# Two different faces of threat. Comparing the neural systems for recognizing fear and anger in dynamic body expressions

Swann Pichon [a], Beatrice de Gelder [b,c], Julie Grèzes [a,*]

[a] *Laboratoire de Neurosciences Cognitives, UMR 960 INSERM, Département d'Etudes Cognitives, Ecole Normale Supérieure, 75005 Paris, France*
[b] *Cognitive and Affective Neuroscience Laboratory, Tilburg University, The Netherlands*
[c] *Martinos Center for Biomedical Imaging, Massachusetts General Hospital, Harvard Medical School, Charlestown, MA, USA*

## ARTICLE INFO

## ABSTRACT

Being exposed to fear or anger signals makes us feel threatened and prompts us to prepare an adaptive response. Yet, while fear and anger behaviors are both threat signals, what counts as an adaptive response is often quite different. In contrast with fear, anger is often displayed with the aim of altering the behavior of the agent to which it is addressed. To identify brain responses that are common or specific to the perception of these two types of threat signals, we used functional magnetic resonance imaging and asked subjects to recognize dynamic actions expressing fear, anger and neutral behaviors. As compared with neutral actions, the perception of fear and anger behaviors elicited comparable activity increases in the left amygdala and temporal cortices as well as in the ventrolateral and the dorsomedial prefrontal cortex. Whereas the perception of fear elicited specific activity in the right temporoparietal junction, the perception of anger triggered condition-specific activity in a wider set of regions comprising the anterior temporal lobe, the premotor cortex and the ventromedial prefrontal cortex, consistent with the hypothesis that coping with threat from exposure to anger requires additional contextual information and behavioral adjustments.

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## Introduction

Watching fear and anger behaviors makes the observer feel threatened and prompts him to prepare an adapted response. It has long been understood that the behavioral manifestations of anger and fear shown in the face, the voice and the whole body help to prepare the body for adaptive action (Darwin, 1872; Frijda, 1986). They also serve as communicative signals by warning observers about potential threats in the environment (de Gelder, 2006). Yet, anger and fear signals are quite different as far as the adaptative behavior they elicit in the observer. In contrast with fear, anger is often displayed with the aim of altering the behavior of the agent to which it is addressed (Frijda, 1986) and therefore appears to be a more interactive signal in the sense that it requires the observer to adapt or regulate his own behavior in tune with the ongoing interaction.

With fear and anger both amounting to threat signals, an important question concerns the specificity of the observers' reaction to perceived anger and fear behaviors in others and this issue has not so far been addressed in the literature. Overall, neuroimaging studies in humans that investigated the perception of fearful facial expressions have reported amygdala and fusiform cortex responses (Morris et al., 1996; Phillips et al., 1997; Vuilleumier et al., 2001). Electro-physiological studies in the monkey's amygdala have also underscored its sensitivity to facial expressions, gaze or vocalizations signaling threat (Hoffman et al., 2007; Kuraoka and Nakamura, 2007). These observations are consistent with the view that the amygdala plays a central role in processing threat related signals and linking them to appropriate defensive and attentional responses (Amaral, 2003; LeDoux, 1995; Vuilleumier et al., 2004). To our knowledge, only few imaging studies directly compared brain evoked responses to fear and anger static facial expressions (Phillips et al. 1999; Whalen et al., 2001; Williams et al., 2005). The results showed that compared with neutral expressions, the perception of both fear and anger faces enhanced amygdala BOLD response, yet fearful expressions seem to evoke the greatest responses. In parallel, neuroimaging studies using fearful and angry facial expressions have often revealed activations in the inferior frontal gyrus and lateral orbitofrontal cortex (IFG BA45 and OFC BA47) (Blair et al., 1999; Fitzgerald et al., 2006; Kesler-West et al., 2001; Sprengelmeyer et al., 1998), consistent with their essential roles in processing emotional expressions (Hornak et al., 1996). Interestingly, Murphy et al. (2003) in their meta-analysis show the highest proportion of lateral OFC activations in studies targeting anger vs. other emotions. Yet as a majority of neuroimaging investigations have been using the same static material, it remains unclear how amygdala and other brain regions are engaged during sensory processing of other emotional signals such as dynamic body-related ones.

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* Corresponding author. Fax: +33 1 44 32 26 86.
 *E-mail address:* julie.grezes@ens.fr (J. Grèzes).

As noted above, anger-based vs. fear-based threat manifestations may trigger rather different adaptive behaviors. Therefore using whole body images rather than only facial expressions may better reveal the underlying neurofunctional similarities in emotion related action structures (de Gelder et al., 2004). Hadjikhani and de Gelder (2003) showed that the perception of body postures expressing fear elicited amygdala and fusiform responses in the same way that did facial expressions. Nevertheless, perceiving fearful body postures was also associated with activations in other affective centers such as the OFC and the insula as well as action-related areas such as the inferior frontal gyrus (IFG) and the premotor cortex (de Gelder et al., 2004). Grosbras et al. (2006) recently used realistic video-clips of hand actions expressing anger and found increased activations in the superior temporal sulcus (STS), the dorsal premotor cortex, the dorsomedial prefrontal cortex (dmPFC), the IFG, the insula and the supramarginal gyrus. Two other experiments investigated the impact of movement on the perception of actions signaling fear and anger (Grèzes et al., 2007; Pichon et al., 2008). The perception of static and dynamic angry and fearful actions was associated with increased responses in the STS, the amygdala and adjacent temporal pole, the inferior frontal cortices, the pre-SMA and the dmPFC. Moreover, the perception of dynamic actions expressing fear specifically engaged the STS extending to the temporoparietal junction (TPJ) and the premotor cortex (Grèzes et al., 2007), whereas the perception of dynamic actions expressing anger increased responses in the anterior temporal cortices, the ventro-medial PFC (vmPFC), the hypothalamus and the premotor cortex. Together, these results showed that besides modulating sensory and emotional regions, the perception of actions expressing a threat is also coupled with increased responses in brain regions associated to motor preparation (Hoshi and Tanji, 2004) and defensive responses (Brown et al., 1969; Graziano and Cooke, 2006).

What remains unclear though is to what extent these responses are characteristic of perceiving a threat or whether some aspects thereof are specific to either fear or anger cues. To investigate this question, we used functional magnetic resonance imaging (fMRI) to record participants' brain haemodynamic activity while they were categorizing videos showing either fear, anger or a neutral action. We tested whether the amygdala is preferentially activated by fear signals. We also aimed at identifying the common and distinct regions associated with the recognition of fear and anger signals. From this, we drew three predictions: first, that the recognition of actions signaling threat increases the amygdala's response; second, that it also enhances the BOLD response in posterior temporal (STS, TPJ, fusiform) as well as inferior frontal (BA45 and BA47) regions; third, that the anterior temporal cortices and OFC are preferentially engaged during the recognition of anger signals.

## Methods

### Participants

16 right-handed volunteers (8 females; mean age = 25.6 years, standard deviation (SD) = 8; and 8 males; mean age = 23.5 years, SD = 2.6) with no neurological or psychiatric history participated in the imaging study. All provided written informed consent according to institutional guidelines of the local research ethics committee and were paid for their participation.

### Stimuli

71 full-light 3 second videos (23 fear, 24 anger and 24 neutral) were used for the present experiment. Videos were chosen from a wider set of stimuli based on the recognition performance obtained in a pilot study. One fear movie was drop because of frequent misclassification. Details about the materials can be found elsewhere (Grèzes et al., 2007; Pichon et al., 2008). The recording of stimuli involved 12 professional actors (6 females, 6 males) performing the simple action of opening a door in front of them, react to a specified encounter and close the door again. The anger and fear versions of this scenario required the actors to react to something or someone that made them angry or frightened them. Recordings were filmed with the camera facing the actors. Importantly, faces were blurred such that only information from the body was available.

In order to control for quantitative differences in movement between the anger, fear and neutral movies, we estimated the amount of movement per video-clip by quantifying the variation of light intensity (luminance) between pairs of frames for each pixel. For each frame, these differences were averaged across pixels that scored (on a scale reaching a maximum of 255) higher than 10, a value which corresponds to the noise level of the camera. These estimations were then averaged for each movie and the resulting scores were used to test the hypothesis of a difference in movement between expressions. Mean estimations of movement for fear, anger and neutral movies (Fig. 1d) were, 40.88 (SD = 7.56), 41.12 (SD = 6.72) and 40.03 (SD = 4.82) respectively. No significant differences were detected between expressions (repeated measures ANOVA, $F(2,44) = 0.43$, $P = 0.613$, Greenhouse–Geisser sphericity correction).

Each movie was also rated by a different group of 39 subjects (27 females; mean age = 22.63 years, standard deviation (SD) = 2.47; and 12 males; mean age = 21.45 years, SD = 2.07) to assess potential differences in emotional intensity between expressions. To collect their responses, we used a 10-graded scale which extremities were labeled "Low" and "High". Subjects could slide a mouse cursor along this scale and the scores collected ranged from 0 to 100. Mean estimations of intensity for fear, anger and neutral movies (Fig. 1f) were, respectively, 48.07 (SD = 13.24), 46.16 (SD = 13.59) and 12.31 (SD = 19). A repeated measure ANOVA revealed a significant difference between expressions ($F(2,74) = 99.18$ $P < 0.001$, Greenhouse–Geisser sphericity correction) and post-hoc $t$-tests (corrected for multiple comparisons) showed that whereas fear and anger movies were equivalently rated ($T(1,37) = 1.59$, $P = 0.36$), they were perceived as more intense than neutral movies (respectively $T(1,37) = 10.51$, $P < 0.001$ and $T(1,37) = 10$, $P < 0.001$).

### Design and fMRI procedure

Our analysis here compared explicit recognition of anger, fear and neutral dynamic body expressions. The full experiment consisted of two tasks, one explicit (recognizing emotions) and one implicit (detecting a color spot in the movie), during which subjects were presented movies of fear, anger or neutral expressions implying the whole body. The comparison between explicit and implicit tasks will be presented elsewhere (Pichon et al. in preparation).

The experiment was divided into two successive scanning runs of 21 min each. Within each run, stimuli were blocked by task and alternated between series of explicit and implicit recognition. At the beginning of each block, subjects were shown instruction on the screen lasting 2 s specifying whether they had name emotions or colors (e.g. "Emotion" or "Color"). Stimuli and null events (5 s) were randomly mixed within blocks. Each task block contained 6 events (including nulls). After each stimulus presentation, subjects were instructed by a response screen (fear/anger/neutral or red/green/blue) to push the corresponding button using a response pad placed in their right hand. Subjects had a delay of 2 s to give their answer. The order of responses was randomized between trials to avoid motor anticipation related effects. A total of 36 blocks per task was presented (142 video-clips + 74 null events). Stimuli were back-projected onto a screen positioned behind the subject's head and viewed through a mirror attached to the head coil. The stimulus was
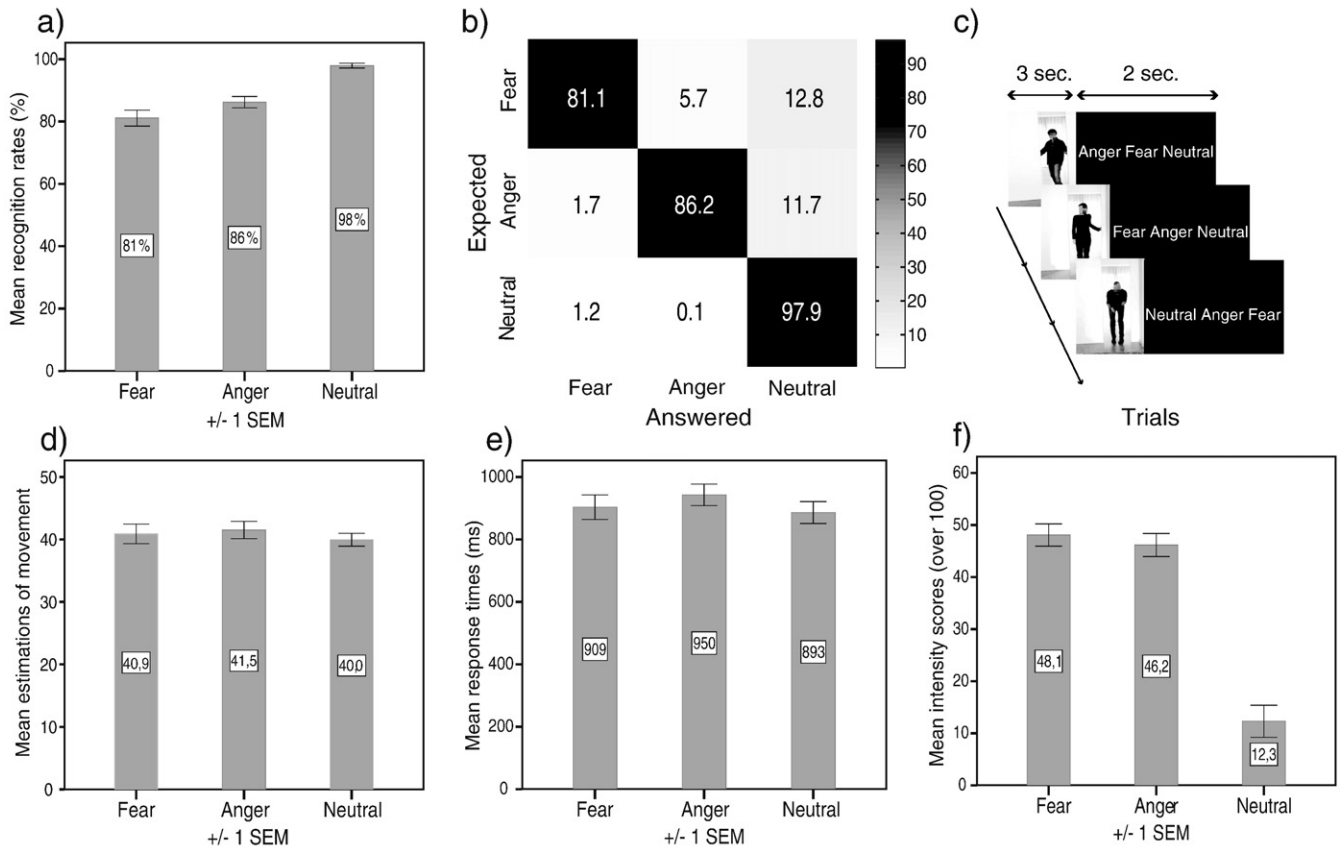
**Fig. 1.** Behavioral results. (a) Mean recognition rate across conditions and (b) confusion matrix showing that all expressions were clearly recognized above chance (percentages displayed take into account omitted responses that are not displayed here). Fear and anger recognition rates were comparable although they both differ from neutral score. (c) Example of 3 trials during which subjects were asked to recognize the emotion expressed in the action. (d) Mean estimations of movement across expressions: these values were estimated by quantifying for each video-clip the variation of light luminance between pairs of frames for each pixel. (e) Mean reaction times. (f) Mean emotional intensity scores across expressions estimated independently of the fMRI experiment by 38 supplementary participants. Error bars represent standard error of the mean (SEM).

centered on the display screen and subtended 10.8° of visual angle vertically and 7.3° horizontally.

### fMRI data acquisition

Gradient-echo T2*-weighted transverse echo-planar images (EPI) with blood oxygenation level-dependent (BOLD) contrast were acquired with a 3 T Siemens Magnetom Trio scanner (Siemens, Erlangen, Germany). Participants used earplugs to attenuate scanner noise and padding was used to reduce head movements. Each volume contained 32 axial slices (repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, 3.5 mm thickness without gap yielding isotropic voxels of 3.5 mm$^3$, flip angle = 90°, field of view (FOV) = 224 mm, resolution = 64*64), acquired in an interleaved manner. An automatic shimming procedure was performed before each scanning session to minimize inhomogeneities of the static magnetic field. We collected a total of 1270 functional volumes for each subject as well as high-resolution T1-weighted anatomical images (TR = 2250 ms, TE = 2.6 ms, slice thickness = 1 mm, 192 sagittal slices, flip angle = 9°, FOV = 256 mm, resolution = 256*256).

### fMRI images processing

Image processing was carried out using SPM2 (Wellcome Department of Imaging Neuroscience; see www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB (Mathworks Inc., Sherborn, MA). The first five volumes of each scanning run were discarded to allow for equilibration effects. The remaining 1260 functional images were reoriented to the AC-PC line, corrected for differences in slice acquisition time using the middle slice as reference, spatially realigned to the first volume by rigid-body transformation, spatially normalized to the standard Montreal Neurological Institute (MNI) EPI template to allow group analysis, resampled to an isotropic voxel size of 2 mm and spatially smoothed with an isotropic 8 mm full-width at half-maximum (FWHM) Gaussian kernel (Friston et al., 1995). To remove low-frequency drifts from the data, we applied a high-pass filter using a standard cut-off frequency of 1/128 Hz.

### fMRI images analysis

A two-stage general linear model was used to examine the effect sizes of each condition and compare them to the group-level. The statistical analyses were carried out using SPM2.

At the subject-level, we performed fixed-effect analyses where task-specific effects were modeled separately for each subject. For each session, we specified a linear model including 7 conditions of interest: 3 conditions corresponding to the explicit recognition of fear, anger, and neutral expressions (F, A, N) and 3 conditions corresponding to the implicit recognition of fear, anger, and neutral expressions; the seventh condition was used to model the instruction screen preceding each block. For the first six conditions, the emotion modeled is the emotion expressed by the actor, and therefore both correct and incorrect responses were included. For each condition, a covariate was calculated by convolving delta functions (representing the onset of each event) with a canonical haemodynamic response function (HRF). The length of each event encompassed

the stimulation and the response period. Six additional covariates were modeled, corresponding to the realignment parameters (the difference between scans in the estimations of the 3 rigid-body translations and the 3 rotations determined from initial spatial registration) in order to capture residual movement-related artifacts. A last covariate represented the mean (constant) over scans. Effects at each brain voxel were estimated using a least squares algorithm to produce condition-specific images of parameter estimates for group-level analysis.

Furthermore, in order to perform correlation analyses between subject's behavioral performances (% of correctly recognized trials) and functional data, we specified another linear model in which subjects' correct and incorrect responses were dissociated. For each session, we specified a linear model including 8 conditions of interest: 3 conditions corresponded to correctly recognized trials of the explicit recognition of fear, anger, and neutral expressions (F, A, N) and 3 conditions corresponding to the implicit recognition of fear, anger, and neutral expressions; the seventh condition modeled the instruction screen preceding each block and the last one the incorrectly recognized trials. Therefore, the parameter estimates for the first 3 conditions in this model reflected the emotion recognized by the participants.

At the group-level, we used a random effect model that allows population based inferences to be drawn. The analysis we report here focused only onto differences between conditions during the explicit task. We performed a repeated measures ANOVA with a three-levels within-subjects factor corresponding to images of parameter estimates obtained at the subject-level for the 3 conditions of the explicit task (F, A, N). A non-sphericity correction was applied for variance differences across conditions or subjects. In this way, the variance estimates at the group-level incorporated appropriately weighted within-subject and between-subject variance effects. After model estimation, we calculated the following contrasts to examine enhanced emotional responses respective to neutral stimuli:

1. We carried out a conjunction analysis between (A vs. N) and (F vs. N) to examine regions that were commonly recruited by the recognition of anger and fear vs. neutral expressions. This test requires that all the comparisons in the conjunction are individually significant (Nichols et al., 2005). The results from the individual contrasts (A vs. N) and (F vs. N) can be found in supplementary materials (Fig. S1 and Tables S2 and S3).
   We then performed two simple regression analyses to identify the brain regions whose activation showed a correlation with the behavioral recognition performances (% of correctly recognized trials) using the magnitude of the effect resulting from the contrast of fear or anger vs. neutral conditions estimated at the subject's level from the model that only included correctly recognized trials.
3. Finally, we searched for responses preferentially elicited by each emotional expression compared to the other one, (A vs. F) and (F vs. A). The volume of comparison was restrained to significant voxels that appeared in the individual contrasts (A vs. N) for anger and (F vs. N) for fear, using inclusive masking procedure with a threshold of $P = 0.001$, uncorrected.

For all statistical maps, we report activations that survived the threshold of $T > 3.39$ ($P < 0.001$, uncorrected) with a minimum cluster extent of 10 contiguous voxels. Given the conservative analyses based on the conjunction null hypothesis, we displayed activations that survived a threshold of $T > 2.75$ ($P < 0.005$, uncorrected) with a minimum cluster extent of 20 contiguous voxels and reported in this table only $P$ values that do not exceed 0.001. We also indicated in tables peaks that survived false discovery rate (FDR) correction ($P < 0.05$) (Genovese et al., 2002). Illustrations of maps were overlaid on the ICBM-152 brain template. Anatomical labeling was performed

with reference to the atlas of Duvernoy (1999) and the anatomy toolbox (Eickhoff et al., 2005). Surface rendering of statistical maps and estimation of Brodmann areas have been carried out using Caret (Van Essen et al., 2001) and the PALS-B12 atlas (Van Essen, 2005), an average brain atlas derived from structural MRI volumes of 12 normal young adults that were adjusted to the ICBM-152 space (Van Essen, 2005).

## Results

### Behavioral results

Examination of the participants' average recognition rate revealed good recognition of the three expressions (mean 88.5%, SD = 4.7). Fear, anger and neutral movies (Fig. 1a) were recognized respectively, 81% (SD = 10.3), 86% (SD = 7.2), and 98% (SD = 2). A repeated measures ANOVA revealed a significant difference between emotions ($F(2,30) = 25.74$ $P < 0.001$, Greenhouse–Geisser sphericity correction) and post-hoc $t$-tests (corrected for multiple comparisons) showed that the latter result was driven by a better recognition of neutral expressions compared to fear ($T(1,15) = 6.76$, $P < 0.001$) and anger ones ($T(1,15) = 6.17$, $P < 0.001$). Importantly, the recognition rates of anger and fear did not differ ($P = 0.089$). Subjects' response times for fear, anger and neutral conditions (Fig. 1e) were, respectively, 909 ms (SD = 162), 950 ms (SD = 142), and 892 ms (SD = 147). Statistical analysis of these scores by repeated measures ANOVA did not reveal any significant differences ($F(2,30) = 2.2$ $P = 0.13$, Greenhouse–Geisser sphericity correction).

### Neuroimaging results

#### Enhanced activity during the recognition of threat signals: (A vs. N) ∩ (F vs. N) (conjunction)

The conjunction (Fig. 2a) revealed that the recognition of fear and anger dynamic signals induced a similar increase of activity in the left amygdala ($xyz_{MNI}$: −18/−6/−16, Fig. 2b). Moreover, in both hemispheres, we observed enhanced activity in the bilateral motion-sensitive visual area MT/V5, in the left fusiform gyrus and the left temporoparietal junction (TPJ). We also detected activations in the right superior temporal sulcus, mainly in its posterior part (pSTS, $xyz_{MNI}$: 56/−50/6 and 60/−38/4) extending to the middle ($xyz_{MNI}$: 50/−20/−10). Finally, we observed activations in the prefrontal cortex (PFC). On the medial wall, a cluster extending from the pre-supplementary motor area to anterior portions of the medial superior frontal gyrus (BA9 and BA10, Fig. 2c) was detected. On the lateral part of the PFC, foci of activation were centered on BA44 and BA45 in the left IFG whereas in the right IFG, they were centered on the orbital part of the IFG, at the junction between BA45 and BA47. Bilateral activations of the lateral OFC (BA47) could also be observed. In the left hemisphere, this cluster was also extending to the deep portion of the frontal operculum at the junction with the anterior insula (Fig. 2d). Post-hoc comparisons of parameter estimates in the left lateral OFC revealed that the response was stronger for anger as compared with fear ($xyz_{MNI}$: −42/22/−10, $T(1,15) = 2.85$, $P < 0.05$; Fig. 2d). The full list of activations is presented in Table 1.

#### Correlations between recognition performances and brain activity

We searched for significant correlations in the whole brain, between subjects' mean correct recognition scores for fear or anger and the corresponding effect magnitude resulting from the contrasts of fear or anger vs. neutral expressions. For fear, the analysis yielded significant correlations in right amygdala and bilaterally in the temporal pole ($P < 0.001$ uncorrected for multiple comparisons and minimum cluster extent of 10 voxels), and in the left amygdala at a lower threshold ($P = 0.002$). In both regions, the estimated difference
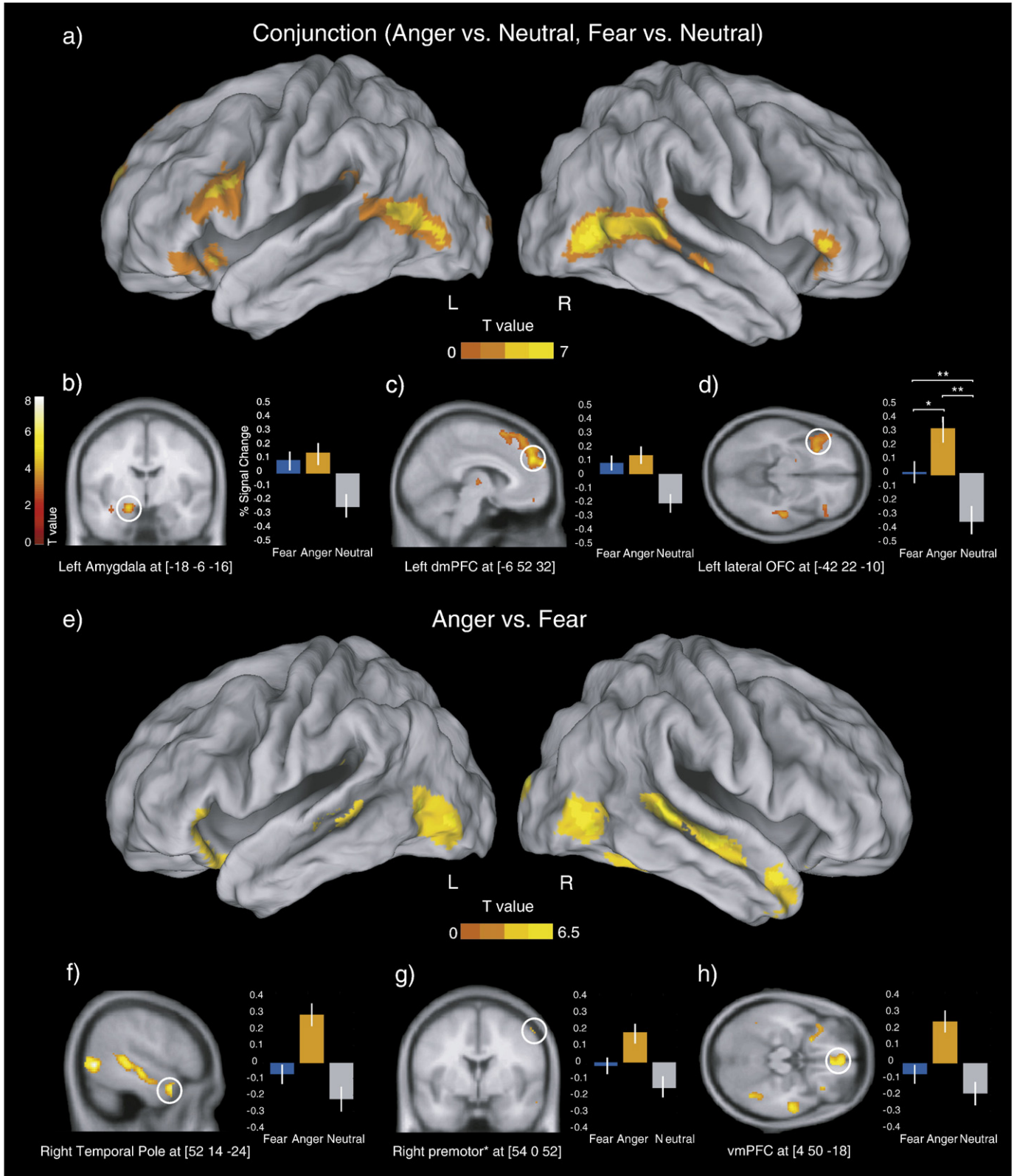
**Fig. 2.** Statistical maps showing common brain areas to fear vs. neutral actions and anger vs. neutral actions, rendered on a partially inflated lateral view of the PALS-B12 atlas (SPM(t) thresholded at $P<0.005$ uncorrected for the present display, cluster extend threshold of 20 voxels). (b) Group (n = 16) average activation of the left amygdala, superimposed on a coronal section of the ICBM-152 average T1-weighted brain. The right histograms represent the percentage signal change (arbitrary units, mean centered, error bars represent SEM) at the local maxima in the left amygdala across conditions (Fear, Anger and Neutral). (c) Group average activation in the left dmPFC and (d) the left lateral OFC extending to the anterior insula, superimposed on sagittal and axial sections of the ICBM-152 average brain (conventions as in b). Paired t-test across conditions showed that the OFC response was higher for anger as compared with fear (*$P<0.05$; **$P<0.005$). (e) Statistical maps showing specific activations to anger vs. fear actions, (SPM(t) thresholded at $P<0.001$ uncorrected for the present display, cluster extent threshold of 10 voxels). (f) Sagittal view of the group average activation in the right temporal pole; (g) coronal view of the group average activation in the right premotor cortex and (h) axial view of the group average activation in the ventromedial PFC (conventions as in (a)).

**Table 1**
Common activations to Anger and Fear, revealed by a conjunction analysis between the contrast (Anger vs. Neutral) and the contrast (Fear vs. Neutral).

| Hemisphere | Anatomical region | MNI coordinates | | | Z value | Size in voxels |
|---|---|---|---|---|---|---|
| | | x | y | z | | |
| L | Medial superior frontal gyrus (dmPFC − BA10) | −8 | 62 | 26 | 4.22 | 1014↓ |
| L | Medial superior frontal gyrus (dmPFC − BA9/BA10) | −6 | 52 | 32 | 4.28 | 1014 |
| L | Medial superior frontal gyrus (dmPFC − BA9) | −6 | 50 | 40 | 3.81 | 1014↓ |
| L and R | Lateral orbitofrontal cortex (BA47) | ±46 | 36 | −12 | 3.16*/3.12* | 436↓/197↓ |
| L | Lateral orbitofrontal cortex (BA47) | −42 | 22 | −10 | 3.44 | 436↓ |
| L | Anterior insula | −30 | 22 | −10 | 3.62 | 436 |
| R | Inferior frontal gyrus (BA45) | 54 | 34 | −2 | 3.73 | 197 |
| L | Inferior frontal gyrus (BA45) | −58 | 22 | 22 | 3.71 | 713 |
| L | Inferior frontal gyrus (BA44) | −46 | 12 | 24 | 3.6 | 713↓ |
| L | Amygdala | −18 | −6 | −16 | 3.98 | 220 |
| L and R | Peri-amygdalar cortex | ±38 | 0 | −22 | 3.25*/3.45 | 220↓/46 |
| L | Thalamus | −6 | −16 | 4 | 3* | 20 |
| R | Pulvinar | 12 | −28 | 0 | 3.51 | 56 |
| R | Superior temporal sulcus − middle part | 50 | −20 | −10 | 3.54 | 1879↓ |
| R | Superior temporal sulcus − posterior part | 60 | −38 | 4 | 4.15 | 1879↓ |
| R | Middle temporal gyrus/superior temporal sulcus | 56 | −50 | 6 | 4.28 | 1879↓ |
| L | Middle temporal gyrus/superior temporal sulcus | −50 | −60 | 12 | 4.03 | 987↓ |
| L and R | Temporoparietal junction − supramarginal gyrus | ±52 | −38 | 26 | 3.31*/3.1* | 87/1879↓ |
| L | Fusiform gyrus | −44 | −46 | −24 | 3.99 | 113 |
| L and R | Middle temporal gyrus (MT/V5) | ±50 | −66 | 2 | 4.24/5.73 | 987/1879 |
| L | Middle temporal gyrus | −46 | −80 | 0 | 3.77 | 987↓ |
| L | Occipital pole | −18 | −102 | 6 | 3.24* | 60 |

$P<0.001$ uncorrected. Results listed survived FDR correction ($P<0.05$) except for *. Subpeaks in clusters marked with ↓.

in the haemodynamic response for fear as compared with neutral expressions was positively correlated with the subjects' ability to recognize fear expressions. The Fig. 3 illustrates the relation between the two variables within the right amygdala at the coordinates $xyz_{MNI}$: 24/2/−20, Pearson($r$) = 0.757, $P<0.001$). The same analysis for anger across the whole brain yielded no significant correlation. The use of a more liberal threshold ($P=0.005$) did not reveal any correlation in the amygdala for anger. Details of regions showing significant correlations are presented in Table 2.
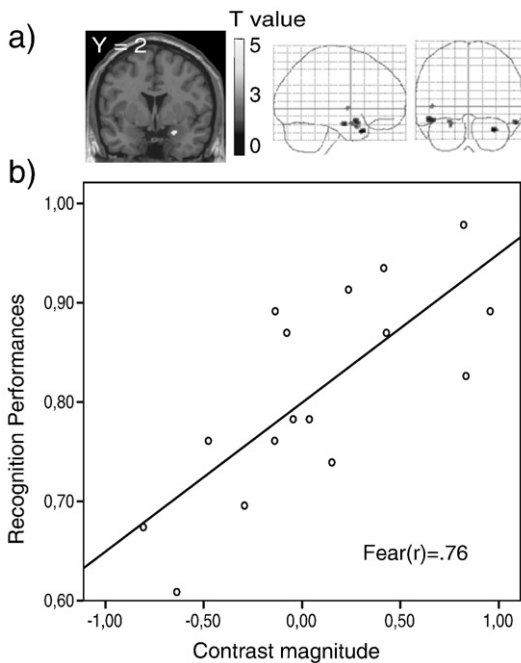


Fig. 3. (a) Correlation analysis performed over the whole brain showing that the better fear is recognized, the more the effect size when contrasting fear vs. neutral expressions is important in right amygdala and bilaterally in the temporal pole (SPM(t) thresholded at $P=0.001$ uncorrected, cluster extend threshold of 10 voxels). No significant correlation was detected for anger expressions across the whole brain. (b) Scatter plot and line of best fit showing the significant positive correlation in the right amygdala at $xyz_{MNI}$: 24/2/−20 (Pearson($r$) = 0.757, $P<0.001$).

*Specific activations for anger (A vs. F) or fear (F vs. A) signals*

To isolate regions specifically engaged during recognition of anger or fear expressions, we compared anger to fear (and vice versa) restraining the volume of comparison to (A vs. N) for anger-specific effects and (F vs. N) for fear-specific effects.

Regions specific to anger expressions as compared to fear ones (A vs. F, Fig. 2e) included the bilateral MT/V5, the fusiform gyrus, the pSTS and left temporoparietal junction. Significant clusters of activity were detected in the right hemisphere along the STS, extending from its posterior part to the temporal pole (from $y = −36$ to $y = 14$, Fig. 2f). Also consistent with expected results, we observed, in the PFC, peaks of activations located in the left lateral orbital gyrus (BA47), in the bilateral posterior orbital gyrus and in the left ventromedial prefrontal cortex (vmPFC, rectus gyrus, Fig. 2h). Finally, activity was revealed in the premotor cortex. As the cluster size of this latter activation was inferior to 10 voxels, we used the coordinates from our previous studies on passive observation of fear and anger ($xyz_{MNI}$: 54/4/40 (Grèzes et al., 2007) and 56/−4/52 (Pichon et al., 2008)) to perform a Small Volume Correction (SVC, 1 cm radius centered onto coordinates mentioned above, Fig. 2g). A cluster at $xyz_{MNI}$: 54/0/52 survived FWE correction for multiple comparisons ($P<0.05$). Details of activations are presented in Table 3.

**Table 2**
Correlation analysis between fear recognition performances and the effect magnitude resulting from the contrast (Fear vs. Neutral).

| Hemisphere | Anatomical region | MNI coordinates | | | Z value | Size in voxels |
|---|---|---|---|---|---|---|
| | | x | y | z | | |
| R | Amygdala | 22 | 8 | −24 | 3.48 | 33 |
| R | Amygdala | 24 | 2 | −20 | 3.39 | 33↓ |
| L | Amygdala | −28 | 2 | −18 | *2.91 | 19 |
| L | Amygdala | −24 | −2 | −16 | *2.81 | 19↓ |
| L | Temporal pole | −30 | 14 | −30 | 3.95 | 21 |
| R | Temporal pole | 50 | 6 | −16 | 3.72 | 60 |
| L | Middle temporal gyrus | −60 | −8 | −20 | 3.71 | 25 |
| R | Posterior insular cortex | 46 | −4 | 0 | 3.32 | 10 |

$P<0.001$ uncorrected, *$P=0.002$ uncorrected. Subpeaks in clusters marked with ↓.

**Table 3**
Brain regions preferentially recruited during the recognition of anger as compared with fear expressions and vice versa.

| Hemisphere | Anatomical region | MNI coordinates | | | Z value | Size in voxels |
|---|---|---|---|---|---|---|
| | | x | Y | z | | |
| *Anger vs. Fear (masked inclusively by Anger vs. Neutral)* | | | | | | |
| R | Ventromedial prefrontal cortex (vmPFC − BA11) | 4 | 50 | −18 | 4.62 | 241 |
| R | Posterior orbital gyrus | 34 | 28 | −20 | 4.08 | 12 |
| L | Posterior orbital gyrus | −26 | 18 | −22 | 4.39 | 457 |
| L | Lateral orbitofrontal cortex (BA47) | −44 | 26 | −6 | 4.23 | 457↓ |
| R | Premotor cortex[a] | 54 | 0 | 52 | 3.61 | 5 |
| R | Temporal pole | 44 | 12 | −38 | 4.32 | 265↓ |
| R | Superior temporal sulcus/temporal pole | 52 | 14 | −24 | 4.87 | 265 |
| R | Superior temporal sulcus − anterior part | 60 | −8 | −14 | 5.18 | 927 |
| L | Superior temporal sulcus − middle part | −60 | −26 | −2 | 4.52 | 159 |
| L and R | Superior temporal sulcus − posterior part | ±56 | −36 | 4 | 3.79/4.82 | 159↓/927↓ |
| L | Temporoparietal junction/supramarginal gyrus | −54 | −38 | 24 | 3.62 | 41 |
| L and R | Fusiform gyrus | ±46 | −50 | −22 | 3.87/4.07 | 51/119 |
| L | Precuneus | −10 | −56 | 36 | 3.97 | 20 |
| L and R | Middle temporal gyrus (MT/V5) | ±50 | −68 | 0 | 4.31/5.62 | 670↓/460 |
| L | Middle occipital gyrus | −44 | −74 | −8 | 4.11 | 670↓ |
| L | Middle occipital gyrus | −44 | −82 | −2 | 4.42 | 670 |
| R | Occipital pole | 22 | −96 | 18 | 4.44 | 130 |
| | | | | | | |
| *Fear vs. Anger (masked inclusively by Fear vs. Neutral)* | | | | | | |
| R | Temporoparietal junction/superior temporal gyrus | 66 | −36 | 26 | 3.71 | 12 |

$P < 0.05$ FDR corrected. Subpeaks in clusters marked with ↓.
  [a] $P < 0.05$ FWE corrected with SVC using a 10 mm sphere radius centered on the premotor coordinates $xyz_{MNI}$: 56/−4/52 from (Pichon et al., 2008).

The direct contrast between fear vs. anger expressions (F vs. A) revealed only one cluster in the right TPJ ($xyz_{MNI}$: 66/−36/26). Details of the activation are presented in Table 3.

## Discussion

The present study was designed to identify the neurofunctional basis of threat perception when observers are faced with fear and anger behaviors. This is the first imaging study that directly compares brain activity elicited by the recognition of dynamic actions signaling fear and anger. Our results clearly indicate that the recognition of fear and anger actions elicits similar activity in amygdala, posterior temporal cortices, dorsomedial and inferior frontal cortices. However, correlation analyses between functional data and behavioral recognition scores show that the magnitude of amygdala response to the perception of fear expressions was a good predictor of subject's mean recognition of fear expressions, but not of anger ones. Finally, the recognition of fear elicited specific responses only in the right TPJ, whereas the recognition of anger revealed specific responses mainly in the anterior part of the temporal cortex, in the premotor cortex and in the vmPFC.

### Similar amygdala activations for fear and anger actions

The recognition of fear and anger actions compared to neutral ones yielded similar haemodynamic response in the left amygdala (Fig. 2b). Previous fMRI studies mainly reported strongest amygdala activations for fear signals (Murphy et al., 2003; Whalen et al., 2001) but our data show a similar magnitude to the recognition of both emotions. One may argue that this pattern arises because anger stimuli are perceived as more intense than fearful ones. This interpretation is refuted by the behavioral results showing that anger actions were perceived as having the same intensity as fearful actions (Fig. 1f). A second objection may be that angry actions contain more body movements than fearful expressions, and therefore enhance amygdala responses to actions signaling anger. Yet, our quantification of movements shows no significant difference between expressions (Fig. 1d).

Our results extend the previous findings of amygdala activations during exposure to fear and angry signals expressed in static faces

(Adams Jr. et al., 2003; Fischer et al., 2005; Morris et al., 1996; Nomura et al., 2004; Whalen et al., 2001; Williams et al., 2004, 2005), static body postures (de Gelder et al., 2004; Hadjikhani and de Gelder, 2003) as well as morphed facial animations (LaBar et al., 2003; Sato et al., 2004). This result is also consistent with amygdala and temporal pole activations during passive observation of dynamic body expressions of fear and anger (Grèzes et al., 2007; Pichon et al., 2008) and corroborates the role played by the amygdala in detecting the occurrence of aversive sensory information (Amaral, 2003; LeDoux, 1995). Together, these arguments support the interpretation that the amygdala response we observe reflects the detection of emotional signals conveyed by threat behaviors. It is however important to notice that we cannot conclude to a threat-specific interpretation since we had no positive emotions to test this assumption. Indeed, it may also be possible that the present response reflects a broader process that evaluates communicative signals (whether positive or negative) and their relevance for social interactions (Brothers et al., 1990; Sanders et al., 2003; Winston et al., 2002).

### Amygdala activation correlates with recognition of fear expressions

At first sight, similar amygdala activations for the recognition of fear and anger dynamic actions contrast with data from functional and neuropsychological studies that have constantly underscored the prevalence of the amygdala involvement for fear signals. But on the other hand, our correlation analysis does indicate a special status for the perception of fear signals. Indeed, across the whole brain, significant correlations were only detected for fear and were restricted to the amygdala and the temporal pole (see Fig. 3), which are heavily interconnected (Amaral and Price, 1984; Kondo et al., 2003). Habel et al. (2007) reported a similar correlation during the recognition of positive and negative emotional expressions, but not during an implicit age discrimination task. Here, we show that this relation is particularly strong in the case of fear, a finding consistent with the severe deficit in recognizing aversive emotions, especially fear, in patients with amygdala or temporal pole lesions (Adolphs et al., 1994, 1995, 2001; Adolphs and Tranel, 1999; Calder et al., 1996). Finally, Williams et al. (2005) have demonstrated that, although the perception of both fearful and angry faces engaged amygdala, only

the autonomic responses associated with fear perception elicited amygdala activity.

*Modulation of temporal regions activity for fear and anger actions*

Recognizing threat behaviors enhanced activations in several regions of the temporal cortex. Increased activity was revealed in the fusiform gyrus, which is often found during faces and body parts processing (Kanwisher et al., 1997; Peelen and Downing, 2005; Schwarzlose et al., 2005; van de Riet et al., 2009). Note that we did not find any significant correlation between the fusiform activity and recognition performances as one may expect based on the literature since amygdala is thought to modulate visual processing in the fusiform during perception of threat (de Gelder et al., 2004; Grèzes et al., 2007; Hadjikhani and de Gelder, 2003; Pichon et al., 2008; Vuilleumier et al., 2001). Although the recognition of fear and anger actions increased the activity in this region, no significant correlation was detected even at a less stringent threshold. One explanation may be that the fusiform activity, which is modulated by the recognition of fear and anger, is not directly linked to the participants' recognition performances. Other temporal regions detected in the conjunction included the middle temporal gyrus (MT/V5/EBA) and the posterior STS. Activation in MT/V5 is a common finding in action perception studies (Decety and Grèzes, 1999) and is consistent with its role in processing visual motion (Maunsell and Van Essen, 1983; Tootell et al., 1995). It may encompass adjacent extrastriate body area (EBA) related activity, a region selectively activated by human body forms (Downing et al., 2001; Peelen and Downing, 2005). The posterior STS has also been frequently highlighted in biological motion studies (see Allison et al., 2000 for review) and shows specific activity for goal-directed actions but also for configural and kinematics information carried by body movements (Bonda et al., 1996; Grossman and Blake, 2002; Perrett et al., 1989; Thompson et al., 2005). As a whole, the joint activation of amygdala and temporal regions encoding biologically relevant visual information is consistent with the view that the amygdala influences the processing of sensory information through projections sent to all levels of the ventral visual pathway (Amaral et al., 2003).

*Modulation of prefrontal regions activity for fear and anger actions*

Fear and anger recognition were also associated with extended activation in the anterior portion of the dmPFC (Fig. 2c). This cluster was restricted to the superior frontal gyrus and did not extend to anterior cingulate regions. Anterior regions of the dmPFC have been associated with various emotional and social tasks, such as retrieval of emotional knowledge, self/other evaluation or mentalizing (Amodio and Frith, 2006; Mitchell et al., 2005; Vogeley et al., 2001), suggesting that the dmPFC may participate in the integration of social knowledge. Yet, the portion of the dmPFC we found active ($yz_{MNI}$: 52/32) has been highlighted by a recent meta-analysis as particularly responsive to the observation of negative emotions (see Van Overwalle, 2008 for review, Fig. 2c). Recent studies that have used dynamic actions signaling fear or anger indeed reported increased dmPFC responses (Grèzes et al., 2007; Grosbras and Paus, 2006; Pichon et al., 2008). Clustering analyses over several functional imaging datasets have also shown that the dmPFC was often found co-activated with limbic regions such as the amygdala, the periaqueductal gray and lateral hypothalamus (Kober et al., 2008), nuclei that are critical for the control of autonomic and endocrine responses, but also for the generation of affective and defensive behaviors in the observer (Brown et al., 1969; McNaughton and Corr, 2004; Panksepp, 1998). Moreover, some authors have pointed out the involvement of this region in protocols investigating the regulation of one's emotional responses (see Ochsner and Gross, 2005 for review, Fig. 2b). It is therefore possible that the dmPFC response we observe reflects an automatic regulative process exerted upon the emotional response elicited by actions signaling threat.

In addition to the dmPFC, the perception of fear and anger also elicited activity in the IFG and its orbital part extending to the lateral OFC (BA 47), the frontal operculum and the anterior insula (Fig. 2d). Interestingly, one study in human reported BA 45 responses for both instrumental and affectively-laden actions whereas BA47 was only reported for affectively-laden actions when compared to instrumental actions (Lotze et al., 2006). Moreover, our previous data also show activity mostly in lateral OFC (BA 47) during passive observation of actions signaling fear and anger (Grèzes et al., 2007; Pichon et al., 2008). Finally, as the orbital regions (area 47/12) in monkeys share strong anatomical connections with inferotemporal visual association cortices (Barbas, 1988; Petrides and Pandya, 2002) and amygdala (Amaral and Price, 1984), it is suggested that this closely linked triadic network may form the anatomical substrate that evaluates the emotional significance of sensory events (Ghashghaei and Barbas, 2002). It is also possible that the anterior insula activation we observe reflects interoceptive process accompanying emotional perception (Craig, 2002).

Although the lateral OFC was activated for perceiving both anger and fear actions as compared to neutral actions, its activity was also significantly higher for anger than for fearful actions. This is consistent with frequent reports of OFC responses during perception of anger signals expressed in faces or body expressions (Sprengelmeyer et al., 1998; Blair et al., 1999; Kesler-West et al., 2001; Murphy et al., 2003 for review; Pichon et al., 2008), and also when one is imagining another's actions leading to indignation or anger (Zahn et al., 2008) or in situations where social rules are violated (Berthoz et al., 2002). Finally, patients showing lesions of the orbitofrontal cortex illustrate the role of this area for recognition of emotional expression, emotional experience and awareness of inappropriate social conduct (Blair and Cipolotti, 2000; Damasio, 1994; Hornak et al., 1996).

*Anger specific activations*

Consistent with the view that coping with someone else's anger behavior involves more demanding social adaptations than someone else's fear behavior, we found additional specific responses for perceiving anger signals in posterior and anterior temporal regions. Behavioral measures argue against the hypothesis that these responses might be accounted by confounds such as movement or perceived intensity (Figs. 1d and f). Activations in anterior regions of the STS have often been associated to speech processing tasks (see Hein and Knight, 2008 for review). For instance, attention to angry prosody (Grandjean et al., 2005) enhances the activity in a location of the right anterior STS ($xyz_{MNI}$: 60/−12/−9) extremely close to the peak we observe from our data ($xyz_{MNI}$: 58/−16/−10). We did find similar activations in our previous studies on passive observation of actions signaling threat (Grèzes et al., 2007; Pichon et al., 2008). Based on the fact that the temporal pole is recruited during retrieval of autobiographical memory (Maguire et al., 2000; Maguire and Mummery, 1999), theory of mind tasks (Brunet et al., 2000; Castelli et al., 2000; Gallagher et al., 2000), and incidental retrieval of emotional context in single word recognition (Maratos et al., 2001), Frith and Frith (2003) have suggested that this region could play a role in the generation of a wider semantic and emotional context for the event being processed, using past experience. The present activity in the temporal pole and the anterior STS, in combination with the previously discussed network, may reflect the fact that anger behavior is a more interactive emotion than fear which requires further evaluation for the observer of the ongoing action as well as additional contextual information.

A specific activation in the right premotor cortex was revealed for perceiving anger when compared to perceiving fear actions. One

possible interpretation is that this activity reflects enhanced motor resonance (Rizzolatti and Craighero, 2004) triggered by the representation of angry actions in sensorimotor cortices. Since anger and fear movies were rated with the same intensity and contained similar amounts of movement, an explanation of their different motor activation is likely to be due to the emotion component. A second interpretation is that the present premotor cortex activation reflects the preparation of an adapted motor action (Hoshi and Tanji, 2004) in response to the perception and the recognition of anger signals. Although the effect is weak, the observed coordinates ($xyz_{MNI}$: 54/0/52) correspond to what one could have expected from previous premotor activation coordinates ($xyz_{MNI}$ fear: 54/4/40; $xyz_{MNI}$ anger: 56/−4/52) revealed during the passive observation of whole body expressions of fear and anger (Grèzes et al., 2007; Pichon et al., 2008). Using facial expressions, Whalen et al. (2001) have also found higher activity in the premotor cortex for perceiving anger as compared to perceiving fear ($xyz_{Talairach}$: −40/−12/53 and 43/−1.5/46). These activations are located at the border between the ventral and the dorsal part of the premotor cortex (Tomassini et al., 2007). In the monkey, stimulation of this part of the premotor cortex (the polysensory zone PZ in the dorsal part of F4), elicits protective movements (Graziano and Cooke, 2006). This region was therefore proposed to play an important role in monitoring approaching stimuli for the guidance of defensive actions. We would like to suggest that the present premotor cortex activation lends support to the hypothesis that being the target of anger signals implies more complex behavioral readjustments than fearful ones.

Finally, the recognition of anger yielded specific responses in the vmPFC and the posterior part of the OFC. The vmPFC was previously reported for passive observation of anger actions (Pichon et al., 2008). In the monkey, the vmPFC and the posterior part of the OFC share dense anatomical connections with amygdala (Ghashghaei and Barbas, 2002) and hypothalamus (Ongur et al., 1998). Both regions presumably play a major role in autonomic and homeostatic regulation but also in the regulation of aggressive and social behaviors in animals and humans (Blair, 2004; Damasio, 1994; Davidson et al., 2000). Indeed, in cats, stimulation of the vmPFC and lateral OFC reduces hypothalamic-dependent aggressive behaviors (Siegel and Edinger, 1983). In human, lesions of the vmPFC impair the ability to make use of somatic states for appropriate decision-making despite appropriate knowledge of their action consequences (Bechara et al., 1996). Although the functional properties of different territories (medial, posterior or lateral) of the OFC are still unclear, we suggest that responses observed in vmPFC and posterior OFC may reflect the increased need for behavioral adaptation. Indeed, knowing the importance of interpersonal and conflict resolution in primates (de Waal, 2000), coping with the anger of others may rely upon the selection of specific behavioral strategies implicating the orbital part of the PFC, particularly strategies that necessitate to adjust one's own behavior on the base of social contingencies.

## Conclusion

We show that viewing fear and anger behaviors elicit comparable activity increases in the amygdala and temporal cortices as well as in the ventrolateral and the dorsomedial prefrontal cortex. We submit that the activity in these areas may reflect the evaluation of the emotional significance of sensory events associated with an automatic regulative process exerted upon the emotional response elicited in the observer by actions signaling threat. Moreover, we observe specific activity when subjects perceived anger signals in a wider set of region comprising the anterior temporal lobe, the premotor cortex and the ventromedial prefrontal cortex. These results provide supports to the hypothesis that coping with threat from exposure to anger as compared to fear signals, requires additional contextual information and additional behavioral adjustments.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2009.03.084.

## References

Adams Jr., R.B., Gordon, H.L., Baird, A.A., Ambady, N., Kleck, R.E., 2003. Effects of gaze on amygdala sensitivity to anger and fear faces. Science 300, 1536.
Adolphs, R., Tranel, D., 1999. Preferences for visual stimuli following amygdala damage. J. Cogn. Neurosci. 11, 610–616.
Adolphs, R., Tranel, D., Damasio, H., 2001. Emotion recognition from faces and prosody following temporal lobectomy. Neuropsychology 15, 396–404.
Adolphs, R., Tranel, D., Damasio, H., Damasio, A.R., 1994. Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. Nature 372, 669–672.
Adolphs, R., Tranel, D., Damasio, H., Damasio, A.R., 1995. Fear and the human amygdala. J. Neurosci. 15, 5879–5891.
Allison, T., Puce, A., McCarthy, G., 2000. Social perception from visual cues: role of the STS region. Trends Cogn. Sci. 4, 267–278.
Amaral, D.G., 2003. The amygdala, social behavior, and danger detection. Ann. N. Y. Acad. Sci. 1000, 337–347.
Amaral, D.G., Price, J.L., 1984. Amygdalo-cortical projections in the monkey (Macaca fascicularis). J. Comp. Neurol. 230, 496.
Amaral, D.G., Behniea, H., Kelly, J.L., 2003. Topographic organization of projections from the amygdala to the visual cortex in the macaque monkey. Neuroscience 118, 1099–1120.
Amodio, D.M., Frith, C.D., 2006. Meeting of minds: the medial frontal cortex and social cognition. Nat. Rev. Neurosci. 7, 268–277.
Barbas, H., 1988. Anatomic organization of basoventral and mediodorsal visual recipient prefrontal regions in the rhesus monkey. J. Comp. Neurol. 276, 313–342.
Bechara, A., Tranel, D., Damasio, H., Damasio, A.R., 1996. Failure to respond autonomically to anticipated future outcomes following damage to prefrontal cortex. Cereb. Cortex 6, 215–225.
Berthoz, S., Armony, J.L., Blair, R.J., Dolan, R.J., 2002. An fMRI study of intentional and unintentional (embarrassing) violations of social norms. Brain 125, 1696–1708.
Blair, R.J.R., 2004. The roles of orbital frontal cortex in the modulation of antisocial behavior. Brain Cogn. 55, 198–208.
Blair, R.J.R., Cipolotti, L., 2000. Impaired social response reversal: a case of 'acquired sociopathy'. Brain 123, 1122–1141.
Blair, R.J.R., Morris, J.S., Frith, C.D., Perrett, D.I., Dolan, R.J., 1999. Dissociable neural responses to facial expressions of sadness and anger. Brain 122, 883–893.
Bonda, E., Petrides, M., Ostry, D., Evans, A., 1996. Specific involvement of human parietal systems and the amygdala in the perception of biological motion. J. Neurosci. 16, 3737–3744.
Brothers, L., Ring, B., Kling, A., 1990. Response of neurons in the macaque amygdala to complex social stimuli. Behav. Brain Res. 41, 199–213.
Brown, J.L., Hunsperger, R.W., Rosvold, H.E., 1969. Defence, attack, and flight elicited by electrical stimulation of the hypothalamus of the cat. Exp. Brain Res. 8, 113–129.
Brunet, E., Sarfati, Y., Hardy-Bayle, M.C., Decety, J., 2000. A PET investigation of the attribution of intentions with a nonverbal task. NeuroImage 11, 157–166.
Calder, A.J., Young, A.W., Rowland, D., Perrett, D.I., Hodges, J.R., Etcoff, N.L., 1996. Facial emotion recognition after bilateral amygdala damage: differentially severe impairment of fear. Cogn. Neuropsychol. 13, 699–745.
Castelli, F., Happe, F., Frith, U., Frith, C.D., 2000. Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. NeuroImage 12, 314–325.
Craig, A.D., 2002. How do you feel? Interoception: the sense of the physiological condition of the body. Nat. Rev. Neurosci. 3, 655–666.
Damasio, A.R., 1994. Descartes' Error: Emotion, Rationality and the Human Brain. Grosset/Putnam, New York.
Darwin, C., 1872. The Expression of the Emotions in Man and Animals. John Murray, London.
Davidson, R.J., Putnam, K.M., Larson, C.L., 2000. Dysfunction in the neural circuitry of emotion regulation — a possible prelude to violence. Science 289, 591–594.
de Gelder, B., Snyder, J., Greve, D., Gerard, G., Hadjikhani, N., 2004. Fear fosters flight: a mechanism for fear contagion when perceiving emotion expressed by a whole body. Proc. Natl. Acad. Sci. U. S. A. 101, 16701–16706.
de Gelder, B., 2006. Towards the neurobiology of emotional body language. Nat. Rev. Neurosci. 7, 242–249.

de Waal, F.B.M., 2000. Primates — a natural heritage of conflict resolution. Science 289, 586–590.

Decety, J., Grèzes, J., 1999. Neural mechanisms subserving the perception of human actions. Trends Cogn. Sci. 3, 172–178.

Downing, P.E., Jiang, Y., Shuman, M., Kanwisher, N., 2001. A cortical area selective for visual processing of the human body. Science 293, 2470–2473.

Duvernoy, H.M., 1999. The Human Brain. Surface, Three-dimensional Sectional Anatomy with MRI, and Blood Supply. Springer-Verlag, Vienna.

Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., Zilles, K., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. NeuroImage 25, 1325–1335.

Fischer, H., Sandblom, J., Gavazzeni, J., Fransson, P., Wright, C.I., Bäckman, L., 2005. Age-differential patterns of brain activation during perception of angry faces. Neurosci. Lett. 386, 99–104.

Fitzgerald, D.A., Angstadt, M., Jelsone, L.M., Nathan, P.J., Phan, K.L., 2006. Beyond threat: amygdala reactivity across multiple expressions of facial affect. NeuroImage 30, 1441–1448.

Frijda, N.H., 1986. The emotions. Cambridge University Press, Cambridge.

Friston, K.J., Holmes, A.P., Worsley, K.J., Poline, J.B., Frith, C.D., Frackowiak, R.S.J., 1995. Statistical parametric maps in functional imaging: a general linear approach. Hum. Brain Mapp. 2, 189–210.

Frith, U., Frith, C.D., 2003. Development and neurophysiology of mentalizing. Philos. Trans. R. Soc., B Biol. Sci. 358, 459–473.

Gallagher, H.L., Happe, F., Brunswick, N., Fletcher, P.C., Frith, U., Frith, C.D., 2000. Reading the mind in cartoons and stories: an fMRI study of 'theory of mind' in verbal and non-verbal tasks. Neuropsychologia 38, 11–21.

Genovese, C.R., Lazar, N.A., Nichols, T., 2002. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. NeuroImage 15, 870–878.

Ghashghaei, H.T., Barbas, H., 2002. Pathways for emotion: interactions of prefrontal and anterior temporal pathways in the amygdala of the rhesus monkey. Neuroscience 115, 1261–1279.

Grandjean, D., Sander, D., Pourtois, G., Schwartz, S., Seghier, M.L., Scherer, K.R., Vuilleumier, P., 2005. The voices of wrath: brain responses to angry prosody in meaningless speech. Nat. Neurosci. 8, 145–146.

Graziano, M.S., Cooke, D.F., 2006. Parieto-frontal interactions, personal space, and defensive behavior. Neuropsychologia 44, 845–859.

Grèzes, J., Pichon, S., de Gelder, B., 2007. Perceiving fear in dynamic body expressions. NeuroImage 35, 959–967.

Grosbras, M.H., Paus, T., 2006. Brain networks involved in viewing angry hands or faces. Cereb. Cortex 16, 1087–1096.

Grossman, E., Blake, R., 2002. Brain areas active during visual perception of biological motion. Neuron 35, 1167–1175.

Habel, U., Windischberger, C., Derntl, B., Robinson, S., Kryspin-Exner, I., Gur, R.C., Moser, E., 2007. Amygdala activation and facial expressions: explicit emotion discrimination versus implicit emotion processing. Neuropsychologia 45, 2369–2377.

Hadjikhani, N., de Gelder, B., 2003. Seeing fearful body expressions activates the fusiform cortex and amygdala. Curr. Biol. 13, 2201–2205.

Hein, G., Knight, R.T., 2008. Superior temporal sulcus — it's my area: or is it? J. Cogn. Neurosci. Electronic Publication.

Hoffman, K.L., Gothard, K.M., Schmid, M.C., Logothetis, N.K., 2007. Facial-expression and gaze-selective responses in the monkey amygdala. Curr. Biol. 17, 766–772.

Hornak, J., Rolls, E.T., Wade, D., 1996. Face and voice expression identification in patients with emotional and behavioural changes following ventral frontal lobe damage. Neuropsychologia 34, 247–261.

Hoshi, E., Tanji, J., 2004. Functional specialization in dorsal and ventral premotor areas. Prog. Brain Res. 143, 507–511.

Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. J. Neurosci. 17, 4302–4311.

Kesler-West, M.L., Andersen, A.H., Smith, C.D., Avison, M.J., Davis, C.E., Kryscio, R.J., Blonder, L.X., 2001. Neural substrates of facial emotion processing using fMRI. Brain Res. Cogn. Brain Res. 11, 213–226.

Kober, H., Barrett, L.F., Joseph, J., Bliss-Moreau, E., Lindquist, K., Wager, T.D., 2008. Functional grouping and cortical-subcortical interactions in emotion: a meta-analysis of neuroimaging studies. NeuroImage Electronic Publication.

Kondo, H., Saleem, K.S., Price, J.L., 2003. Differential connections of the temporal pole with the orbital and medial prefrontal networks in macaque monkeys. J. Comp. Neurol. 465, 499–523.

Kuraoka, K., Nakamura, K., 2007. Responses of single neurons in monkey amygdala to facial and vocal emotions. J. Neurophysiol. 97, 1379.

LaBar, K.S., Crupain, M.J., Voyvodic, J.T., McCarthy, G., 2003. Dynamic perception of facial affect and identity in the human brain. Cereb. Cortex 13, 1023–1033.

LeDoux, J.E., 1995. Emotion: clues from the brain. Annu. Rev. Psychol. 46, 209–235.

Lotze, M., Heymans, U., Birbaumer, N., Veit, R., Erb, M., Flor, H., Halsband, U., 2006. Differential cerebral activation during observation of expressive gestures and motor acts. Neuropsychologia 44, 1787–1795.

Maguire, E.A., Mummery, C.J., 1999. Differential modulation of a common memory retrieval network revealed by positron emission tomography. Hippocampus 9, 54–61.

Maguire, E.A., Mummery, C.J., Büchel, C., 2000. Patterns of hippocampal-cortical interaction dissociate temporal lobe memory subsystems. Hippocampus 10, 475–482.

Maratos, E.J., Dolan, R.J., Morris, J.S., Henson, R.N.A., Rugg, M.D., 2001. Neural activity associated with episodic memory for emotional context. Neuropsychologia 39, 910–920.

Maunsell, J.H., Van Essen, D.C., 1983. Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. J. Neurophysiol. 49, 1127–1147.

McNaughton, N., Corr, P.J., 2004. A two-dimensional neuropsychology of defense: fear/anxiety and defensive distance. Neurosci. Biobehav. Rev. 28, 285–305.

Mitchell, J.P., Neil Macrae, C., Banaji, M.R., 2005. Forming impressions of people versus inanimate objects: social-cognitive processing in the medial prefrontal cortex. NeuroImage 26, 251–257.

Morris, J.S., Frith, C.D., Perrett, D.I., Rowland, D., Young, A.W., Calder, A.J., Dolan, R.J., 1996. A differential neural response in the human amygdala to fearful and happy facial expressions. Nature 383, 812–815.

Murphy, F.C., Nimmo-Smith, I., Lawrence, A.D., 2003. Functional neuroanatomy of emotions: a meta-analysis. Cognitive Affect. Behav. Neurosci. 3, 207–233.

Nichols, T., Brett, M., Andersson, J., Wager, T., Poline, J.B., 2005. Valid conjunction inference with the minimum statistic. NeuroImage 25, 653–660.

Nomura, M., Ohira, H., Haneda, K., Iidaka, T., Sadato, N., Okada, T., Yonekura, Y., 2004. Functional association of the amygdala and ventral prefrontal cortex during cognitive evaluation of facial expressions primed by masked angry faces: an event-related fMRI study. NeuroImage 21, 352–363.

Ochsner, K.N., Gross, J.J., 2005. The cognitive control of emotion. Trends Cogn. Sci. 9, 242–249.

Ongur, D., An, X., Price, J.L., 1998. Prefrontal cortical projections to the hypothalamus in Macaque monkeys. J. Comp. Neurol. 401, 480–505.

Panksepp, J., 1998. Affective Neuroscience: The Foundation of Human and Animal Emotions. Oxford University Press, New York.

Peelen, M.V., Downing, P.E., 2005. Selectivity for the human body in the fusiform gyrus. J. Neurophysiol. 93, 603–608.

Perrett, D.I., Harries, M.H., Bevan, R., Thomas, S., Benson, P.J., Mistlin, A.J., Chitty, A.J., Hietanen, J.K., Ortega, J.E., 1989. Frameworks of analysis for the neural representation of animate objects and actions. J. Exp. Biol. 146, 87–113.

Petrides, M., Pandya, D.N., 2002. Comparative cytoarchitectonic analysis of the human and the macaque ventrolateral prefrontal cortex and corticocortical connection patterns in the monkey. Eur. J. Neurosci. 16, 291–310.

Phillips, M.L., Young, A.W., Senior, C., Brammer, M., Andrew, C., Calder, A.J., Bullmore, E.T., Perrett, D.I., Rowland, D., Williams, S.C., Gray, J.A., David, A.S., 1997. A specific neural substrate for perceiving facial expressions of disgust. Nature 389, 495–498.

Phillips, M.L., Williams, L., Senior, C., Bullmore, E.T., Brammer, M.J., Andrew, C., Williams, S.C., David, A.S., 1999. A differential neural response to threatening and non-threatening negative facial expressions in paranoid and non-paranoid schizophrenics. Psychiatry Res. 92, 11–31.

Pichon, S., de Gelder, B., Grèzes, J., 2008. Emotional modulation of visual and motor areas by dynamic body expressions of anger. Social Neurosci. 3, 199–212.

Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. Annu. Rev. Neurosci. 27, 169–192.

Sanders, M.J., Wiltgen, B.J., Fanselow, M.S., 2003. The place of the hippocampus in fear conditioning. Eur. J. Pharmacol. 463, 217–223.

Sato, W., Kochiyama, T., Yoshikawa, S., Naito, E., Matsumura, M., 2004. Enhanced neural activity in response to dynamic facial expressions of emotion: an fMRI study. Brain Res. Cogn. Brain Res. 20, 81–91.

Schwarzlose, R.F., Baker, C.I., Kanwisher, N., 2005. Separate face and body selectivity on the fusiform gyrus. J. Neurosci. 25, 11055–11059.

Siegel, A., Edinger, H.M., 1983. Role of the limbic system in hypothalamically elicited attack behavior. Neurosci. Biobehav. Rev. 7, 395–407.

Sprengelmeyer, R., Rausch, M., Eysel, U.T., Przuntek, H., 1998. Neural structures associated with recognition of facial expressions of basic emotions. Proc. Biol. Sci. R. Soc. 265, 1927–1931.

Thompson, J.C., Clarke, M., Stewart, T., Puce, A., 2005. Configural processing of biological motion in human superior temporal sulcus. J. Neurosci. 25, 9059–9066.

Tomassini, V., Jbabdi, S., Klein, J.C., Behrens, T.E.J., Pozzilli, C., Matthews, P.M., Rushworth, M.F.S., Johansen-Berg, H., 2007. Diffusion-weighted imaging tractography-based parcellation of the human lateral premotor cortex identifies dorsal and ventral subregions with anatomical and functional specializations. J. Neurosci. 27, 10259–10269.

Tootell, R.B., Reppas, J.B., Kwong, K.K., Malach, R., Born, R.T., Brady, T.J., Rosen, B.R., Belliveau, J.W., 1995. Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. J. Neurosci. 15, 3215.

van de Riet, W.A.C., Grezes, J., de Gelder, B., 2009. Specific and common brain regions involved in the perception of faces and bodies and the representation of their emotional expressions. Soc. Neurosci. 4, 101–120.

Van Essen, D.C., 2005. A Population-Average, Landmark- and Surface-based (PALS) atlas of human cerebral cortex. NeuroImage 28, 635–662.

Van Essen, D.C., Drury, H.A., Dickson, J., Harwell, J., Hanlon, D., Anderson, C.H., 2001. An integrated software suite for surface-based analyses of cerebral cortex. J. Am. Med. Inform. Assoc. 8, 443.

Van Overwalle, F., 2008. Social cognition and the brain: a meta-analysis. Human Brain Mapping Electronic Publication.

Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happé, F., Falkai, P., Maier, W., Shah, N. J., Fink, G.R., Zilles, K., 2001. Mind reading: neural mechanisms of theory of mind and self-perspective. NeuroImage 14, 170–181.

Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J., 2001. Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. Neuron 30, 829–841.

Vuilleumier, P., Richardson, M.P., Armony, J.L., Driver, J., Dolan, R.J., 2004. Distant influences of amygdala lesion on visual cortical activation during emotional face processing. Nat. Neurosci. 7, 1271–1278.

Whalen, P.J., Shin, L.M., McInerney, S.C., Fischer, H., Wright, C.I., Rauch, S.L., 2001. A functional MRI study of human amygdala responses to facial expressions of fear versus anger. Emotion 1, 70–83.

Williams, L.M., Brown, K.J., Das, P., Boucsein, W., Sokolov, E.N., Brammer, M.J., Olivieri, G., Peduto, A., Gordon, E., 2004. The dynamics of cortico-amygdala and autonomic activity over the experimental time course of fear perception. Brain Res. Cogn. Brain Res. 21, 114–123.

Williams, L.M., Das, P., Liddell, B., Olivieri, G., Peduto, A., Brammer, M.J., Gordon, E., 2005.

BOLD, sweat and fears: fMRI and skin conductance distinguish facial fear signals. NeuroReport 16, 49–52.

Winston, J.S., Strange, B.A., O'Doherty, J., Dolan, R.J., 2002. Automatic and intentional brain responses during evaluation of trustworthiness of faces. Nat. Neurosci. 5, 277–283.

Zahn, R., Moll, J., Paiva, M., Garrido, G., Krueger, F., Huey, E.D., Grafman, J., 2008. The neural basis of human social values: evidence from functional MRI. Cereb. Cortex Electronic Publication.