

Amygdala activation when one is the target of deceit: Did he lie to you or to someone else?

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The ability to figure out whether a person is being honest or deceitful is an important part of social competence. Reactions to deceit may however differ depending on whether one is being deceived oneself or observes a deceitful exchange between others. In the present study, we investigated whether personal involvement influenced the neural responses associated with the detection of deceit. Subjects watched videos of actors lifting a box and judged whether the actors had been misled about the real weight of the box. Personal involvement was manipulated by having the participants themselves among the actors. The critical finding was that there was activity in amygdala and fusiform gyrus only for the condition in which participants observed themselves being deceived. In contrast, the superior temporal sulcus and anterior cingulate cortex were activated irrespective of whether the participants detected that the experimenter had deceived themselves or another. These four brain areas are all interconnected and are part of the discrete neural system subserving social cognition. Our results provide direct evidence, using judgments of deceit in a social context, that the crucial factor for amygdala activation is the involvement of the subjects because they are the target of the deceit. We interpret the activation of the amygdala in this situation as reflecting the greater affective reaction when one is deceived oneself. Our results suggest that when one is personally involved, deceit is taken as a potential threat.
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Introduction

Successful social interactions depend on the ability to predict and explain the mental states of other people, such as desires, beliefs and intentions. It is particularly important to be able to distinguish whether a person is being honest or deceitful. To do so,

one needs to process information that is relevant and directly available; this mainly consists in the movements of the agent in space and time in the physical and social environment (Barresi and Moore, 1996). According to Humphrey (1983), the human ability for perceiving subtle expressions and behaviors partly developed from the increasing competence in deceiving and manipulating each other among members of a social group.

In a recent experiment, Grèzes et al. (2004) explored the brain mechanisms involved in detecting deception from the perception of the non-verbal dynamic behavior of actors. When subjects detected deceptive intention, there was activity in the amygdala and in the anterior cingulate cortex. We suggested that the observer may have felt that the intention to deceive was directed towards him, and that as a result, the activations in the anterior cingulate gyrus and amygdala reflected the observer's emotional response of being deceived. In other words, we hypothesized that the critical factor might be personal involvement.

Two recent studies suggest that personal involvement might indeed be crucial. In a recent fMRI study, subjects were scanned while they read stories in which they or someone else either intentionally or accidentally violated social norms (Berthoz et al., 2003). Activation in the amygdala was only found when the participants read stories that narrated their own intentional transgression of social norms. In the second study, activation in the anterior cingulate was specifically found when subjects viewed faces which were making eye contact and when they heard their own name (Kampe et al., 2003).

Our previous experiment did not allow the conclusion that personal involvement is crucial for deceit (Grèzes et al., 2004). In the present experiment, we therefore manipulated whether the subject was or was not the target of deceit. Subjects were scanned while watching videos of themselves or of others lifting a box and were instructed to judge the presence of deceit. In the two conditions of interest, subjects judged whether the experimenter had misled them or another about the real weight of a box. Two comparison conditions were included in which the subjects judged the presence of deceit in the other direction that is whether the

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subjects themselves or the other actors misled the experimenter. The design was therefore factorial, with effects of self/other and direction of deceit. This enabled us to look for activations that related to who was the target of deceit. We were specifically interested in whether there were activations in the amygdala and in the cingulate that only occurred when one is the target of deceit.

Materials and methods

Subjects

Six subjects (3 men and 3 women, with ages of 26–35 years old) with no neurological or psychiatric history participated in the imaging study. All gave informed consent according to procedures that had been approved by the Joint Ethics Committee of the National Hospital for Neurology and Neurosurgery (UCLH NHS Trust) and Institute of Neurology (UCL).

Stimuli

Six actors (3 men and 3 women) were videotaped over 50 trials of lifting and carrying a box of varying weights (1, 6, 12 or 18 kg). Each recording started with the box placed in the middle of the scene and about 1 m from the right edge of the table. The actor entered on the left, lifted the box by its side handles, walked towards the table, placed the box on the table and left the room. During the first part of the filming session, the experimenter gave the exact weight of the box so that the actor had a correct expectation of the weight. However, randomly and on 10% of the trials, the experimenter misled the actor by providing false information about the weight. As a consequence, the actor had a false expectation of the weight. In the second part of the filming session, the experimenter gave the exact weight of the box, but the actor was instructed to pretend that the box had a different weight. In this way, we created videos in which the actors had deceptive intentions. Six actors were used to assess variability in observer performance due to individual difference in actor styles of lifting and carrying. We edited video recordings of 3 s concentrating on

the lifting phase. Using the after-effect software, we blurred the face of the actors on each movie in order to hide facial and emotional expression, so that only body information was provided.

Since the subjects for the fMRI experiment were the actors, the video recording session and the fMRI study were 2 years apart to minimize memory effects. The stimuli used during the fMRI experiment consisted of color video recordings of the actors performing the action of lifting and carrying a box of different weights. During the scanning session, the videos were viewed by projection onto a mirror mounted onto the head-coil in the scanner. Each trial started by the display of an instruction panel for 2 s. Then the subjects viewed videos (3.5 s each) of themselves (Self, S) or of another actor (Other, O). At the end of each video, a screen was presented for 1.5 s on which was displayed one of the following questions: “the Experimenter lied to You” (ES), “the Experimenter lied to the Actor” (EO), “You lied to the Experimenter” (SE), “the Actor lied to the Experimenter” (OE). Below the question was displayed the answers ‘Yes’ and ‘No’ (see Fig. 1).

The perceptual properties that allow the subjects to perform the task correspond to the action kinematics of the actors while lifting a box. As the experiment was designed to study the effect of being the target of deceit, we concentrate on the conditions where the experimenter either gave the correct weight of the box (e.g., Fig. 2, line A) or misled the actors about the weight of the box (e.g., Fig. 2, line B). When the experimenter misled the actor, the actual weight of a box differed from the expected one (Fig. 2, line B). As a consequence, postural readjustments occurred, and the amount of readjustment specified the difference between the expected and actual weight. The subjects had to detect these postural readjustments in order to decide whether the actors have been misled or not. The information provided in the movies did not differ between self and other conditions.

The subjects were required to decide (forced choice) between them by making key-press with their right fingers. The location of the two words (on the right and left part of the screen) was randomized. This forms a 2*2*2 factorial design (Self versus Other, Toward the Actor versus Toward the Experimenter, Presence versus Absence of lie) (see Table 1). We delayed the

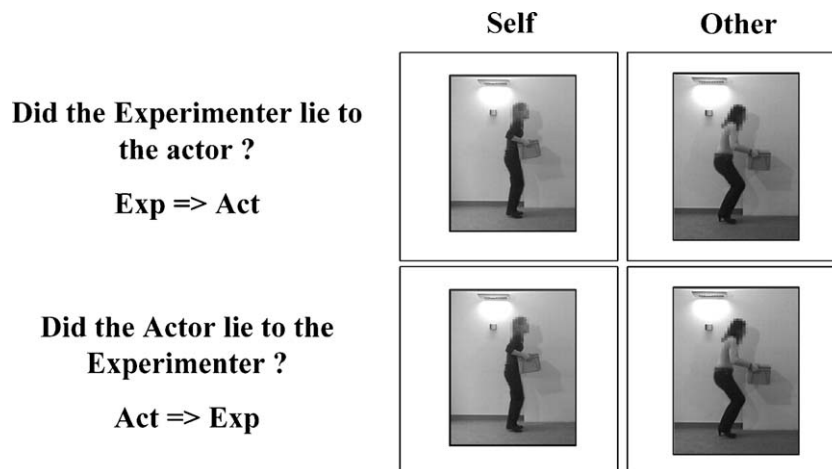


Fig. 1. The subjects watched videos of themselves or of actors lifting a box. They had to judge whether the experimenter lied to them or to the actors about the weight of the box, or whether they or the actors were deceiving the experimenter about the weight of the box. Each trial corresponds to the presentation of a color movie of 3.5 s followed by a screen of 1.5 s on which the words ‘Yes’ and ‘No’ were displayed. The position of the two words on the screen was randomized across trials so as to avoid motor preparation during the observation phase. The subjects were required to decide (forced choice) whether the actor was deceived or had a deceptive intention by making key-press with the right fingers.

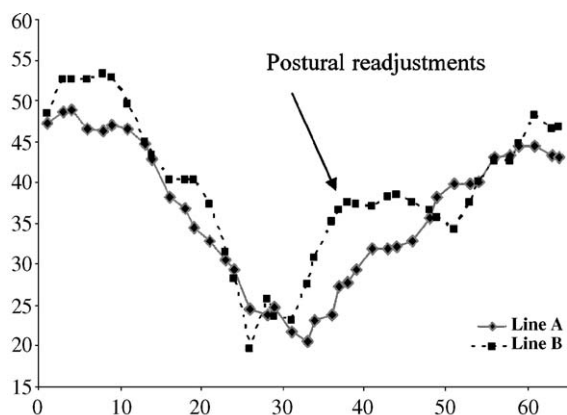


Fig. 2. Perceptual properties that allow the observer to make his judgment. The amount of movement per video-clip and per condition can be assessed by measuring the difference in movements between pairs of frames for each pixel. This difference is coded in terms of light intensity variation and averaged across pixels that scored higher than 10 (corresponding to the noise level of the camera). With this procedure, the temporal profiles frame by frame for each condition can graphically represented. Line A represents the temporal profile for the actor n°7 lifting a box of 1 kg, whereas line B represents the same actor expecting a box of 1 kg, but lifting a box of 18 kg. The difference in the shape between the two profiles provides a measure of the postural readjustments.

responses on purpose so as to ensure that the subjects responded at the same time at the end of the observation period. Furthermore, by varying the location of the response cues, we deliberately prevented the subjects from preparing their responses during the observation period. As a result, our design was not appropriate for detecting any reaction time advantages in making judgments about oneself compared with others.

The study was carried out in two scanning sessions. One hundred and ninety two video films (64 self, 64 actor 1, 64 actor 2) intermixed with 80 null events were randomly presented with an inter-trials interval of 7 s. Twenty five percent of the videos involved deceptive intention from the actor, and 25% involved the actor being deceived by the experimenter.

Behavioral analysis

The mean judgments per subject were converted into a measure of sensitivity [d'] independent of any response bias (Macmillan and Creelman, 1991). Four different d' values were computed: two for the ability to correctly detect deceit when one or the actor is the target of a lie, two for the ability to correctly detect deceit when one or the actor is deceiving. ANOVAs were performed on these measures, where the actors (self or other) and the target of deceit (the actor or the experimenter) were within participant factors. Only effects surviving $P < 0.05$, in the absence of higher order interactions, are reported. We excluded trials with reaction times more than 1.5 s (3.6% of the total trials) both from the behavioral and imaging analysis, as the motor response was performed during the following trial.

Imaging and image processing

Imaging was performed with a 1.5-T Siemens SONATA scanner (Siemens, Erlangen, Germany). Each scanning session was composed of 2 functional runs. For each of them, gradient-

echo T_2^* -weighted transverse echo-planar images (EPI) with blood oxygenation level-dependent (BOLD) contrast were acquired. Each volume comprised 36 axial slices (2.4 mm thickness with 1.35 mm gap and 3*3 mm in-plane resolution, TE = 50 ms, flip angle of 90°, field of view of 36 cm, matrix of 64*64). Each volume was acquired sequentially in a descending direction and continuously during the two functional runs of 16 min each. An automatic shimming procedure was performed before each scanning session. A total of 295 functional volumes were collected for each subject and for each functional run with an effective repetition time (T_R) of 3.24 s/volume. At the end of the scanning session, a T1-weighted structural image was acquired.

The first five volumes of each functional run were discarded to allow for T1 equilibration effects. Images were realigned, slice-time corrected, normalized to the MNI standard echo-planar image template with a re-sampled voxel size of 2*2*2 mm and smoothed with a Gaussian kernel with full-width half maximum of 6 mm (Ashburner and Friston, 1997).

Statistical analysis of imaging data

After pre-processing, statistical analysis was carried out using the general linear model (Friston et al., 1995) using Statistical Parametric Mapping (SPM2; Wellcome Department of Imaging Neuroscience, London, UK). The data were separated according to whether the trials were correctly or incorrectly judged (mean correct = 66.9% for Self and 71.3% for Other). In a first model, we found that the difference between correct and incorrect responses drove brain activations in our contrasts of interest. We therefore chose to select only the correct trials in order to avoid this possible confound. The correctly judged trials were modeled as eight effects of interest and defined as follows.

Two represented the trials where subjects perceived themselves performing actions either with a correct expectation as the experimenter did not mislead them (ESn) or with a false expectation as the experimenter did mislead them (ESy).

Two represented the trials where subjects perceived themselves as performing genuine actions (SEn) or faked ones (SEy).

Two represented the trials where subjects perceived another actor performing actions with a correct expectation as the experimenter did not mislead him (EOn) or a false expectation as the experimenter misled him (EOy)

Two represented the trials where subjects perceived another actor performing genuine actions (OEn) or faked ones (OEy).

The BOLD response to the video onset for each event type was modeled by a box-car waveform of 4.5 s (1.88 TR) convolved with the hemodynamic response function and its temporal derivative to account for any temporal shifts in the response of the stimuli

Table 1
Experimental conditions

Abbreviations	
ESn	The Experimenter (E) didn't lie to You (S)
ESy	The Experimenter (E) did lie to You (S)
SEn	You didn't lie to the Experimenter (E)
SEy	You did lie to the Experimenter (E)
EOn	The Experimenter (E) didn't lie to the Actor (O)
EOy	The Experimenter (E) did lie to the Actor (O)
OEn	The Actor (O) didn't lie to the Experimenter (E)
OEy	The Actor (O) did lie to the Experimenter (E)

(Friston et al., 1998). Also included for each session were error trials, missed ones, the instruction period and the six covariates to capture residual movement-related artefacts (the 3 rigid-body translations and the 3 rotations determined from initial registration) and a single covariate representing the mean (constant) over scans. The data were high-pass filtered with a frequency cut-off at 140 s.

We performed a random effects analysis. Images of parameter estimates for each condition of interest were created for each subject (first-level analysis) and were then entered into a second-level analysis using ANOVAs with the 8 HRFs comprising a factor. The following four T contrasts were calculated at the random level.

- 1) The main effects of the actors (Self + Others) being the target of deceit $[(ESy - ESn) + (EOy - EOn)] - [(SEy - SEN) + (OEy - OEn)]$.
- 2) The interaction of Self being the target of deceit $[(ESy - ESn) - (EOy - EOn)] - [(SEy - SEN) - (OEy - OEn)]$.
- 3) The main effect of the actors (Self + Others) deceiving the experimenter $[(SEy - SEN) + (OEy - OEn)] - [(ESy - ESn) + (EOy - EOn)]$.
- 4) The interaction of Self deceiving the experimenter $[(SEy - SEN) - (OEy - OEn)] - [(ESy - ESn) - (EOy - EOn)]$.

Statistical Parametric maps (SPMs) of the T statistic were constructed using a generalized Greenhouse–Geisser correction. The statistical parametric maps were thresholded at $P < 0.001$ (uncorrected for multiple comparisons), except for the amygdala and the anterior cingulate cortex, where, based on our a priori hypothesis, where we used $P < 0.005$ (uncorrected). These maps were overlaid on the MNI template and on the normalized structural images of each subject and labeled using the atlas of Duvernoy (1999).

A limitation of the present study is that we only tested six subjects. The reason was that we needed to obtain videos of the subjects as actors and to scan the same subjects 2 years later. The limitation of the present study is therefore that there may be false negatives because of reduced sensitivity. On the other hand, results that are positive with random effects of six subjects should be reliable.

Results

Behavioral analysis

The subjects were able to detect deception above a chance level. The mean judgments per subject were converted into a measure of

sensitivity [d'] independent of any response bias (Macmillan and Creelman, 1991). The subjects were significantly sensitive to deceit ($d' = 1.183$, t test $P < 0.0001$). Subjects tended to be less accurate at detecting when they themselves were the target of a lie ($d' = 0.924$) than when they were lying ($d' = 1.145$), or the other was the target of a lie ($d' = 1.243$) or the other was lying ($d' = 1.422$). The ANOVAs on the d' measures revealed no significant difference in the d' measures for judgments about one's own actions ($d' = 1.035$) and of others ($d' = 1.333$) [$F(1,5) = 0.595$, $P = 0.475$] nor for judgments about being the target of a lie ($d' = 1.084$) or lying to the experimenter ($d' = 1.284$), [$F(1,5) = 0.483$, $P = 0.518$], and no interaction between the two factors [$F(1,5) = 0.042$, $P = 0.845$]. However, there was a tendency for an interaction between Agent (Self or Other) and Target (Actors or Experimenter) on mean accuracy [$F(1,5) = 0.502$, $P = 0.077$].

As explained in the methods, the design was not suitable for looking for differences in RT.

Neuroimaging results

Self being the target of deceit

We next analyzed the data to identify the neural network specifically engaged when the subjects detected that they themselves (Self only) were the target of deceit. The following interaction was calculated $[(ESy - ESn) - (EOy - EOn)] - [(SEy - SEN) - (OEy - OEn)]$. This analysis highlighted activations in the left amygdala and the right fusiform gyrus (see Table 2, Figs. 3 and 4).

Actors as the target of deceit

We first analyzed the data to identify the neural network engaged when the subjects detected that the actors (Self and Others) were the target of deceit. The following main effect was calculated $[(ESy - ESn) + (EOy - EOn)] - [(SEy - SEN) + (OEy - OEn)]$. This analysis showed activations in the anterior cingulate cortex and in the right superior temporal sulcus (see Table 2, Fig. 5).

Actors deceiving

The neural network engaged when the subjects detected that the actors (Self and Others) were deceiving the experimenter was identified by calculating the following main effects $[(SEy - SEN) + (OEy - OEn)] - [(ESy - ESn) + (EOy - EOn)]$. This contrast revealed activations bilaterally in the lateral orbitofrontal gyrus, in the cingulate sulcus, in the putamen and the insula in the left hemisphere (see Table 3).

Table 2

Brain regions showing amplitude differences when the subjects judged that both they themselves and the others were misled by the experimenter

Brain regions	Talairach coordinates				Cluster
	x	y	z	Z score	
<i>The Actors (Self + Others) being misled by the Experimenter: [(ESy - ESn) + (EOy - EOn)] - [(SEy - SEN) + (OEy - OEn)]</i>					
R Medial superior frontal/anterior cingulate gyrus	4	48	24	3.83	124
R Superior temporal sulcus	52	-50	22	3.69	19
<i>Self being misled by the Experimenter: [(ESy - ESn) - (EOy - EOn)] - [(SEy - SEN) - (OEy - OEn)]</i>					
R fusiform	46	-36	-20	3.27	45
L amygdala*	-10	-4	-16	2.97	17

$P < 0.001$ non-corrected.

* $P = 0.001$ (a priori hypothesis).

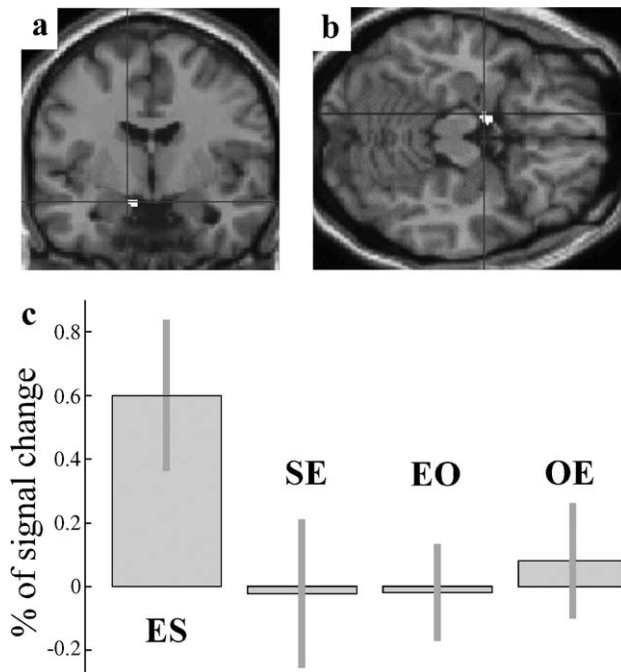


Fig. 3. Region showing amplitude difference only when subjects judged that they were the target of deceit. (a) Group ($n = 6$) average activation of the amygdala superimposed on a coronal section of the MNI brain. (b) Group ($n = 6$) average activation of the amygdala superimposed on a transversal section of the MNI brain. (c) Histograms representing the percentage of signal change at the local maximum in the amygdala ($x, y, z = -10 - 4 - 16$). The first histogram corresponds to the difference between the trials where subjects judged that the experimenter misled them (ESy) versus did not (ESn); the second stands for the trials where subjects judged that they misled the experimenter (SEy) versus they did not (SEn); the third represents the trials where subjects judged that the experimenter misled the other actor (EOy) versus did not (EOn); the fourth stands for the trials where subjects judged that the other actor misled the experimenter (OEy) versus did not (OEn).

Self deceiving

Finally, to identify the neural network engaged specifically when the subjects detected that they themselves (Self only) were deceiving the experimenter, the following interaction was calculated $[(SEy - SEn) - (OEy - OEn)] - [(ESy - ESn) - (EOy - EOn)]$. This analysis highlighted bilateral activations in the lateral orbitofrontal gyrus (see Table 3).

The activations for the comparison conditions (contrasts 3 and 4) are given in Table 3 for the sake of completeness. However, since the study was designed to study the effect of being the target of deceit (contrasts 1 and 2), they are not further discussed.

Discussion

We hypothesized that in social situations, one's reactions to deceit might differ depending on whether one is directly involved by virtue of being the target compared with simply being a witness. In the present experiment, we were specifically interested in the activations associated with detecting that the experimenter had lied to the subject compared with activations when the subject detected that the experimenter had lied to another. So as to control for the judgment of a lie, these activations were contrasted with those elicited when the observer detected that the actor was deceiving the experimenter.

Our critical findings were two. First, there was activity in the amygdala (AM) and fusiform gyrus (FG) only when subjects detected that they themselves were the target of deceit. Second, there was activity in the superior temporal sulcus (STS) and anterior cingulate cortex (ACC) when subjects detected that the actions reflected deceit on the part of the experimenter both to themselves and to another. These four brain areas are all interconnected (Stefanacci and Amaral, 2002) and are part of the discrete neural system subserving social cognition (Brothers, 1990).

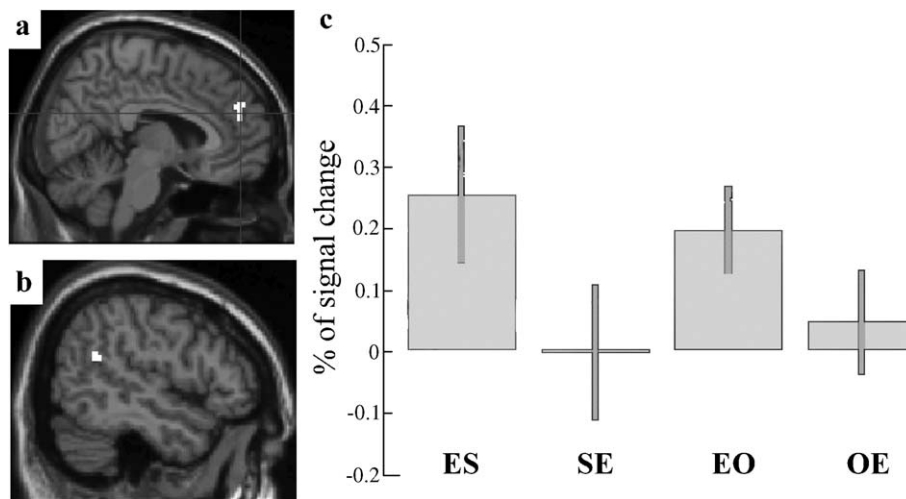


Fig. 4. Regions showing amplitude difference when subjects judged that they themselves and the others were deceived by the experimenter. (a) Group ($n = 6$) average activation of the rostral anterior cingulate cortex/superior frontal cortex superimposed on a sagittal section of the MNI brain. (b) Group ($n = 6$) average activation of the right superior temporal sulcus superimposed on a sagittal section of the MNI brain. (c) Histograms representing the percentage of signal change at the local maximum in the rostral anterior cingulate cortex ($x, y, z = 2, 50, 28$), other conventions as in Fig. 3c.

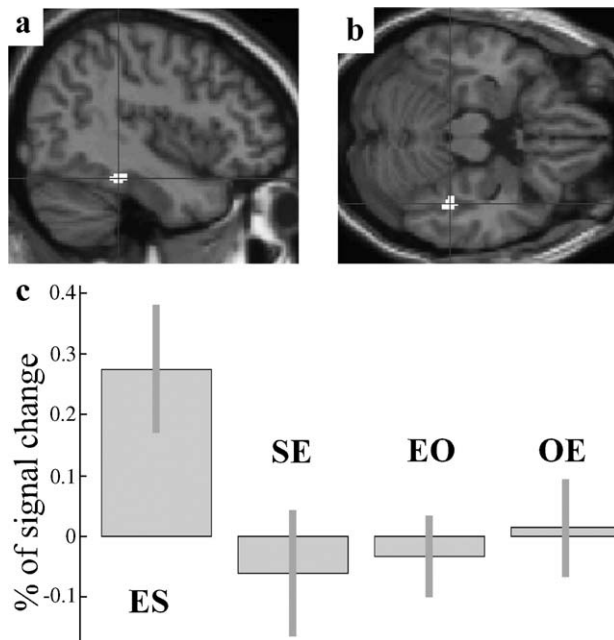


Fig. 5. Region showing amplitude difference only when subjects judged that they were the target of deceit. (a) Group ($n = 6$) average activation of the fusiform gyrus superimposed on a sagittal section of the MNI brain. (b) Group ($n = 6$) average activation of the fusiform gyrus superimposed on a transversal section of the MNI brain. (c) Histograms representing the percentage of signal change at the local maximum in the fusiform gyrus ($x, y, z = 6, -36, -20$); other conventions as in Fig. 3c.

Self being the target of deceit

When the subjects detected specifically that they themselves were directly involved by being the target of deceit, there was activity in the amygdala (AM) and fusiform gyrus (FG). The amygdala has been shown to be activated during the perception and the recognition of emotional static faces (e.g., Winston et al., 2002) and bodies (de Gelder et al., 2004). However, it is also activated when subjects make judgments of mental states through the perception of a person's eyes (Baron-Cohen et al., 1999) or when they view computer animations of simple geometrical shapes whose movement patterns selectively evoked mental state attribution (Castelli et al., 2000; Schultz et al., 2003). This region is said to play a key role in fast and automatic evaluation of the social

significance of an event, as for example when it is threatening (Dolan, 2002; Adolphs, 2003; Schwartz et al., 2003).

The fusiform gyrus appears to be specialized for the recognition of different kinds of objects. This includes animate agents, as a body-selective fusiform region has been identified from static displays (Hadjikhani and de Gelder, 2003; Peelen and Downing, 2005), and from video and point-light displays of moving humans (Bonda et al., 1996; Beauchamp et al., 2003). Activity in the fusiform gyrus has also been found in mentalizing tasks (Castelli et al., 2000; Schultz et al., 2003). In the present study, subjects had to detect deceit from full body motor actions. This region has strong connections with amygdala in monkeys (Amaral et al., 1992) and in humans (Smith et al., 2004), and it has recently been proposed that it is part of the circuitry of social cognition (Schultz et al., 2003).

In the present study, the judgments were of social deception. This is one example of a potential hostile situation, in that a person seeks to convince another to believe something that they know to be false. Therefore, one needs to be acute in perceiving and distinguishing whether a person is honest or deceitful. Amaral (2003) has pointed out that the projections of amygdala to visual cortical areas have a typical pattern of feedback-type projections which appear to modulate information processing by enhancing neural responses (Hupe et al., 2001). Due to the role of the amygdala in the evaluation of social significance of events and in emotional responses, these feedback projections to visual areas, including the fusiform gyrus, have been suggested to act to modulate visual attention (Amaral, 2003). This is important where visual information is processed during relevant social situations and further and finer grained computations must be performed (Schultz et al., 2003; Hadjikhani and de Gelder, 2003).

However, the question arises as to why the activity in the amygdala and fusiform gyrus was specific to the situation in which the subjects detected that they were the target of deceit. Our hypothesis was that activation of the amygdala in our previous study (Grèzes et al., 2004) reflected the fact that our subjects felt that the deceit was directed at them. For this reason, in the present study, we specifically compared the activations depending on who was the target of deceit. Our result indicates that the crucial factor is personal involvement.

There are other indications that personal involvement is a crucial factor. First, the perception of direct gaze is associated with a greater correlation between activity in the amygdala and fusiform gyrus when compared to averted gaze, irrespective of the head

Table 3

Brain regions showing amplitude difference when the subjects judged that both they themselves and others mislead the experimenter

Brain regions	Talairach coordinates			Z score	Cluster
	x	y	z		
<i>The Actors (Self + Others) misleading the Experimenter: [(SEy - SE_n) + (OEy - OE_n)] - [(ESy - ES_n) + (EOy - EO_n)]</i>					
L Anterior/lateral orbital gyrus	-34	56	-12	3.88	44
R Anterior/lateral orbital gyrus	36	56	-6	3.55	54
R Cingulate sulcus (motor part?)	18	-4	50	3.72	24
L Putamen	-20	-14	16	3.48	51
L Short insular gyrus	-34	10	-4	3.43	16
<i>Self misleading the Experimenter: [(SEy - SE_n) - (OEy - OE_n)] - [(ESy - ES_n) - (EOy - EO_n)]</i>					
L Anterior/lateral orbital gyrus	-34	56	-14	4.78	200
R Anterior/lateral orbital gyrus	36	60	-4	4.24	87

$P < 0.001$ non-corrected.

direction (George et al., 2001). This may be because direct gaze is a means of establishing personal interaction. Second, Berthoz et al. (2003) have demonstrated that the amygdala is specifically activated when subjects judge verbal accounts of their own deliberate social transgressions. This suggests that they feel negative emotions when considering their own transgressions compared with those of others. Finally, Gloor (1972) reported that amygdala stimulation induces subjective experiences of behavioral attitudes of others that the patients perceive as being directed at them (Gloor, 1972; cited by Brothers, 1990).

Our findings are consistent with this, but go beyond the previously obtained results by providing direct evidence, using judgments of deceit in a suggested social context, that the crucial factor for amygdala activation is the involvement of the subjects because they are the target of the deceit. We interpret the activation of the amygdala in this situation as reflecting the greater affective reaction when one is deceived oneself. This could be directly tested by recording psycho-physiological measures. Finally, we cannot rule out the possibility that this affective reaction is due to the fact that the subjects were re-experiencing the original episode in which they were deceived, even though the gap between filming and viewing the films was 2 years.

Actors as the target of deceit

Our other finding relates to deceit whether directed at the subject or another person. In our experiment, the observers watched a person picking up the box and used a disruption in the kinematics as evidence to infer the mental state of the actor and judge that the person had been deceived. We found activations in the superior temporal sulcus and the anterior cingulate cortex when the subjects detected that the experimenter had deceived themselves or another. Several neuroimaging studies have shown that the superior temporal sulcus is involved, not only in the perception of biological motion (Allison et al., 2000), but also in the attribution of mental states (Winston et al., 2002; Schultz et al., 2003; Saxe and Kanwisher, 2004). Furthermore, Samson et al. (2004) have reported evidence that in neurological patients, the temporo-parietal junction, including the posterior part of the STS, is necessary for reasoning about the beliefs of others. By contrast, though imaging data support a role for the ACC in the understanding of mental states (Frith and Frith, 1999), evidence from a neurological patient suggests that its contribution is not essential (Bird et al., 2004).

The ability to detect a disruption in the kinematics implies a prediction of the expected kinematics and the detection of an error in prediction. There is evidence that both the STS and the ACC play a role in making such predictions. Saxe et al. (2004) reported enhanced activity in the STS when a target person walks across a room and appears to stop behind a bookcase longer than expected. It has also been shown that activity in the STS is more prolonged when an observer's prediction has been violated (Pelphrey et al., 2003). Activity has also been reported in the ACC, as well as the STS, when subjects make predictions about the responses of another person (Ramnani and Miall, 2004). Furthermore, it is well established that it is possible to record an error signal in the ACC when the outcomes of action are not as predicted (Rushworth et al., 2004).

We therefore suggest that the activity in the STS and ACC relates to the subject's perception that an action did not unfold as expected, associated with the inference that the experimenter has

deceived themselves or someone else. Thus, these areas may provide a mechanism for the understanding of false beliefs whether one's own or another's. In the same way, the ACC and anterior insula would provide a mechanism for the perception of feelings whether one's own or those of others (Jackson et al., 2005; Singer et al., 2004; Wicker et al., 2003).

Conclusion

In our experiment, subjects made judgments concerning deceit. We varied the target of deceit, that is, whether it was the subject who was being deceived or someone else. The finding was that the amygdala was only activated when the subjects detected that they themselves had been deceived. Previous animal and human studies have shown activity in the amygdala in response to threat. Our results suggest that humans perceive deception as a threat, but only when it is aimed at themselves.

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