to the right anterior STG.

(including expressions) from the eye region may be compared to a theory of mind task. If one has to judge whether someone is friendly or hostile, one explicitly engages in the attribution of mental states to the other person. In this respect, our results revealed the activation of a network of brain areas that fits well with the social/emotional brain delineated on the basis of animal and human studies [1,11,17,19]. According to this model, social and emotional behaviour required in two-way communication is critically dependent on a specialised circuit involving the amygdala and the prefrontal, orbito-frontal, cingulate, somatosensory and temporal pole cortices.

Indeed, the main effect of emotion attribution revealed two different foci in the dorso-medial prefrontal cortex were activated (Table 1a, Fig. 2). The more dorsal one (−4, 45, 34) has a location similar to a region consistently found specifically activated by "theory of mind" tasks in several previous neuroimaging studies ([12,23,27,30], see [10,26] for a review). Interestingly, a very recent study demonstrated increased activation of this particular area when subjects perceived horizontally averted gazes [14]. The second focus is more ventral and can be related to emotion processing. Several studies found similar medial prefrontal activation related to the experience of pleasant or unpleasant emotions when the inducing stimuli involved the presentation of slides, film clips, or recall of memories of emotional events [17,36,43]. It has also been suggested that areas of the medial prefrontal cortex are involved in accessing both affective and non-affective schematic mental models of personal and social relevance [46]. The presence of these medial prefrontal activations detected in the contrasts between emotional and fixation distance judgement conditions suggest that this brain region is indeed specifically involved when emotion processing is required.

Therefore, activation of this network is consistent with a role of these structures in the process of understanding the social signals accompanying gaze. Our task required the explicit attribution of friendly or hostile intent and therefore includes the recognition of two basic emotional states (happy and angry). We note that attribution of emotions and social traits may also occur automatically, indeed the same brain systems may be activated in implicit social judgements (for review see [37]). Although the anterior cingulate cortex is known to be involved both in cognition and emotion, our activation focus lies in what has been termed the affective part of the anterior cingulate gyrus (see [13] for a review). Activity of this part of the brain in the main effect of emotion perception and attribution further supports its role in emotional processing.

Activity in medial prefrontal regions and in the anterior cingulate gyrus has also been reported in previous neuroimaging studies involving problem solving and decision-making [28,34]. In our study, the small mismatch in task difficulty between emotional and non-emotional conditions could thus explain these activations. However, it is remarkable that the brain regions highlighted here have been all previously reported in neuroimaging studies on emotion processing. Therefore, it is unlikely that the difference in difficulty is the only factor responsible for these activities.

The orbitofrontal cortex is known to play a pre-eminent role in the processing of social stimuli [16]. Specifically, our activated focus lies in a sector of orbitofrontal cortex that is critical in linking perceptual representation of stimuli with representations of their emotional and social significance (for a recent review see [1]). Direct gaze is known to be a cause of electrodermal response and patients with damage to this orbitofrontal region fail to generate the anticipatory electrodermal response to affectively salient cues [7,20]. Here the task and stimuli ensured both social and emotional salience.

The temporal pole (Ba 38) was also found bilaterally activated in the main effect of emotion perception and attribution, regardless of the direction of gaze (Table 1a). Temporal pole is considered a high order visual cortical area and has reciprocal connections to the amygdala, the hippocampus and the prefrontal cortex [22]. In this study, eye-gaze was both attentionally and emotionally salient, so the present findings are consistent with a role for the temporal pole in evaluating the emotional and attentional meaning of visual stimuli. Such evaluation may include retrieval of past emotional experiences for the purpose of assessing the significance of the current stimulus and guiding the behavioural response [36]. Consistent with our findings, several neuroimaging studies which engaged subjects in mentalising tasks reported bilateral activation of the temporal poles (see [26] for a review).

As stated above, the amygdala is implicated in the processing of emotion [10,17,36,44] as well as in the monitoring of gaze [32,49], which may itself have emotional significance. In the present study, amygdala activity was only found when we contrasted direct gaze with averted gaze processing with non-emotional faces (DGC − AGC, not reported here) and when we contrasted emotional with non-emotional averted gaze processing (AGE − AGC, in Table 1). This is coherent with its involvement in both roles (direct gaze and emotion processing) and further supports its critical role in social intelligence. The lack of amygdala activation in contrasts factoring out activity related solely to direct gaze perception (DGE − DGC) and emotional processing (DGE − AGE) does not contradict these conclusions since the amygdala activity is likely to be present in both conditions and thus cancel out.

Beside these common activations, simple effects of emotion attribution ((DGE − DGC) and (AGE − AGC)) revealed areas of greater activation depending on the presence of a direct or averted gaze (Table 1b and c). This is in line with our hypothesis that direction of gaze has an impact on emotional processing, and it was statistically explored with an interaction analysis. Since conditions DGE/DGC and AGE/AGC differed in task and in the presence or absence of emotional expression, we also compared activities in the DGE and AGE conditions (Table 2).

The surprising finding of this study is the bilateral activation of the anterior part of the superior temporal gyrus (STGa, Ba 22) both in the contrast manipulating the judgement (emotional versus non-emotional) keeping gaze constant (DGE − DGC) and in the contrast manipulating gaze direction (direct versus averted) keeping the emotional judgement constant (DGE − AGE, see Tables 1 and 2). Furthermore, this focus of activation in the STGa was also found in the right hemisphere in the interaction analysis that aims to isolate brain areas selectively activated by interpretation of emotions that are personally directed.[2] This result is consistent with our hypothesis that the brain activates specific regions in response to the combination of direct gaze perception and emotion attribution.

Eye-contact generates a bi-directional relation and the emotional expression gives intentionality to the actor. This means that subjects had to engage in a "second-person" intentional relation, i.e. involving the perception of an action (here an emotion) performed by another organism and directed to the perceiver [28]. It has been argued that the system specialised in processing second-person relations through eye-contact may be the evolutionary and developmental precursor to the human Theory of Mind module [4]. The neural activity within STGa observed in this study could be a component of the brain structures underlying such a system and provides suggestive evidence that the brain has evolved specific structures to process emotional/social information directed towards the perceiver.

Few functional imaging studies investigated the role of the anterior superior temporal cortical areas in human. So far, STG activity has been related predominantly to processing of language [8]. The anterior STG, however, has not previously been reported as implicated in the processing of emotionally salient stimuli, although STG activation is reported by Calder et al. [14] in a contrast between direct and averted gaze in neutral faces. Our study provides the first evidence of cerebral structures selectively involved when we experience and read the emotion in the eyes of someone focusing on us. Emotions of others become particularly salient when they are directed towards ourselves. Although most previous studies of emotion processing have employed facial expression stimuli looking straight at the subject (e.g. [36,44]), such studies have failed to isolate this personal involvement. Studies employing only emotional expressions with eye contact cannot disambiguate the processes involved in understanding emotional states per se from processes involved in emotion decoding where the observer is implicated as the recipient of the expressed emotion. Our study gives a new insight into brain structures that may be responsible for the receptive aspects of emotional communication that accompanies social interactions. An interesting support to this view comes from a neuroimaging study that demonstrated a specific hypoperfusion at rest in the anterior STG region in autistic children, as compared to age-matched controls [50]. This is consistent with the fact that one of the main deficits in autism is an impairment in the ability to read another's intentions or mental states and a tendency to avoid eye-contact [38].

For further readings see [2,9,18,29,35,39].

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