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Self-identification and empathy modulate error-related brain activity during the observation of penalty shots between friend and foe

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The ability to detect and process errors made by others plays an important role in many social contexts. The capacity to process errors is typically found to rely on sites in the medial frontal cortex. However, it remains to be determined whether responses at these sites are driven primarily by action errors themselves or by the affective consequences normally associated with their commission. Using an experimental paradigm that disentangles action errors and the valence of their affective consequences, we demonstrate that sites in the medial frontal cortex (MFC), including the ventral anterior cingulate cortex (vACC) and pre-supplementary motor area (pre-SMA), respond to action errors independent of the valence of their consequences. The strength of this response was negatively correlated with the empathic concern subscale of the Interpersonal Reactivity Index. We also demonstrate a main effect of self-identification by showing that errors committed by friends and foes elicited significantly different BOLD responses in a separate region of the middle anterior cingulate cortex (mACC). These results suggest that the way we look at others plays a critical role in determining patterns of brain activation during error observation. These findings may have important implications for general theories of error processing.

Keywords: self-identification; error; reward; empathy; MFC

INTRODUCTION

The ability to recognize our own errors and their consequences, and to use this information to modify our future behaviors, is important for many forms of learning ranging from the acquisition of basic motor skills to the more sophisticated refinement of complex social and interpersonal abilities. Neuroscientific investigations conducted over the last two decades have provided converging evidence that sites in the medial frontal cortex (MFC) are critically involved in error processing (see Ridderinkhof *et al.*, 2004 for review). For example, data from a number of experiments indicate that action execution errors typically result in a negative deflection in event-related brain potentials (ERP) at a latency of ~100 ms (Falkenstein *et al.*, 1991; Gehring *et al.*, 1993). Source localization of this event-related negativity (ERN), as well as data from fMRI experiments, suggest that sites in the MFC form the brain basis of this error-processing mechanism (Holroyd and Coles, 2002; Ridderinkhof *et al.*, 2004 for meta-analysis; Holroyd *et al.*, 2005; Kennerley *et al.*, 2006). Additionally, a feedback-related negativity (FRN), thought to be distinct from the ERN (Gehring and Willoughby, 2004) can be observed

following negative feedback. This signal has a similar scalp distribution to the ERN but occurs at a longer latency (~250 ms) (Miltner *et al.*, 1997). Critically, areas within the MFC have also been shown to be responsive to *observation* of errors committed by others (Van Schie *et al.*, 2004; De Bruijn *et al.*, submitted for publication).

While the general functional basis of error processing is largely agreed upon, most experiments conducted to date have defined errors in a very narrow, and indeed problematic way. In each of the experiments cited above the *commission* or *observation* of an action error was perceived as a negative event, i.e. errors resulted in worse performance, decreased monetary rewards or both. While the reason for this association is obvious, self-generated errors committed in the real world are usually associated with negative affective consequences, it renders the resulting MFC activations difficult to interpret in light of recent theories of MFC activity. Currently, researchers have linked MFC activity to both action errors and the negative affective consequences associated with their commission (Miltner *et al.*, 1997; Holroyd and Coles, 2002; Nieuwenhuis *et al.*, 2004). One may pose the question, does activation of the MFC result from the execution/observation of action errors *per se*, the negative affective consequences which typically follow such events, or both? An additional limitation of contemporary error-execution paradigms is that the results are not necessarily

Received 15 January 2008; Accepted 1 August 2008

Advance Access publication 20 September 2008

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useful for understanding observed errors committed in a social context. In such situations, the affective consequences of an observed error can be either positive or negative depending on who commits the error.

In the present experiment, we tried to separate out these two confounding factors by creating a design in which, in the one case, observed action errors would have negative affective consequences, whereas in the other case, similar errors would have positive affective consequences. More specifically, our experiment uses the idea of socially constructed realities to provide a framework in which to investigate error processing. It has been suggested that, through social interactions, people continuously define and redefine their subjective realities (Macionis and Plummer, 2002). One way in which we do this is by forming attachments to groups based on defining concepts such as nationality, family or gender. Indeed, scientists have attempted to quantify the extent to which we identify with such groups. This tendency has been termed 'self identification'. Research on this topic suggests that, to the extent that we identify with a given group we tend to adopt their views, goals and interpretation of the world (cf. Wann and Branscombe, 1993; Troop and Wright, 2001; Wann *et al.*, 2001). For example, it is likely that members of Allied Nations reacted to reports of D-day with a smile whereas members of Axis nations probably reacted with a frown. Other examples of self-identification are readily found in the domain of sports where mistakes of an opponent (team) are typically received with much enthusiasm, whereas similar mistakes of a team member generally result a negative response or evaluation. Typically, whereas for self generated errors, affective consequences are generally negative, for observed errors the evaluation largely depends on the context and whether you do or do not self-identify with the person making the mistake. While it is easy to see how identification with others could introduce very strong and specific biases in behavior, it is currently unclear how such behavioral biases might be supported neurally.

In order to determine whether the MFC is mainly activated by the affective component that typically accompanies errors or to the error *per se*, irrespective of the emotional consequence, we conducted an action observation experiment in which full brain fMRI was recorded at 3 T while strong Dutch and German soccer fans watched virtual penalty shootouts between their national team (friend) and a rival team (foe). Our primary hypothesis was that observation of action errors would elicit more MFC activity than goals, regardless of the valence of the associated psychological consequences. This would argue for a functional role of the MFC in the processing action errors, irrespective of context and the emotional consequences for the observer. The second hypothesis, however, predicts that error processing in the MFC is mainly a reflection of the negative results that usually accompany action errors. In the latter case MFC would need to be activated differentially to action errors committed by an opponent (foe) and a preferred own team (friend).

Table 1 Sample questions from the questionnaires used in the experiment.

Measure	Sample Question
IRI-PT	I try to look at everybody's side of a disagreement before I make a decision.
IRI-FS	After seeing a play or movie, I have felt as though I were one of the characters.
IRI-EC	I believe there are two sides to every question and try to look at them both.
IRI-PD	In emergency situations, I feel apprehensive and ill at ease.
SFQ	I view myself as a soccer fan.
SSIS	How big a fan of the Dutch soccer team would you say you are?
Love	How much do you love the Dutch/German soccer team.
Dislike	How much do you dislike the German/Dutch soccer team.

PT = Perspective Taking Subscale, FS = Fantasy Subscale, EC = Empathic Concern Subscale, PD = Personal Distress Subscale, SFQ = Sports Fandom Questionnaire. Participants were asked how much they loved and disliked their and the opponent team.

These questions and hypotheses are important to emerging theories of observational learning as well as joint action which posit a critical reliance on our ability to distinguish correct from incorrect behavior in order to adjust future actions to avoid possible negative affective consequences already experienced by another. In order to better understand the functional role of the MFC in error processing and possible differences that exist between individuals in this respect, we included questionnaires to investigate whether differences in MFC activation would be correlated with measures of empathy and self identification (Table 1). Empathy was assessed using the Interpersonal Reactivity Index (IRI), a 28 item questionnaire which contains four seven-item subscales designed to measure four facets of empathy (Davis, 1980). These include perspective taking (tendency to adopt the viewpoint of others), empathic concern (tendency to experience compassion), personal distress (tendency to experience discomfort in response to distress experienced by others) and fantasy (tendency to imagine oneself in fictional situations). The perspective taking and fantasy subscales are designed to measure the nonaffective, cognitive aspects of empathy and the empathic concern and personal distress scale assess the emotional aspects of empathy (Davis *et al.*, 1994; Alterman *et al.*, 2003; Lawrence *et al.*, 2006; Rankin *et al.*, 2006). We assessed self identification using the Sport Spectator Identification Scale (SSIS) which we modified to test the extent to which Dutch participants were fans of the Dutch national soccer team and German participants were fans of the German national soccer team.

MATERIALS AND METHODS

Subjects

A total of 22 participants (19–43 years old, mean age 24 years, one female, 21 male, two left-handed, 17 Dutch fans, five German fans) participated in the fMRI experiment. Because events were coded relative to the fandom of the

participants (e.g. a Dutch player is a friend of a Dutch fan but a foe of a German fan and vice versa), whether a subject was a Dutch or German fan was not a confounding factor. All participants were healthy adults (self-report) and gave written informed consent according to the institutional guidelines set forth by the local ethics committee (CMO region Arnhem-Nijmegen, the Netherlands) prior to the experiment. Subjects were compensated at the rate of 10 Euros per hour for their participation.

Stimuli

Video clips of individual penalty shots were recorded during penalty shootouts made using the XBOX 360 version of the 2006 FIFA (Fédération Internationale de Football Association) World Cup soccer game (Electronic Art Nederland B.V., Hoensbroek, the Netherlands). Average duration of each penalty shot was 5 s. A coaxial cable connected the Xbox 360 to the ASUS AGP-V3800Pro V31.40H graphics card of a standard computer running on Microsoft Windows 2000, transferring the video-sync and video without audio through a composite-video signal. The video was digitally recorded on the computer with ASUS digital VCR 2.5, using a resolution of 720×480 pixels. Every penalty shot was converted to an AVI video clip using EZ Video Converter 1.2, with the original frame rate and Ligos Indeo Video 5.11 video codec. Only players who were on the Dutch and German national teams during the actual World Cup 2006 were included. All clips were made using the same virtual stadium at the same time of day and in identical weather conditions. Additionally, shots were matched across teams for shot angle and direction in which the keeper moved.

Clip selection

A total of five participants (19–24 years old; one female, one left-handed) participated in a separate experiment, to judge clarity of results of the clips. Participants were shown 470 candidate video clips (selected on the basis of technical realism from a pool of 600 original clips by a certified soccer referee). While seated in a chair behind a table, subjects watched the clips on a computer screen from a distance of 80 cm, with the screen subtending the same visual angle as in the fMRI setting. Participants rated the video clips on clarity of results, using a 3-point Likert scale (1 = goal, 2 = miss, 3 = unclear). These data were used to select only video clips with an unambiguously clear result (either a goal or a miss) for use in the fMRI experiment. After the pilot study, 35 goals and 35 misses were selected for each of the two teams (the Netherlands, Germany), matching them across teams in terms of shot angles and direction in which the keeper moved. The video clips were then divided into two games between Germany and The Netherlands. Each game consisted of seven rounds of penalty shootouts between the two teams, resulting in a winner per round and a winner per game. To avoid predictability, the clips were arranged in

different scenarios in which we varied total number of kicks in which the shootout was decided (6–14), duration of shootout rounds ($M = 1.67$ min, $s.d. = 0.43$), beginning team, and last team to shoot and whether a round would end on the basis of a goal or a miss.

Procedure

Prior to scanning, subjects completed questionnaires assessing handedness, team identification with their national soccer team (SSIS-Voetbal, an 8-point Likert scale, based on the SSIS; Wann and Branscombe, 1993), soccer fandom [SFQ-Voetbal, an 8-point Likert scale, adapted from the Sport Fandom Questionnaire (SFQ; Wann *et al.*, 2001)] and general empathy (a 5-point Likert scale and Dutch translation of the IRI; Davis, 1980). Following scanning, subjects completed an exit questionnaire in which they reported their team preferences by ordinal ranking the teams [from most (1) to least (4) liked] and reported the degree to which they liked and disliked each of the teams (scale of 1–100). Results were analyzed with SPSS, version 15.

All data was acquired during a single fMRI scanning session which lasted approximately 1.5 h ($M = 77.8$ min., $s.d. = 1.6$ min.). Video stimuli were presented using a projector and viewed by subjects lying in the scanner bed through a custom made mirror (Figure 1). All stimuli were delivered using Presentation software version 9.90 (Neurobehavioral Systems, Davis, CA, USA) run on a Dell Workstation (Austin, TX, USA). Subjects were instructed to concentrate on the video clips while in the scanner. Following 20% of trials, subjects were queried concerning the outcome of the previously viewed penalty shot. The response screen contained a green square on the right side

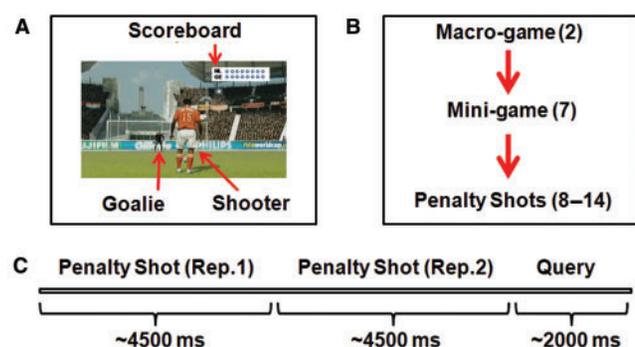


Fig. 1 (A) Frame capture taken from the beginning of one of the penalty shot videos illustrating the perspective from which actions were viewed. The scoreboard in the upper right quadrant was updated with green (goal) and red (miss) circles in the appropriate rows following each shot. (B) Illustration of the general structure of the scanning run. Participants viewed two macro-games between the Dutch and German teams. Each macro-game consisted of seven mini-games. Between mini-games, participants were updated on the overall score between the Netherlands and Germany. Each mini-game was similar in structure to an actual penalty-shootout with the winner being decided based on current FIFA guidelines (see Methods section). (C) Timecourse of a single penalty shootout within a mini-game. Notably, each clip was shown twice to ensure participants could accurately categorize misses and goals. Queries concerning the outcome (miss or goal?) followed 20% of the trials.

and a red square on the left side, or vice versa, where green symbolized 'goal' and red symbolized 'miss'. Subjects responded with an fMRI compatible gamepad using either the left or right index finger depending on the result of the video and the location of the red and green squares. Each of the two macro-games started with a Start clip (35 s), showing the stadium and the lineup of both teams and ended with a cheering clip (20 s), showing the winning team cheering and the losing team grieving. Each macro-game was introduced by a text screen indicating the number of the game (1–4) and the teams playing (Netherlands–Germany, Germany–Netherlands). Within each macro-game, each of the seven penalty shootouts were introduced by a text screen indicating the number of the game (1–7) and the current number of penalty shootouts won by each team. The shootout then proceeded in the following manner. A video of a player of team A taking a shot on goal was played two times in a row (duration = 10 s). This was followed, in 20% of the trials by a quiz regarding the outcome of the observed action (duration = 2 s). The same sequence of events was repeated, in this case featuring a player of team B taking the penalty kick. This procedure repeated until a winner was established. Following the standard FIFA regulations for penalty shootouts, teams took turns in taking penalty kicks, until each team had taken five kicks. In the case that one team scored more goals than the other could possibly reach with all of their remaining kicks (e.g. 3-0 after three kicks each), the shootout ended. If however, at the end of five kicks both teams had scored an equal number of goals (e.g. 4-4), the shootout continued with rounds of one kick until one side scored and the other missed. A scoreboard indicating the progress of the teams within a shootout round was overlaid in the upper right quadrant of the shootout clips. The order of macro-games and penalty shootouts were randomized, as was the selection of individual clips within the penalty shootouts (although, the sequence of goals and misses within each penalty shootout was predetermined based on the final score). The end of each of the macro-games was marked by presentation of the cheering clip followed by a text screen indicating which team had won the macro-game. All text screens were presented in the native language of the participant. Brain signal measured during observation of penalty shots was subsequently entered into SPM2 for analysis.

Design

The results of an observed clip (Goal, Miss), Team (Friend, Foe) and Self-Identification as measured by an adapted version of the SSIS (mean SSIS scores; Wann and Branscombe, 1993) administered prior to fMRI scanning were treated as within-subjects variables. Soccer fandom as measured by an adaptation of the SFQ (mean SFQ scores; Wann *et al.*, 2001) and empathy as measured by the IRI (mean IRI scores; Davis, 1980) were also measured. Based on the results of the SSIS, we were able to assign the videos within the

shootouts as Friend or Foe. Differential anterior cingulate cortex (ACC) activity was considered the primary dependent variable of interest.

fMRI data acquisition

All imaging data was collected at the F.C. Donders Centre for Cognitive Neuroimaging (Nijmegen, The Netherlands). Functional images were acquired on a Trio 3T whole-body MR scanner (Siemens, Erlangen, Germany) using an ascending slice acquisition sequence and a birdcage head coil (TR = 2.50 s, TE = 35 ms, 90° flip-angle, 34 axial slices, slice-matrix size = 64 × 64, slice thickness = 3 mm, slice gap = 0.5 mm, FOV = 22.4 mm, voxel size = 3.5 × 3.5 × 3.5 mm). A single scanning block lasted ~80 min, depending on the reaction times of the participants ($M = 78.25$ min, $s.d. = 2.29$). Following echo planar image (EPI) acquisition, a T₁-weighted 3D MPRAGE sequence (volume TR = 1960 ms, TE = 4.43 ms, 8° flip-angle, 176 coronal slices, slice-matrix size = 256 × 208, slice thickness = 1.0 mm, voxel size = 1 × 1 × 1 mm) was acquired.

fMRI data analysis

Functional data were preprocessed and analyzed using SPM2 (<http://www.fil.ion.ucl.ac.uk/spm>). All functional data were first corrected for motion artifacts using the bilinear interpolation method and coregistered with the high resolution T₂-weighted anatomical image. Images were then normalized to the Montreal Neurological Institute (MNI) template with a resolution of 2 × 2 × 2 mm, and smoothed in three dimensions using a 6 × 6 × 6 mm Gaussian kernel. The following events were modeled: Goal_Friend, Miss_Friend, Goal_Foe, Miss_Foe. In general, these events were modeled in terms of the actual videos of penalty shots viewed by the participants. The precise temporal window over these video events differed depending on which contrasts were analyzed. In the first analysis, events were modeled as the entire time during which videos of soccer shots (both repetitions) were played in a given condition. This broad model was used in contrasts designed to compare activity during general observation of the self-identified and nonself-identified teams (e.g. Friend > Foe and Foe > Friend). In the second analysis, events were modeled as the second half of the first repetition of each movie. This portion of the movie included the outcome (error/goal) and was designed to achieve better signal strength in areas related to error observation. This second, more focused model was used in comparisons of BOLD signal relating to error and reward processes. In all cases, brain responses were first modeled separately for individual subjects using the general linear model and subsequently entered into random effects analyses using SPM2. The data was high-pass filtered to remove potential unwanted effects of scanner drift. This potential confound was further addressed by ensuring that events of interest (misses and goals) were equally likely to occur both early and late in the scanning session. In the second-level analysis, contrasts

were created according to the logic of the hypotheses described in the Introduction section. Based on previous research, we restricted our error processing region of interest to the medial frontal cortex. Initial analysis of the fMRI data revealed that, in general, activation in the ACC was significantly higher when viewing foes as compared to friends (see Discussion section). For this reason, we avoided comparisons in which BOLD signal during Friend and Foe were directly compared without a baseline (i.e. Goal_Foe, Goal_Friend, etc.). Instead, we investigated ACC activation during processing of errors using an intersection analysis. Using a technique adopted in previous research (Newman-Norlund *et al.*, 2007) we calculated the intersection of statistical parametric maps for (Miss_Foe–Goal_Foe) and (Miss_Friend–Goal_Friend) to localize brain areas in which BOLD signal was related to observation of misses independent of the affective consequences and the intersection of (Goal_Foe–Miss_Foe) and (Miss_Friend–Goal_Friend) to localize brain areas in which BOLD signal was related to the affective consequences independent of action outcome. Cluster sizes adopted to correct for multiple comparisons were based on voxels in EPI space. Individual comparisons in these intersections were thresholded at $P < 0.01$, 5-voxel extent, so that the resulting intersection had a chance of $P < 0.001$ of occurring by chance. We adopted a threshold of $P < 0.001$ uncorrected, 5-voxel extent for activations in the contrasts designed to localize MFC sites in which misses elicited greater activation when committed by either friends or foes (e.g. [MISS_{FRIEND}–GOAL_{FRIEND}]–[MISS_{FOE}–GOAL_{FOE}], and the reverse contrast). Such thresholds are justified in light of the fact that we had specific *a priori* hypotheses concerning activation in the medial frontal cortex. Taken together with the fact that we find strong correlations between MFC activations and subscales of the IRI, it is unlikely these activations are false positives (Type I errors). All reported activations falling outside the MFC were minimally significant at $P < 0.001$ uncorrected, 10-voxel extent, which is more typically adopted for whole brain analyses in the absence of specific predictions. Coordinates in MNI space were converted into Talairach space using the nonlinear method of C.M. Lacadie and colleagues (submitted for publication). All regression analyses reported in the current article were conducted using the first eigen-variate which were extracted from the second-level analyses models (random effects models, SPM.mat) using the VOI toolbox in SPM2. Here, we report bivariate Pearson correlations between eigen-variate and the IRI (and subscales when appropriate) and SSIS.

RESULTS

Behavioral results

The mean ranking of the teams according to the exit form was Friend ($M = 1.00$, $s.d. = 0.00$) and Foe, ($M = 2.00$, $s.d. = 0.94$). In order to test whether fans strongly liked

Table 2 Minimum, maximum, mean value and standard deviations for questionnaires used in the current experiment.

Measure	Minimum	Maximum	Mean	Standard Deviation
IRI-PT	2.14	4.43	3.48	0.67
IRI-FS	2.00	4.57	3.44	0.65
IRI-EC	2.14	4.29	3.38	0.54
IRI-PD	1.13	4.00	2.41	0.54
SFQ	2.00	8.00	5.62	1.67
SSIS	3.13	7.13	4.91	1.10
Love-friend	20.00	100	86.40	16.62
Dislike-friend	1.00	30.00	5.08	7.70
Love-foe	1.00	70.00	25.72	22.28
Dislike-foe	1.00	100.00	42.00	35.78

their own teams and disliked the opposition teams we performed two separate repeated measures ANOVAs on the scores of love for and dislike of the teams, as measured by the exit forms. A significant difference was found in how much subjects loved the teams (Huynh–Feldt Epsilon-corrected $F_{2,78,58.33} = 49.10$, $P < 0.001$). Results of the Helmert contrasts indicated that subjects loved their own team (Friend) more than the other team (Foe) ($F_{1,21} = 118.24$, $P < 0.001$). Similarly, a significant difference was found in how much subjects disliked the teams (Huynh–Feldt Epsilon-corrected $F_{2,16,45.43} = 12.95$, $P < 0.001$), with dislike scores for foes being significantly higher than those for other teams ($F_{1,21} = 9.06$, $P < 0.01$) (Table 2). Bivariate Pearson's correlations between the questionnaires are also reported (Table 3).

Accuracy and reaction time data obtained from the forced choice (Goal–Miss) questions which followed 20% of the trials were subjected to statistical analysis in SPSS. A repeated measures ANOVA using accuracy as the dependent variable, team as within-subjects variable and empathy subscales as covariates revealed a nonsignificant main effects of Team (Huynh–Feldt Epsilon-corrected $F_{1,71,25.69} = 0.66$, $P = 0.66$) and empathy subscales (Huynh–Feldt Epsilon-corrected $F_{1,15} < 0.71$, $P > 0.41$) and no significant interaction effects between Team \times empathy subscales (Huynh–Feldt Epsilon-corrected $F_{1,71,25.69} < 2.34$, $P > 0.12$). Similarly, when using reaction times as the independent variable, the main effects of Team (Huynh–Feldt Epsilon-corrected $F_{1,59,27.08} = 0.44$, $P = 0.60$) and empathy subscales (Huynh–Feldt Epsilon-corrected $F_{1,17} < 0.66$, $P > 0.43$), as well as all interaction terms were insignificant (Huynh–Feldt Epsilon-corrected $F_{1,59,27.08} < .337$, $P > .64$).

fMRI results

To distinguish between theories of MFC function based on error observation and their consequences we first determined brain areas evincing greater signal strength during observation of errors as compared to observation of goals. First, we calculated the intersection ($(MISS_{FRIEND} - GOAL_{FRIEND}) \cap (MISS_{FOE} - GOAL_{FOE})$), with results from

Table 3 Pearson correlations between various measures used in the current experiment. Significant correlations (2-tailed, $P < .05$) are shown in bold.

Measure	Value	IRI-EC	IRI-PT	IRI-FS	IRI-PD	SSIS	Love(FR)	Dislike(FR)	Love(FO)
IRI-EC	Pear. Corr.	1	—	—	—	—	—	—	—
	Sig (2-tail)	—	—	—	—	—	—	—	—
IRI-PT	Pear. Corr.	0.504	1	—	—	—	—	—	—
	Sig (2-tail)	0.010	—	—	—	—	—	—	—
IRI-FS	Pear. Corr.	0.304	−0.097	1	—	—	—	—	—
	Sig (2-tail)	0.139	0.645	—	—	—	—	—	—
IRI-PD	Pear. Corr.	0.278	0.178	0.273	1	—	—	—	—
	Sig (2-tail)	0.178	0.394	0.187	—	—	—	—	—
SSIS	Pear. Corr.	0.013	−0.121	−0.032	0.113	1	—	—	—
	Sig (2-tail)	0.953	0.583	0.885	0.609	—	—	—	—
Love(FR)	Pear. Corr.	0.100	0.057	0.044	−0.103	0.059	1	—	—
	Sig (2-tail)	0.643	0.792	0.839	0.632	0.804	—	—	—
Dislike(FR)	Pear. Corr.	−0.122	−0.154	0.115	0.090	−0.314	−0.032	1	—
	Sig (2-tail)	0.571	0.473	0.594	0.676	0.177	0.860	—	—
Love(FO)	Pear. Corr.	−0.457	−0.228	−0.262	−0.330	−0.418	−0.112	0.537	1
	Sig (2-tail)	0.025	0.285	0.216	0.115	0.066	0.563	0.006	—
Dislike(FO)	Pear. Corr.	0.374	0.063	0.233	0.376	0.457	0.364	0.057	−0.450
	Sig (2-tail)	0.071	0.789	0.273	0.070	0.043	0.074	0.787	0.024

FO = foe,

each individual comparison thresholded at $P < 0.01$ uncorrected, 10 voxels (see fMRI data analysis section). This test revealed that BOLD signal in the right anterior cingulate cortex (vACC: Talairach coordinates [10, 33, −5]) and left pre-supplementary motor area (pre-SMA): Talairach coordinates [−6, 29, 39], was significantly correlated with observation of action errors (Figure 2) independent of the psychological consequences of their observation. Activation in these areas was also significant in the comparison MISS_{ALL}–GOAL_{ALL}, further corroborating their involvement in processing of observed errors. In order to test whether error-related activity in these areas was correlated with our social measures, individual scores on the IRI and SSIS were regressed against individual fMRI results in the MISS_{ALL}–GOAL_{ALL} contrast. BOLD signal at the vACC site identified in the intersection analysis contrast was significantly predicted by scores on the empathic concern subscale of the IRI. Specifically, BOLD signal negatively covaried with empathic concern $B = -0.544$, $P = 0.009$. Collapsed across the Friend/Foe dimension, activity in the pre-SMA site identified in this comparison was significantly and negatively correlated with the empathic concern subscale of the IRI, $B = -0.580$, $P = 0.005$. When tested separately for Friend and Foe we found that pre-SMA response to misses committed by friends covaried significantly with empathic concern ($B = -0.639$, $P = 0.001$), whereas pre-SMA response to misses committed by foes did not ($B = -0.386$, $P > 0.05$). Activity at other sites found active in the MISS_{ALL}–GOAL_{ALL} comparison (Table 4) were not significantly correlated with any subscales of the IRI.

Notably, activity in this contrast at these two MFC sites was not significantly correlated with the self-identification scores obtained from the SSIS (vACC, $B = -0.194$, $P = 0.388$; pre-SMA, $B = -0.140$, $P = 0.533$). In order to test for areas responding differentially to observed errors as a function of

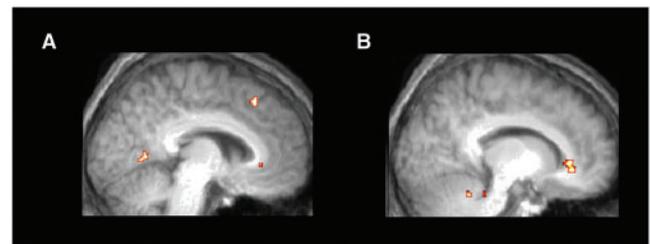


Fig. 2 Medial frontal sites at which BOLD signal was found to be significantly different in the contrast Misses–Goals, independent of fandom ($P_{\text{conjunction}} < .0001$ uncorrected, 10-voxel extent). (A) pre-SMA site (Talairach coordinates [−6, 29, 39]) (B) ventral anterior cingulate cortex site (Talairach coordinates [10, 33, −5]). Results are overlaid on the average normalized brain of the 23 participants.

the broader categorical metric of self-identification, we compared miss-related activity for friends to miss-related activity for foes using the contrast ($[\text{MISS}_{\text{FRIEND}} - \text{GOAL}_{\text{FRIEND}}] - [\text{MISS}_{\text{FOE}} - \text{GOAL}_{\text{FOE}}]$). A single site in the left anterior cingulate cortex (Talairach coordinates [−13, 34, 13]) [dorsal to the vACC site reported above, and referred to in this article as middle anterior cingulate cortex (mACC)] showed increased BOLD signal for observation of errors committed by friends relative to errors committed by foes, $P < 0.005$ uncorrected, 10-voxel extent (Figure 3, Table 4). The size of this effect was positively correlated with individuals' scores on the personal distress subscale of the IRI, $B = 0.552$, $P = 0.008$ (Figure 4, Table 4). The reverse contrast, ($[\text{MISS}_{\text{FOE}} - \text{GOAL}_{\text{FOE}}] - [\text{MISS}_{\text{FRIEND}} - \text{GOAL}_{\text{FRIEND}}]$), did not reveal any areas in MFC that were more active for errors committed by foes relative to those committed by friends.

In order to isolate areas in the MFC showing greater activation following observed actions (of any sort) with negative affective consequences we calculated the intersection ($\text{GOAL}_{\text{FOE}} - \text{MISS}_{\text{FOE}} \cap (\text{MISS}_{\text{FRIEND}} - \text{GOAL}_{\text{FRIEND}})$).

A similar conjunction of the reverse contrasts, ($\text{MISS}_{\text{FOE}} - \text{GOAL}_{\text{FOE}} \cap (\text{GOAL}_{\text{FRIEND}} - \text{MISS}_{\text{FRIEND}})$) was used to localize brain areas associated with positive affective consequences of observed actions. No significant voxels survived

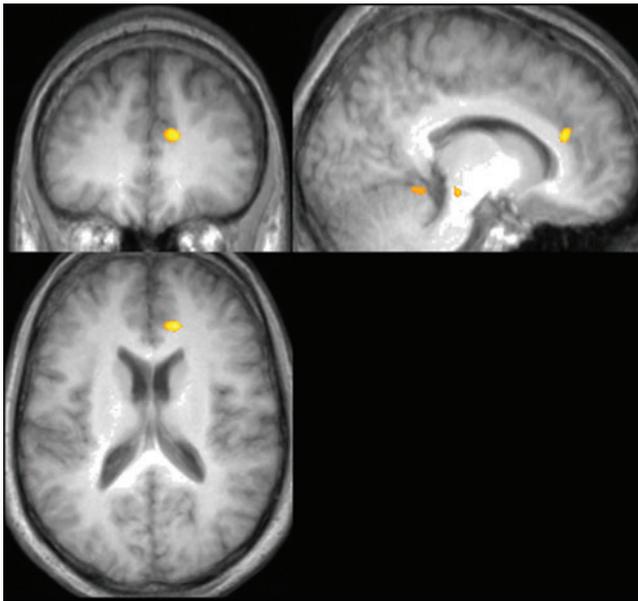


Fig. 3 Results from the contrast ($\text{MISS}_{\text{FRIEND}} - \text{GOAL}_{\text{FRIEND}} - (\text{MISS}_{\text{Foe}} - \text{GOAL}_{\text{Foe}})$, $P < .005$ uncorrected (for illustration purposes, see Table 4 for exact P -values), revealed a site in the left dorsal anterior cingulate cortex (Talairach coordinates $[-13, 34, 13]$), where response to errors was significantly greater when observing friends vs foes. The size of the difference in this contrast was positively correlated with the personal distress subscale of the IRI. Results are overlaid on the average normalized brain of the 23 participants.

these intersection analyses, even when the most lenient significance threshold ($P < 0.05$ uncorrected, 3-voxel extent) was adopted, suggesting that the MFC was not modulated by the affective consequences of error observation.

Additional contrasts were examined to characterize differences in BOLD signal associated with observation of players (collapsed across successful and unsuccessful penalty shots) with which participants either did or did not self-identify. A random effects analysis of activity in the contrast ($\text{Friend}_{\text{ALL}} - \text{Foe}_{\text{ALL}}$) revealed significant activations at sites in the bilateral fusiform gyrus and the right inferior frontal gyrus extending into the border with ventral premotor cortex, $P < 0.001$ uncorrected, 10-voxel extent (Figure 5, Table 4).

DISCUSSION

The primary goal of the current experiment was to assess the role of medial prefrontal areas in the processing of errors and their affective consequences independent of one another. Two sites in the medial frontal cortex, vACC and pre-SMA, responded to the observation of errors made by friend and foe regardless of the valence of the affective consequences associated with these actions. BOLD signal recorded at both of these sites during error observation was significantly correlated with participants' scores on the empathic concern subscale of the IRI. Although error-related activity at these sites did not correlate with our continuous measure of self-identification, an effect of this variable was seen in the differential mACC activity in response to observing friends (as opposed to foes) commit an error. These results have important implications for theoretical

Table 4 Table of brain activations in comparisons of interest used to address hypotheses in the current experiment. All coordinates are for peak values in a cluster and are reported in Talairach space.

Brain Area	z-score	p.unc.	size	x	y	z
$\text{MISS}_{\text{ALL}} - \text{GOAL}_{\text{ALL}}$						
TPJ	3.73	<.001	26	63	-39	29
IFG (p.oper.)	3.60	<.001	51	-43	39	-13
aITG	3.57	<.001	12	36	6	-19
thalamus	3.54	<.001	10	-6	-12	-6
putamen	3.42	<.001	12	11	-10	0
pre-SMA	2.62	=.004	5	-6	29	39
vACC	3.14	=.001	84	10	33	-5
$\text{MISS}_{\text{FRIEND}} - \text{GOAL}_{\text{FRIEND}} - [\text{MISS}_{\text{FOE}} - \text{GOAL}_{\text{FOE}}]$						
thalamus	3.80	<.001	78	-4	-8	0
aITG	3.80	<.001	18	-42	-13	-21
mACC	3.58	<.001	7	-13	34	13
hippocampus	3.55	<.001	16	21	-27	-13
$\text{Friend}_{\text{ALL}} - \text{Foe}_{\text{ALL}}$						
fusiform gyrus	4.17	<.001	1000	-38	-74	-9
fusiform gyrus	3.68	<.001	269	41	-55	-9
IFG (p.oper.)	3.32	<.001	28	40	9	21

Results were thresholded at $P < 0.001$, uncorrected for multiple comparisons, minimum cluster size of 10. Values in bold represent instances in which P -values greater than or equal to .001 and/or cluster sizes smaller than 10 voxels were considered significant based on *a priori* predictions. TPJ, temporoparietal junction; IFG (p.oper.), inferior frontal gyrus, pars opercularis; aITG, anterior inferior temporal gyrus; vACC, ventral anterior cingulate cortex; mACC, middle anterior cingulate cortex; IPL, inferior parietal lobe, SMG, supramarginal gyrus.

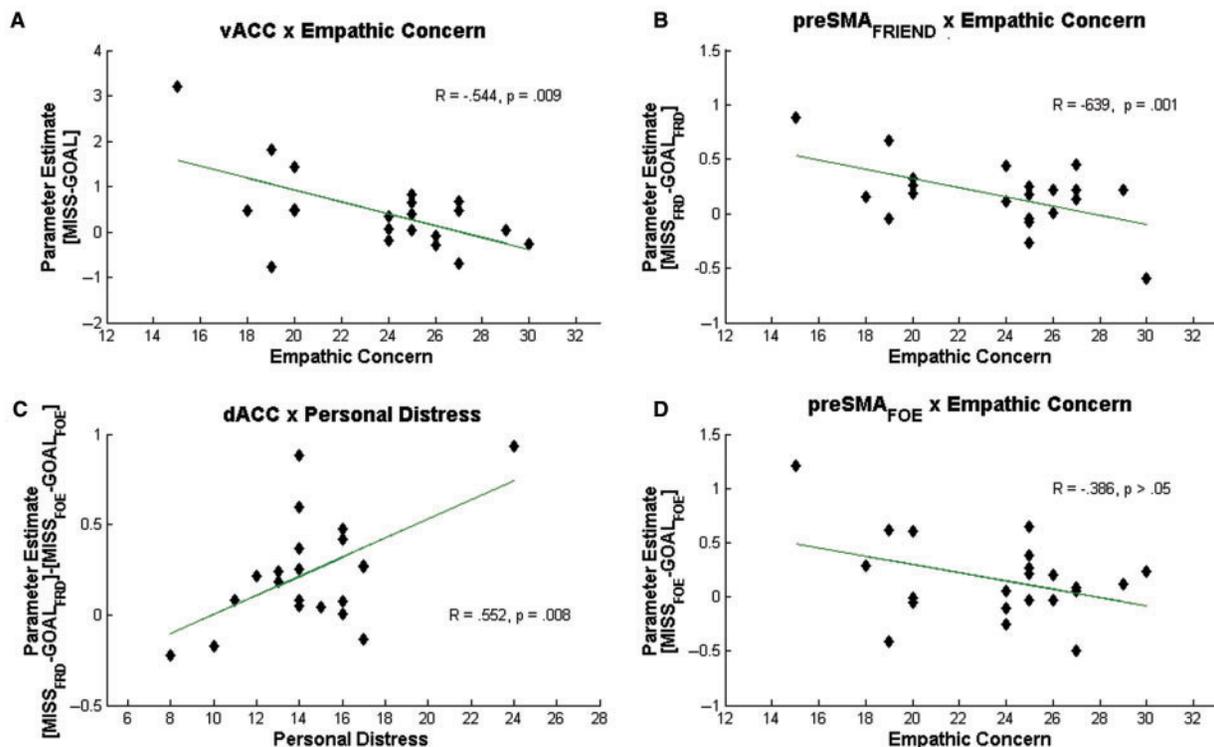


Fig. 4 Correlations between BOLD signal at MFC sites and subscales of the IRI. (A) Difference in BOLD response to errors in vACC (Talairach coordinates [10, 33, -5]) was negatively correlated with scores on the empathic concern subscale of the IRI. (B) Differences in BOLD response to errors committed by friends vs foes in dorsol anterior cingulate cortex (dACC) (Talairach coordinates [-13, 34, 13]) were positively correlated with personal distress subscores of the IRI. (C and D) Error-related activity was negatively correlated with pre-SMA (Talairach coordinates [-6, 29, 39]) activity for friends but not for foes.

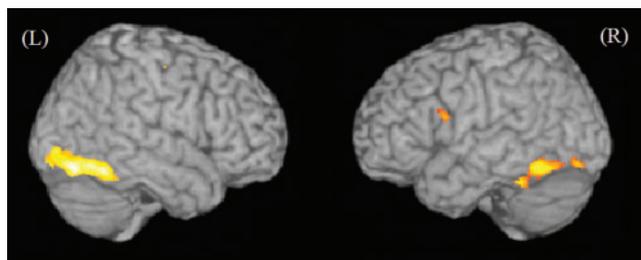


Fig. 5 Figure showing bilateral fusiform gyrus and right inferior frontal gyrus (pars opercularis) associated with the contrast Friend_{ALL} > Foe_{ALL}, $P < .001$ uncorrected, 10-voxel extent.

discussions concerning the role of MFC in the processing of errors and negative feedback which can best be understood by examining their relation to earlier research on mental representations and empathy.

Error observation, social learning and pre-SMA

In the current experiment pre-SMA activity associated with the observation of action errors was not modulated by the valence of the consequences. In a recent fMRI experiment conducted by De Bruijn and colleagues (submitted for publication) participants observed what was ostensibly another person (but actually a computer mimicking the behavior of a real participant) make errors in a simple computer game in which they were required to precisely lineup a

moving triangle with a stationary target of varying size. Comparison of brain activity associated with observation of errors to brain activity associated with observation of correct trials revealed signal difference at a pre-SMA site precisely overlapping with the area reported in the current experiment. Activation in the area around BA 32/6/8 has often been reported in studies in which participants actually commit errors (for a review see Ridderinkhof *et al.*, 2004). Importantly, Ridderinkhof and colleagues showed that this area was not only activated following response errors, but also following pre-response conflict, decision uncertainty and negative feedback. These findings have led to the recent interpretation that the posterior MFC signals the need to change behavior in order to optimize future outcomes (Ullsperger *et al.*, 2004). Interestingly, the current study shows that the same area is also activated by the observation of errors, in the absence of a requirement for behavioral adjustments from the observer. As such, the current findings are in line with a recent ERP study demonstrating an ERN in response to errors made by others (Van Schie *et al.*, 2004). One may argue/speculate that the pre-SMA activations in response to observed errors may help to predict future performance and may thus play a role in observation based learning. However, additional research is needed to clarify the precise role of pre-SMA in error processing and its relationship to observation based learning.

Errors and empathy in the vACC

Brain activity at the vACC site ($z < 2$) was also found to be associated with error observation in the current experiment. This site is not typically considered an error processing region *per se*, but rather is believed to be involved in empathy and emotional aspects of cognition (Bush *et al.*, 2000; Jackson *et al.*, 2006). In general, the attribution of such a role is consistent with the current results which suggest that differences in vACC signal associated with observation of errors were significantly modulated by affective (i.e. empathy) rather than cognitive components of error processing. This idea is further corroborated by experiments involving emotion processing which show modulation of activity at similar sites by autonomous and visceral aspects of emotion (Bush *et al.*, 2000; Koski and Paus, 2000; Paus, 2001) as opposed to the analytical/dispassionate processing of errors.

The dissociation between cognitive and affective aspects of error processing is furthermore illustrated by subpopulations showing abnormalities in ACC activity, such as obsessive-compulsive disorder (OCD) patients. In these individuals, the ACC has been found to be hyperactive at rest, during symptom provocation, and after commission of errors in cognitive tasks (Ursu *et al.*, 2003). Using an error commission paradigm, Fitzgerald and colleagues (2005) found that OCD patients showed higher error-related activity in vACC sites ($z < -6$) which were nearly overlapping with the vACC region associated with error observation in the present study. These authors suggest that, while OCD patients may be as sensitive to errors as healthy controls (hence, no difference in dorso-caudal ACC and pre-SMA activity), that subsequent affective responses to these errors may be of a quantitatively different nature. Based on these findings, vACC activity might reflect an affective component of error processing consistent with a recent meta-analysis of neuroimaging studies of emotion showing greater activity in the vACC for responses to aversive stimuli (Wager *et al.* 2003), as well as fMRI and ERP studies implicating the vACC in affective responses to errors (Kiehl *et al.*, 2000; Luu *et al.*, 2000a, b; Luu *et al.*, 2003; Luu and Pederson, 2004).

Self-identification and medial ACC

One of the main predictions of the current experiment was that the MFC's response to errors should be modulated by the social construct of self-identification. Although we found no significant correlations between brain activity and SSIS scores, activity in medial ACC was greater during observation of errors committed by friends than by foes. This suggests that, at a more discrete level, self-identification does modulate error-related brain activity. Our results suggest that the mechanism behind this effect may be related to individual differences in empathy as measured by the IRI. Specifically, the size of this difference was positively correlated with participants' scores on the personal distress subscale of the IRI, which is thought to measure the egocentric emotional reactivity and anxiety of an individual in response

to observed negative experiences of others. This finding is consistent with results from a recent fMRI experiment by Lawrence and colleagues (2006). These researchers found an area of anterior cingulate cortex (Talairach coordinates: $[-14, 26, 15]$), close to the area found in the present experiment (Talairach coordinates: $[-13, 34, 13]$), in which BOLD signal was significantly positively correlated with personal distress and negatively correlated with measures of social skills. According to Lawrence and colleagues, increased blood flow at this anterior cingulate site may represent participants' attempts to regulate their own autonomic arousal. This theory is based on the fact that activations at similar ACC sites have been reported in relation to the representation and modulation of states of autonomic arousal (Frith and Frith, 2003). In addition, as the personal distress scale is a measure of *self-oriented* negative emotional experience (Joireman *et al.*, 2002; Guarino *et al.*, 2007; Tangney *et al.*, 2007) this positive correlation between personal distress scores and size of difference between mACC activation following errors by friend compared to errors by foe does fit with our suggestion that self-identification is at play here. Observation of errors committed by friends (persons with whom the observer is likely to share a common goal) in the current experiment likely elicited greater personal distress and possibly greater attempts to regulate this response in our participants.

Observation of friends

Another indication of the discrete level at which self-identification was at play, was the greater brain activity during observation of actions made by friends as compared to those made by foes. Two sites of activation were associated with viewing players (in general) with whom the participant self-identified, namely the fusiform gyrus and inferior frontal gyrus (pars opercularis). BOLD signal was greater in these areas during perception of Friends in comparison to Foes. Activity in the fusiform gyrus has been traditionally associated with responses to human faces (Puce *et al.* 1996; Kanwisher *et al.* 1997; Haxby *et al.*, 2000; Kanwisher and Yodel, 2006 for review). It has also been shown that BOLD signal in this area may be modulated by familiarity of faces, although these results are less consistent. Some experiments have shown greater activation for familiar faces *vs* unfamiliar ones (Lehmann *et al.*, 2004; Avidan and Behrman, 2005) while others have shown the reverse effect (Rossion *et al.*, 2003) or no difference at all (Eger *et al.*, 2005; Pourtois *et al.*, 2005). The finding in the current experiment could be due to the participants' higher familiarity with faces on their national teams. Importantly, the fusiform gyrus has been shown to respond not only to faces, but also to the perception of whole body movements (Peelen and Downing, 2004). While the movements of players in the game were designed to appear realistic, moves from individual players were not recorded and built into individual Dutch and German player models. Thus, the relatively greater response of the fusiform

gyrus when viewing friends was likely not related to perception of familiar player movements, but rather to the familiar appearance (e.g. facial characteristics, build and team colors) of the soccer players. This finding is important because it is consistent with the idea that virtual soccer avatars in the video game were perceived as being familiar persons as opposed to completely novel actors. This finding supports the idea that use of virtual reality avatars may be a viable method for studying brain correlates of social observation and in this way contributes to ongoing debates concerning the use of virtual reality in psychology (Tarr and Warren, 2002; Sanchez-Vives and Slater, 2005).

In addition to the fusiform gyrus, the right pars opercularis was also activated to a greater extent when viewing friends as compared to foes. Various researchers have suggested that the mirror neuron system (MNS) plays a critical role in the simulation of other persons' movements during action observation in a variety of contexts (Fadiga and Craighero, 2005; Molnar-Szakacs *et al.*, 2006). Critically, such MNS mediated simulation appears to be greatest when the actor is perceived as maximally similar to the observer, e.g. biological stimuli typically activate the MNS, while robotic stimuli do not (Tai *et al.*, 2004). And observation of movements made by animals (perhaps because such movements do not belong to the observer's motor repertoire) does not drive the MNS in the same manner as observation of human movements (Buccino *et al.*, 2004). The current results are consistent with the idea that the human MNS responds maximally to actions perceived as being made by similar others in that the right pars opercularis was maximally responsive when viewing players with which the participant self-identified. Because action kinematics were identical in friend and foe conditions, differences in BOLD signal are not likely due to differences based on the biological characteristics or the actors or on any experience the participants may have had with such movements. In general, this result suggests that the response of the right anterior MNS is modulated by top down processing, such as the context in which an action is embedded. This conclusion is consistent with recent data demonstrating modulation of right inferior frontal gyrus (IFG) activation by contextual manipulation. In a recent experiment, this area was found to be preferentially activated during the preparation and execution of complementary actions, e.g. actions coordinated with another person (Newman-Norlund *et al.*, 2007). This activity may have reflected the recognition of an action and the calculation of an appropriate motor response based on the social context in which the action was embedded. Of course, the participants in the current experiment were not calculating motor responses based on the observed actions. These results could be reconciled by modifying the role assigned to the right IFG by other researchers. One possibility is that this area is responsible for a more general process of integrating actions of self and other in situations where the actions of the other are judged as

important/salient to the observer, or where the actor and observer share similar goals. It must also be noted that differences in attention to various aspects of the complex social scene (e.g. goalie, ball, goal or player) may have partially driven some of the current findings in the comparison of friend and foe. Although, the lack of significant reaction time or accuracy differences in the queries following 20% of trials argues against this. Future experiments might acquire more sensitive measures of attention, for example using eye-tracking.

Empathic concern

An important part of our endeavor involved the analysis of correlations between activity in our critical contrasts and the social measure of empathy. Our data demonstrate that right vACC and pre-SMA activity following observation of errors in general negatively covaried with participants' scores on the empathic concern subscale of the IRI. Empathic concern is operationalized as the tendency to experience feelings of sympathy and compassion for unfortunate others (Davis, 1980). Empathic concern is, in a manner of speaking, related to the experience of a complementary emotional response (e.g. feeling compassion for an injured child) as opposed to a mirroring of emotion. Importantly, this statement is fully consistent with studies showing a relationship between the MNS (Carr *et al.*, 2003; Cox, 2007) which has been implicated in the computation of both imitative *and complementary* responses (Newman-Norlund *et al.*, 2007, 2008) responses, and empathy.

Here, we propose that empathic concern can alternatively be interpreted as a disposition to regulate negative affect, both when trying to comfort an emotionally distressed other and in situations of intrapsychic emotional distress (Berne, 1964; Stewart and Joines, 1996; Hamers and Sebregts, 2002). In line with this view, recent theoretical papers (Decety and Lamm, 2006) discussing the functional anatomical basis of empathy concluded that empathy relies both on bottom-up information processing to allow the experience of emotions in another person, as well as the top-down capacity to regulate the perceived emotion. In the current experiment, empathic concern may have been involved in the regulation of evoked negative affect in response to an observed miss. Specifically, participants with a stronger disposition towards empathic concern may have been better able to regulate this experience of increased distress, resulting in attenuation of vACC activity during observation of misses, and hence a smaller BOLD signal difference following observation of errors compared to goals in general. Supporting evidence for this logic comes from Eisenberg *et al.* (2004), who demonstrated that individuals who can regulate their own emotions are more likely to experience empathy in social interactions with others. The same inverse relationship was also found in OCD patients who show limited capacity for empathic concern and have high negative affect as well as a hyperactive vACC during rest

and following commission of errors (DSM-IV; Shedler and Westen, 2004; Fitzgerald *et al.*, 2005). The distinction between bottom-up and top-down mechanisms in empathy may help to explain why empathic concern attenuated vACC activity following misses of both friend and foe, but only attenuated pre-SMA activity when observing friend. Furthermore, as we will explain below, the same model might also explain why, in previous studies, *positive* correlations between empathy and activation of the ACC were found.

In a recent fMRI study by Cheng *et al.* (2007), physicians who practice acupuncture were compared to naive participants while observing movies in which needles were being inserted into different body parts. While activation in dorsal anterior cingulate cortex was stronger for control subjects than for physicians and positively correlated with the amount of discomfort that subjects experienced, activation in vACC was stronger for physicians than controls and was negatively related to the amount of discomfort that participants experienced during video observation. These findings suggest that vACC is mainly involved in down-regulating the emotional response which was done more affectively by physicians than controls. Interestingly, similar results have been reported for the experience of social pain resulting from social exclusion from an online game (Eisenberger *et al.*, 2003). Furthermore, consistent with the complementary perspective in empathic concern (e.g. feeling compassion for an injured child), preliminary findings from our laboratory (Karremans *et al.*, unpublished data) indicate that reminding people of a secure attachment figure (e.g. his/her partner) reduces pain and stress-related brain activation in conditions of socially exclusion. These and other findings lead to the tantalizing hypothesis that physical and social pain may actually share a common neural and computational basis (Eisenberger and Lieberman, 2004). Coming back to the present study, the reason why vACC and pre-SMA, sites which often show coactivation during error processing tasks (Fitzgerald *et al.*, 2005; Mars *et al.*, 2005), show a different pattern of correlations with empathic concern may simply be because of the greater sensitivity of the vACC to the down-regulation of negative affect. That is, subjects with a high disposition towards empathic concern are better able to regulate their emotional response to the observation of a miss than subjects with lower empathic ability (Eisenberg *et al.*, 2004). Hence, a possible explanation why enhanced empathic concern may have attenuated pre-SMA activation to misses might be because down-regulation in the vACC spread to this more dorsal region of medial frontal cortex.

Lastly, we would like to address the apparent contradiction between the current findings and the previous research finding a positive correlation between empathic concern and activation in the ACC (e.g. Singer *et al.*, 2004). As already indicated, heightened empathy may either enhance the bottom-up properties of perceiving negative emotions in others, or support the top-down suppression of negative affect (cf. Decety and Lamm, 2006). It is well conceivable

that depending on the situation, the task or the nature of the stimulus (e.g. whether subjects have any sense of control) subjects may select different strategies for processing emotional content in others. This may influence the balance between bottom-up and top-down processes, which in turn will affect the direction of the relation between empathic concern and activation in the ACC. We hypothesize that in conditions that induce or allow subjects to select a regulatory strategy, empathic ability will correlate negatively with activation in vACC and possibly pre-SMA. On the other hand, when conditions demand a lack of control or emotional regulation, we should expect levels of empathic concern to correlate positively with activation in vACC and pre-SMA. This might be a topic of investigation for future studies.

Positive vs negative affective consequences

It must be noted that the conjunction analyses in which we attempted to isolate areas responsive to actions with either positive (goal of a friend and miss of an enemy) or negative affective consequences (miss of a friend and goal of an enemy) did not reveal any significant activations even when a very lenient threshold was adopted. One potential explanation for this lack of finding is that the affective value of misses made by the opposing team was not equal to the affective value of goals made by the favored team. This hypothesis is supported by research on gloating which suggests that for such an equivalence to be achieved, an individual must envy the position of the other team (cf. Shamay-Tsoory *et al.*, 2007). It is entirely possible that participants in the current experiment did not envy the foe team and this could account for the lack of a result in the conjunction analysis. Another possible explanation for this finding is that some effects were diluted by the inclusion of trials in which misses and goals were not interpreted as being particularly meaningful (for example, a goal or miss at the beginning of a mini-game vs the end of a mini-game). Previous literature has shown that the magnitude of an error does indeed affect the neural response (Holroyd *et al.*, 2004). Accordingly, future explorations of this sort might record physiological variables like heart rate and breathing, and use these to categorize events in terms of their affective value.

General conclusion

In the present experiment, the brain correlates of error observation were disentangled from the brain correlates of negative consequences typically associated with them. Our results indicate that sites in the MFC, including vACC and pre-SMA respond to observed errors similarly regardless of whether the error is interpreted as a positive or negative event, and that the strength of such responses was significantly modulated by participants' capacity for empathic concern. Our results also indicate that self-identification, at the most general level, impacts the brain's response to action observation in general (e.g. bilateral fusiform gyrus and

right pars opercularis), and observation of errors in particular (mACC). These results extend findings from previous literature on error observation using electro-encephalography (EEG) (van Schie *et al.*, 2004) and comment on theories of error processing in which the MFC is ascribed a central role. The ability to interact with and learn from the observation of conspecifics depends critically on our ability to represent them as distinct entities. The current experiment raises the tantalizing possibility that our own personal views of others may bias action monitoring systems in a powerful way. Future experiments might compare the neural basis of error observation in situations where learning is likely to be either beneficial or harmful. Also, experiments in which participants are allowed the opportunity to adjust their own behavioral plans based on observation of errors could further specify the dynamics of human error processing mechanisms. Insights provided by such experiments may have applications for theories which relate the perception and categorization of social entities (as friend or foe) to their influence on specific socio-cognitive processes.

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