How social is error observation? The neural mechanisms underlying the observation of human and machine errors

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Recently, it has been shown that the medial prefrontal cortex (MPFC) is involved in error execution as well as error observation. Based on this finding, it has been argued that recognizing each other's mistakes might rely on motor simulation. In the current functional magnetic resonance imaging (fMRI) study, we directly tested this hypothesis by investigating whether medial prefrontal activity in error observation is restricted to situations that enable simulation. To this aim, we compared brain activity related to the observation of errors that can be simulated (human errors) with brain activity related to errors that cannot be simulated (machine errors). We show that medial prefrontal activity is not only restricted to the observation of human errors but also occurs when observing errors of a machine. In addition, our data indicate that the MPFC reflects a domain general mechanism of monitoring violations of expectancies.

Keywords: error; action observation; medial prefrontal cortex; simulation

INTRODUCTION

To function appropriately in our social world, we constantly have to interpret each other's behaviour. By now, there is converging evidence that this interpretation relies on simulation processes. Moreover, it has been shown that we activate similar brain regions when we perform and observe actions (Rizzolatti *et al.*, 2001; Rizzolatti and Craighero, 2004; Iacoboni, 2005) or when we experience and observe other bodily states such as emotions (Wicker *et al.*, 2003), pain (Botvinick *et al.*, 2005; Lamm *et al.*, 2011) and touch (Keysers *et al.*, 2004). In sum, it seems that we rely on embodied simulation mechanisms to understand other's behaviour. Recently, it has been shown that the brain system involved in error commission, namely the medial prefrontal cortex (MPFC) (Ridderinkhof *et al.*, 2004; Ullsperger and von Cramon, 2004), is also activated when we observe other humans making errors (Shane *et al.*, 2008; de Bruijn *et al.*, 2009; Newman-Norlund *et al.*, 2009). This shared brain activity has led to the hypothesis that an analogous embodied simulation mechanism might be at hand at this more cognitive level, namely to understand each other's errors (van Schie *et al.*, 2004; Bates *et al.*, 2005; Bekkering *et al.*, 2009). Here, we investigate whether shared activation in brain areas involved in error commission and error observation necessarily rely on simulation. Logically, error simulation can only take place when we observe an error that we can make ourselves. Therefore, we compared the neural mechanisms involved in the observation of human errors (i.e. errors that we can simulate) and machine errors (i.e. errors that we cannot simulate). More precisely, we used functional brain imaging while participants observed daily life human–machine interactions that resulted in correct or erroneous outcomes. The cause for these errors could be 2-fold. First, the person caused the error by incorrectly operating the machine (human error). Second, the error could be caused by a malfunctioning of the machine (machine error). If MPFC activity is only present in the human error condition, this would imply that

simulation is necessary for the occurrence of MPFC activity in error observation, if on the other hand MPFC is also activated during the observation of machine errors, the role of this brain region in error observation should be considered more general. Further, implementing this paradigm allows us to identify other brain areas uniquely related to the observation of errors performed by biological agents compared with nonbiological agents.

METHODS

Participants

Twenty-three participants (19 females) participated in the experiment [mean age = 21.3 years, standard deviation (s.d.) = 2.2 years]. Four participants were excluded from the analysis due to motion artifact. All participants were paid €25 for their participation. They were all right handed as was measured by the Edinburgh Inventory (Oldfield, 1971). All participants gave written informed consent and had no history of neurological disorders. Ethical approval was given by the Medical Ethical Review Board of the Ghent University hospital.

Stimuli and design

The experiment was implemented using Presentation software (Neurobehavioral Systems, Albany, NY). Every trial consisted of a short movie, showing a daily situation of a human–machine interaction. All videos were rated by an independent group of participants before the functional magnetic resonance imaging (fMRI) experiment (see Supplementary Material for more details). Eight different situations were presented in the fMRI study (coffee machine, elevator, photocamera, electronic garage door, semi-automatic doors, vending machine, photocopier and digital clock). A complete description of our stimulus materials is shown in Figure 1 and Table 1. According to the characteristics of the human–machine interaction, three conditions were specified. First, the person could perform a correct action after which the machine would produce the correct outcome (CORRECT). For example, in the coffee machine situation, the person would press the correct button on the machine after which the machine would pour the coffee correctly into the cup. Second, the person could perform an incorrect action resulting in an incorrect outcome (HUMAN ERROR). In the example of the coffee machine, the person would press the button corresponding to two cups of coffee.
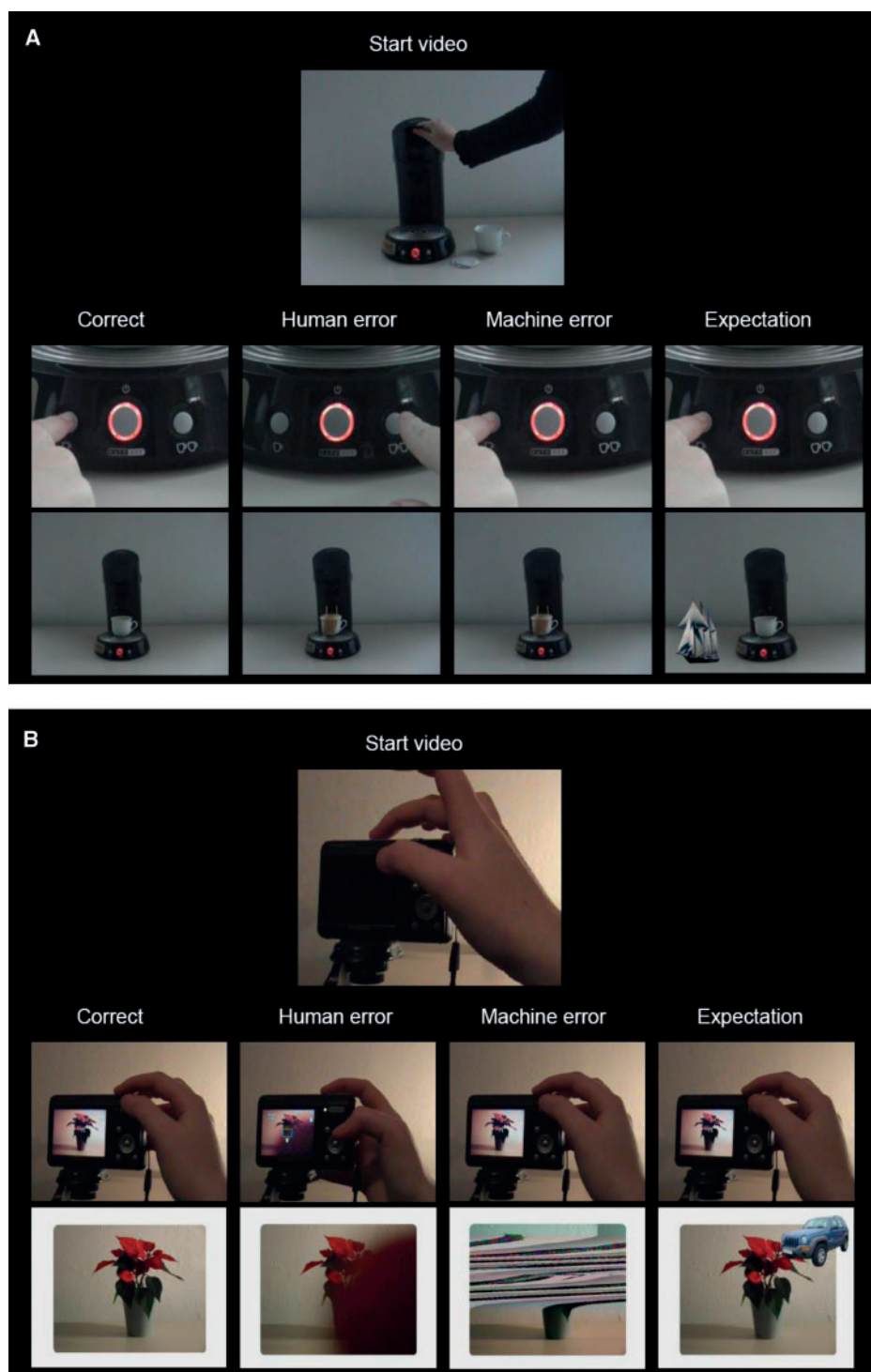
Fig. 1 Frames for start situation, moment of the action and moment of the outcome (from top to bottom) for four situations. (**A**) Coffee machine; (**B**) photocamera; (**C**) vending machine; (**D**) photocopier. For every situation the four conditions (correct, human error, machine error and expectation) are represented from left to right.

As a result, too much coffee is being poured into the cup and the coffee is spilled. Third, the person could perform a correct action, leading however to an incorrect outcome produced by the machine (MACHINE ERROR). Considering the above-mentioned example, the person would press the button for one cup of coffee, but nevertheless too much coffee is poured into the cup and again the coffee is spilled. See http://users.ugent.be/~cdesmet/materials.html for the video clips related to the coffee machine situation.

Human errors become apparent from the moment the person performs the incorrect action. The erroneous result of this action will thus be expected. Machine errors on the other hand are not caused by an incorrect human action. Therefore, these errors are not expected in the series of ongoing events. An additional difference between human errors and machine errors is thus the predictability of the erroneous outcome. However, because this problem is inherent to the characteristics of the errors (namely a machine error will always be unexpected,
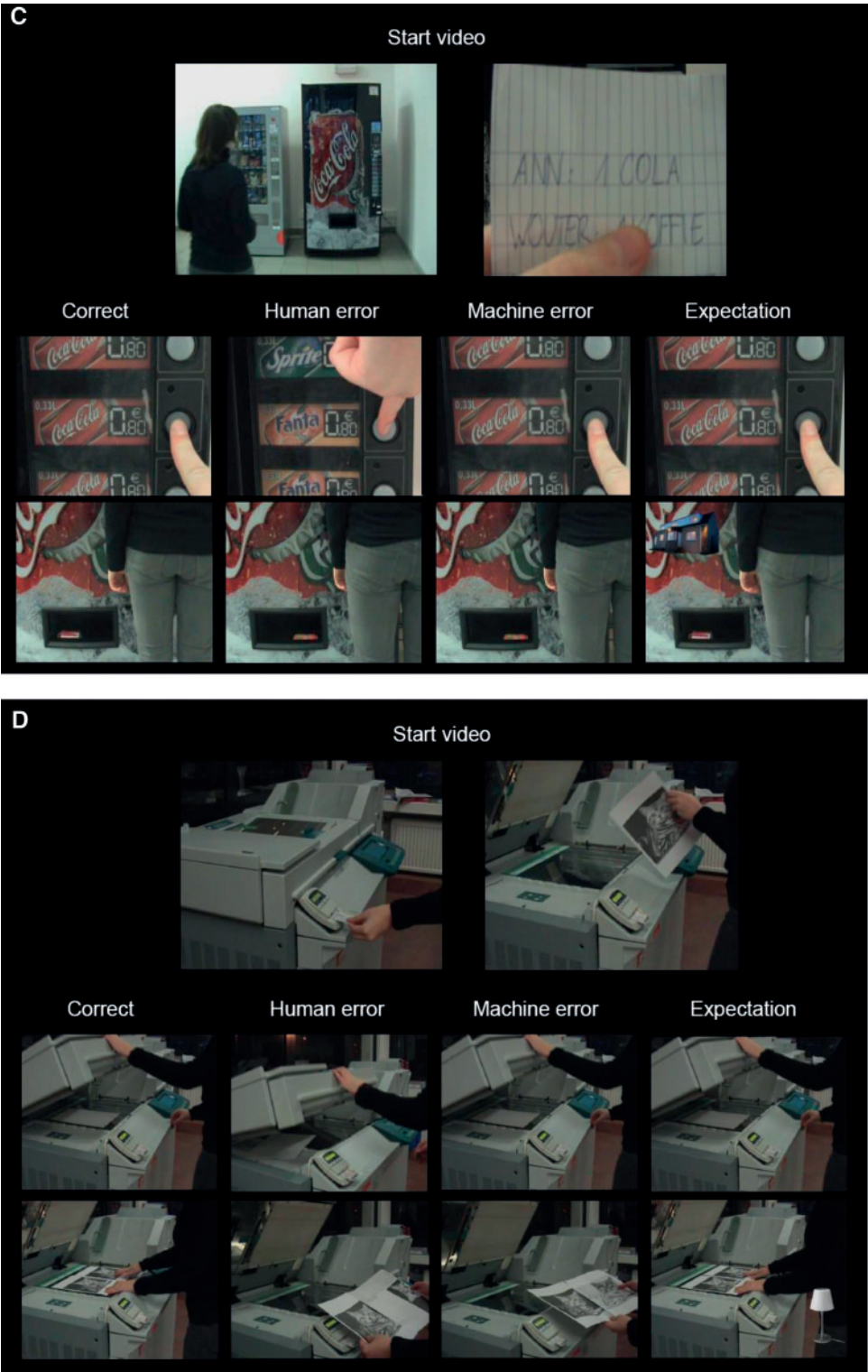
Fig. 1 Continued.

whereas a human error is the result of an incorrect action), we controlled for this issue by including an extra condition in which the correct action and outcome were presented but where an unexpected object, unrelated to the situation, appeared on the screen (EXPECTATION). In the above example, this would mean that there is an unrelated picture (e.g. a chair) presented in one of the quadrants of the screen at the moment the coffee is poured into the cup. Eight different objects were used in the eight different situations. Furthermore, over the whole experiment, the objects were presented equally often in each quadrant of the computer screen. The picture remained on the screen until the movie ended. If a difference in brain activity between human errors and machine errors can be explained by the unexpected nature of a machine error, we should also find this activity in the expectation condition.

Table 1 Description of the different moments (start video, moment of the action and moment of the outcome) for every condition (correct, human error, machine error and expectation) and for each situation

Situation	Start video	Correct	Human error	Machine error	Expectation
Coffee machine	Coffee machine is shown. Next to the machine are a coffee pad and an empty cup. Person approaches machine and positions pad and cup in the machine.	Person presses the button with a 'one-cup indicator'. (22) The coffee is poured into the cup until the cup is full. (33)	Person presses the button with a 'two-cup indicator'. (23) Coffee for two cups of coffee is poured into the cup. As a result, the coffee is spilled. (36)	Person presses the button with a 'one-cup indicator'. (22) Coffee for two cups of coffee is poured into the cup. As a result, the coffee is spilled. (36)	Person presses the button with a 'one-cup indicator'. (22) The coffee is poured into the cup until the cup is full and a picture of a ship is shown at the bottom left corner of the screen. (34)
Elevator	Person with suitcase approaches elevator and pushes button to call for the elevator. The elevator arrives and the person with the suitcase enters the elevator.	The elevator button is pushed. (22) The door of the elevator is closed. (27)	The suitcase is blocking the closure of the door. The person pushes the button to close the door. (10) The elevator door starts to close but pushes against the suitcase and opens again. (15)	The elevator button is pushed. (20) The elevator door closes but immediately opens again. (25)	The elevator button is pushed. (22) The door of the elevator is closed and a picture of a green bucket is presented at the right upper corner of the screen. (26)
Photocamera	A camera on a tripod is shown in front of a flower in a flowerpot. A hand approaches the camera and switches on the machine.	The button to take a picture is pressed. (16) The flower is correctly photographed as is shown by a printout of the picture. (18)	The button to take a picture is pressed but the person places a finger before the objective. (14) The flower is photographed but the finger also appears on the printout. (17)	The button to take a picture is pressed. (16) The flower is photographed but the printout shows a noise pattern instead of the flowerpot. (18)	The button to take a picture is pressed. (16) The flower is correctly photographed as is shown by the printout and a picture of a blue car is shown at the upper right corner of the screen. (18)
Electronic garage door	Person walks to a garage door and pulls out a paper from her trousers pocket. The paper says 'code: 4455'.	The person enters the correct code to open the garage door. (11) The garage door opens. (24)	The person enters the code '5566' instead of '4455'. (12) The garage door does not open. (19)	The person enters the correct code to open the garage door. (11) The garage door opens halfway and then closes again. (23)	The person enters the correct code to open the garage door. (11) The garage door opens and a picture of a black shoe is visible at the bottom right corner of the screen. (24)
Semi-automatic doors	Person walks to a badge reader next to the electronic sliding doors of the faculty building.	The person holds the correct badge 'admission card university Ghent' before the doors. (2) The doors open and the person enters the building. (4)	The person holds the wrong card (a bank card) before the badge reader. (2) The doors do not open. The person walks away. (4)	The person holds the correct badge 'admission card university Ghent' before the doors. (2) The doors do not open. The person walks away. (4)	The person holds the correct badge 'admission card university Ghent' before the doors. (2) The doors open, the person enters the building and a picture of a ninepin is shown at the upper right corner of the screen. (5)
Vending machine	Person approaches vending machine. She puts a coin in the machine and reads out a paper that says 'ANN: 1 COLA'.	The button for 'cola' is pushed. (20) One can of cola is delivered. Person takes out her change and the can. (25)	The button for 'fanta' is pushed. (20) One can of fanta is delivered. Person takes out her change and the can. (25)	The button for 'cola' is pushed. (20) One can of fanta is delivered. Person takes out her change and the can. (25)	The button for 'cola' is pushed. (20) One can of cola is delivered and a picture of a house is presented at the upper left corner of the screen. The person takes out her change and the can. (25)
Photocopier	Person approaches photocopier and places pay card in the machine. She holds an image of a cat.	The person places the image in the scanner part and pushes the copy button. (14) A copy of the image is printed and compared with the original image. (39)	The person places the image in the scanner part. However, half of the paper hangs out the scanner part. The copy button is pushed. (7) A copy of half the image is printed and compared with the original image. (28)	The person places the image in the scanner part and pushes the copy button. (11) A copy of the image is printed and compared. However, the colours of the image are inversed compared with the original image. (36)	The person places the image in the scanner part and pushes the copy button. (14) A copy of the image is printed and compared with the original image. A picture of a lamp is shown at the bottom right corner of the screen. (38)
Digital clock	A digital clock with a flickering display showing '0:00' is visible. Then a watch is shown with the hour (6:00).	The person sets the digital clock to 6.00. (16) The digital clock shows 6.00. (20)	The person sets the digital clock to 3.00. (18) The digital clock shows 3.00. (20)	The person sets the digital clock to 6.00. (17) The digital clock shows 3.00. (20)	The person sets the digital clock to 6.00. (16) The digital clock shows 6.00 and a picture of a chair is shown at the bottom left corner of the screen. (17)

The timing of the moment of the action and outcome are always reported in seconds between brackets.

There were three blocks of 32 unique trials (8 situations × 4 conditions), resulting in 96 experimental trials. The order of the 32 trials within each block was randomized for each block. The duration of each movie was dependent on the situation and the condition (mean duration = 28.22 s, s.d. = 9.50 s; for correct: 28.25 s, s.d. = 9.81 s; for human errors: 26.00 s, s.d. = 9.78 s; for machine errors: 29.50 s, s.d. = 9.50 s; for expectation: 28.63 s, s.d. = 9.84 s). However, for each situation, we constructed a video clip that was very similar for the four conditions (correct, human error, machine error and expectation), and only the crucial event was changed (e.g. the moment of the action). In this way, the movies belonging to the different conditions were kept as equal as possible. The moment of the action started on average 14.72 s

after the start of the video clip (for correct: 15.38 s, s.d. = 6.65 s; for human errors: 13.25 s, s.d. = 6.98 s; for machine errors: 14.88 s, s.d. = 6.60 s; for expectation: 15.38 s, s.d. = 6.65 s). The mean time at which the outcome took place was 22.75 s after the start of the video (for correct: 23.75 s, s.d. = 10.47; for human errors: 20.50 s, s.d. = 9.52; for machine errors: 23.38 s, s.d. = 10.28; for expectation: 23.38 s, s.d. = 10.31). The mean interval between both moments was 8.03 s (for correct: 8.38 s; for human errors: 7.25 s; for machine errors: 8.50 s; for expectation: 8.00 s). To make sure that participants paid attention to the videos, we occasionally asked a question about the previously presented video clip. Over the whole experiment, eight questions were asked. These questions were divided over the eight different situations and over the four conditions. The questions always comprised multiple choices of four possibilities. The questions were presented in white on a black background. The trials preceding a question were discarded from the analysis, resulting in 88 experimental trials.

Procedure

Participants were lying in the scanner while they attentively watched the movies. Each trial started with the presentation of a fixation cross for a duration of 200 ms, after which the movie started. The intertrial interval was varied in a pseudologarithmic fashion. Using steps of 300 ms, 50% of the trials used a jitter ranging from 200 to 1100 ms, 30% of the trials used a jitter ranging from 1400 to 2300 ms, and 20% of the trials used a jitter ranging from 2600 to 3500. The mean interval was 1250 ms. When a question was presented on the screen, participants had to respond by means of two response boxes that were placed on their upper legs. Responses were given with the index and middle fingers of each hand. The mapping of the responses to the different answers of the multiple choice question was indicated on the screen. A short break was inserted in the middle of the experiment.

fMRI methods

The experiment was carried out on a 3T scanner (Siemens Trio) using an 8-channel radiofrequency head coil. Subjects were positioned head first and supine in the magnet bore. First, 176 high-resolution anatomical images were acquired using a T1-weighted 3D MPRAGE sequence [repetition time (TR) = 2530 ms, echo time (TE) = 2.58 ms, image matrix = 256 × 256, field of view (FOV) = 220 mm, flip angle = 7°, slice thickness = 0.90 mm, voxel size = 0.9 × 0.86 × 0.86 mm (resized to 1 × 1 × 1 mm)]. Whole-brain functional images were collected using a T2*-weighted echo planar imaging (EPI) sequence, sensitive to BOLD contrast (TR = 2000 ms, TE = 35 ms, image matrix = 64 × 64, FOV = 224 mm, flip angle = 80°, slice thickness = 3.0 mm, distance factor = 17%, voxel size 3.5 × 3.5 × 3 mm, 30 axial slices). The amount of EPI images differed slightly per subject due to the self-paced initiation of trials where a question was imposed.

All data were analyzed using SPM5 (http://www.fil.ion.ucl.ac.uk/spm/software/spm5/). To account for T1 relaxation effects, each EPI sequence started with two dummy scans. First, all functional images were spatially realigned using rigid body transformation. After the realignment the images were slice time corrected using the first slice as a reference. The structural image of each subject was co-registered with their mean functional image. Further, all functional images were normalized to the Montreal Neurological Institute (Montreal, Quebec, Canada) T1 template. The images were resampled into 3.5 mm^3 voxels and spatially smoothed with a Gaussian kernel of 8 mm (full-width at half maximum). A high pass filter of 128 s was applied during fMRI data analysis. Statistical analyses were performed using the general linear model implemented in SPM5. We distinguished correct trials,

human error trials, machine error trials and expectation trials. Because human errors are defined at the moment of the action (the moment the button is pressed in the coffee machine situation) and machine errors at the moment of the outcome (the moment the coffee is spilled in the coffee machine situation), we defined both moments as separate regressors in the general linear model, resulting in 8 regressors (4 conditions × 2 moments). When comparing different conditions in the whole-brain contrasts, both moments (moment of the action and moment of the outcome) of one condition were always compared with both moments of the other condition. Both a canonical hemodynamic response function (HRF) and the first time derivative were modelled on these moments. We computed contrast images by comparing the parameter estimates for the regressors containing the canonical HRF. To account for residual movement effects, six regressors defining head movement were included in the model. A familywise error correction (FWE) was used with $P < 0.05$. All clusters containing more than five voxels were reported in the results section. First, we will describe three whole-brain contrasts revealing activation related to human errors, machine errors and the occurrence of unexpected events, respectively. Second, we performed a conjunction analysis on these three whole-brain contrasts. This conjunction analysis reveals which brain areas are commonly activated by the three selected brain contrasts applying a FWE correction with a threshold of $P < 0.05$. Further, we plotted the percent signal changes for the different conditions in the overlapping cluster in the medial frontal wall (peak coordinates = 6, 24, 57). The region of interest analysis was carried out using the MARSBAR toolbox constructed for SPM5 (Brett et al., 2002).

RESULTS

We computed whole-brain contrasts to examine brain activation related to human errors, machine errors and the occurrence of unexpected events. To this aim, we subtracted brain activity in the correct condition from that in the human error condition, the machine error condition and the expectation condition, respectively. The first part of the analysis focuses on MPFC activation (however for a complete list of activations for each contrast and for the conjunction analysis, Table 2). As expected, brain activation related to human errors was found in the MPFC. In particular, the activation was located in the presupplementary motor area (pre-SMA) (BA8, 6, 30, 57, $z = 6.24$). Very similar MPFC activation was also found for machine errors. As in the first contrast, the activation peak was located in the pre-SMA (BA8, 6, 24, 57, $z = 5.51$). Interestingly, the third contrast (subtracting correct situations from unexpected events) also revealed MPFC activation. Here, the activation cluster was even more extended than in the previously described contrasts. More precisely, a region stretching from the SMA (BA 6), over the pre-SMA (BA 8) into the rostral cingulate zone (RCZ, BA 32) was revealed (peak coordinates: −3, 18, 48, $z = 6.27$). The conclusions based on these results are 2-fold. First, the data suggest that the activation in the MPFC is not specific for the observation of human errors. Second, the MPFC activation is not uniquely related to the observations of errors but rather to the observation of a surprising or unexpected event. See Figure 2 for an overview of MPFC brain activation and Figure 3 for left and right cortical renderings.

Although the cause of the human error (i.e. the human incorrect action) can be simulated whereas the cause of the machine error (i.e. a malfunctioning of the machine) cannot be simulated, it is important to notice that all video clips entail predictive processes and simulation processes. First, from the start scene of the video a general goal can be predicted. For example, the view of the coffee machine will lead to the expectation of making/drinking a cup of coffee. At the moment of the action (erratic in the human error condition and correct in all other conditions), this goal can be violated (due to the erratic action in the

Table 2 MNI coordinates of whole-brain contrasts

	Peak coordinates	Z-score	Cluster size
Human error (human error−correct)			
MPFC (pre-SMA, BA8)	6, 30, 57	6.24	60
Right inferior frontal gyrus	54, 30, 0	6.68	239
Left inferior frontal gyrus	−60, 18, 15	5.45	53
Right precentral gyrus (premotor cortex)	30, −9, 57	4.85	7
Left inferior parietal lobe	−42, −42, 51	7.01	246
Right inferior parietal lobe	60, −48, 39	5.49	126
Left inferior parietal lobe	−60, −51, 36	5.10	36
rMTG (extending in the LOTC)	54, −66, 6	6.18	267
lMTG	−57, −57, 6	5.77	219
Machine error (machine error−correct)			
MPFC (pre-SMA, BA 8)	6, 24, 57	5.51	26
Right inferior frontal gyrus extending into the right anterior insula	54, 21, 9	5.93	126
Left inferior frontal gyrus	−54, 21, 12	4.88	13
Left anterior insula	−33, 24, 0	4.86	7
lMTG	−57, −57, 6	5.28	46
Expectation (expectation−correct)			
MPFC (pre-SMA + RCZ) + SMA	−3, 18, 48	6.27	428
Left inferior frontal gyrus + left anterior insula	−51, 15, −3	5.98	150
Right inferior frontal gyrus + right anterior insula	45, 18, 3	5.66	142
Left inferior frontal sulcus	−45, 6, 39	5.89	136
Left middle frontal gyrus	−39, 57, 12	5.31	36
Right middle frontal gyrus	27, 63, 24	4.93	21
Left inferior parietal lobe	−33, −60, 51	6.04	289
Right inferior parietal lobe	33, −60, 51	5.16	38
Precuneus	18, −78, 48	4.73	5
Fusiform gyrus	33, −51, −12	6.08	66
lMTG	−60, −54, 15	5.77	70
Right middle occipital gyrus	39, −84, 15	5.17	50
Left middle occipital gyrus	−33, −90, 9	5.14	19
Human versus Machine (human error−machine error)			
Right precentral gyrus (premotor cortex)	24, −6, 57	5.50	55
Left precentral gyrus (premotor cortex)	−21, −9, 60	5.63	49
Left PCG	−36, −36, 45	6.21	211
Right SPL	15, −54, 66	5.35	26
rMTG	54, −69, 9	5.21	40
lMTG	−42, −75, 9	6.82	160
Conjunction ((human error−correct) ∩ (machine error−correct) ∩ (expectation−correct)			
MPFC (pre-SMA, BA 8)	6, 24, 57	4.98	6
Right inferior frontal gyrus	51, 18, 6	5.09	12
lMTG	−57, −57, 9	5.05	15

Anatomical assignments were made using the Duvernoy's (1999) human brain atlas (although we use the term parietal lobe instead of parietal gyrus). The distinction between SMA/pre-SMA and RZC were made based on the description in Picard and Strick (1996).

human error condition) or fulfilled (due to the correct action in all other conditions) and the action can be simulated. Further, at the moment of the outcome the initial goal can be tested again. Moreover, the outcome can be in accordance with the goal (as is the case in the correct condition) or violate the goal (as is the case in the human error condition and the machine error condition). In addition, the outcome can be compared with the previously executed action. More specifically, the outcome can be expected based on the action (as is the case in the correct condition and the human error condition) or the outcome can violate the previous action (as is the case in the machine error condition). The moment of the action and the moment of the outcome thus form key moments in these violations or fulfilments of predictions. Keeping in mind our conclusion that MPFC activation might be related to the observation of unexpected events, it seems informative to describe the MPFC activation at these two time points for the different conditions. To this aim, we performed a signal change analysis in the part of the MPFC where the three previously described contrasts showed an overlap in activation. This overlap was defined by computing a conjunction null analysis on all three contrasts (pre-SMA, BA 8, peak coordinates = 6, 24, 57, z = 4.98, extent = 6, the whole of the activated region was taken for the percent signal change analysis). Note that the following statistics are not entirely orthogonal to the contrast used to define the region of interest, so they are

reported with the caveat that the data are not independent. Paired comparisons showed that when the action violated the initial goal the percent signal change was increased. Moreover, for human errors the percent signal change at the moment of the action was larger than the percent signal change at the moment of the action for the correct movie clip [$F(1,18) = 39.10$, $P < 0.001$], whereas the percent signal changes at the moment of the action for machine errors and the expectation condition did not differ from the percent signal change at the moment of the action for the correct condition (Fs < 1). Further, for all situations in which the outcome violated the initial goal, the percent signal change was increased compared with the situation where the outcome mapped the initial goal. More precisely, for machine errors and human errors, the percent signal change at the moment of the outcome was substantially larger than that of the correct condition at the moment of the outcome [machine errors: $F(1,18) = 47.42$, $P < 0.001$, human errors: $F(1,18) = 6.47$, $P < 0.05$]. In addition, machine errors at the moment of the outcome showed larger percent signal changes than human errors at the moment of the outcome, [$F(1,18) = 37.66$, $P < 0.001$]. This can be explained by the fact that at the moment of the outcome machine errors violate the previously executed action and the initial goal whereas for human errors the outcome does violate the initial goal but is in accordance with the previously executed action. This
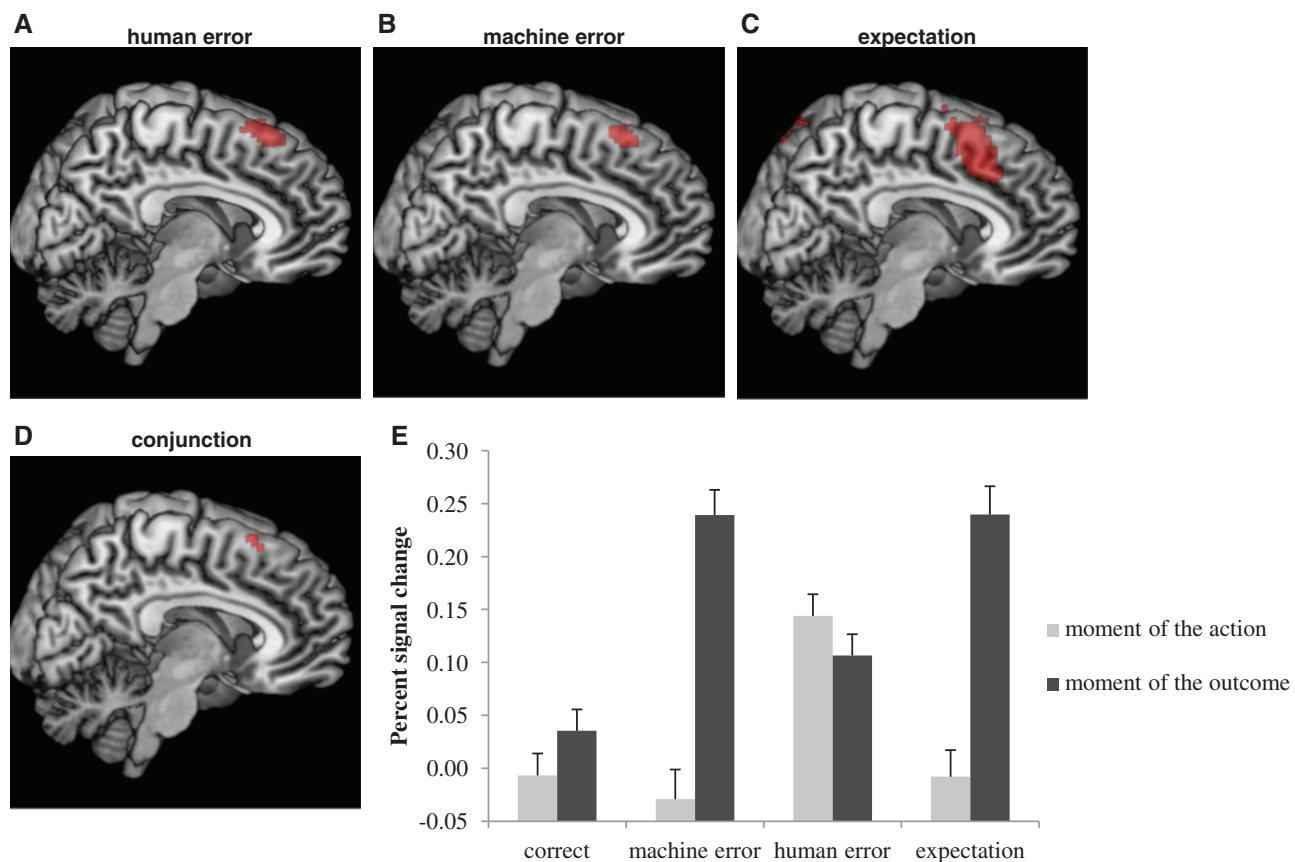
Fig. 2 Results of the fMRI analyses. For (**A**), (**B**) and (**C**), both moments (moment of the action and moment of the outcome) of one condition were compared with both moments of the other condition. Smoothed slices acquired via MRIcron are shown at x = 6. (**A**) Sagittal view of MPFC activity related to the contrast human errors–correct, MNI peak coordinates = 6, 30, 57. (**B**) Sagittal view of MPFC activity related to the contrast machine errors–correct, MNI peak coordinates = 6, 24, 57. (**C**) Sagittal view of MPFC activity related to the contrast expectation–correct, MNI peak coordinates = −3, 18, 48. (**D**) Brain activity related to the conjunction analysis performed on the contrasts specified in (**A**), (**B**) and (**C**) (A ∩ B ∩ C), MNI peak coordinates = 6, 24, 57. (**E**) Percent signal changes for the area obtained in the conjunction analysis (MNI peak coordinates = 6, 24, 57) for the correct, the human error, the machine error and the expectation condition at the moment of the action and the moment of the outcome.
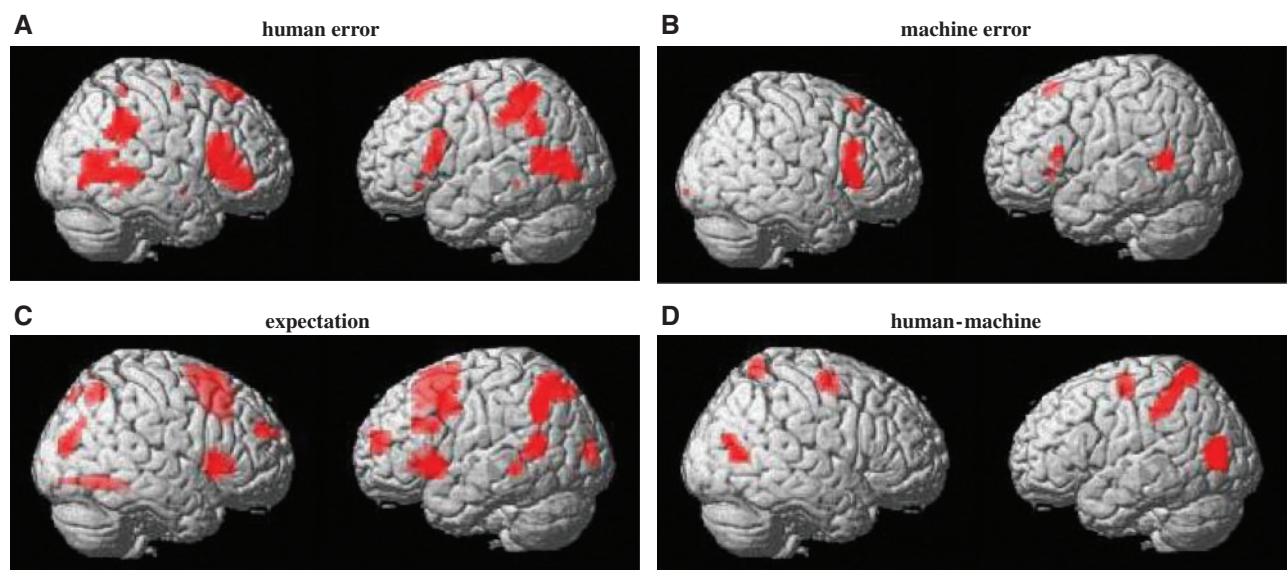

Fig. 3 Left and right cortical surface renderings for the contrasts. (**A**) Human errors–correct; (**B**) machine errors–correct; (**C**) expectation–correct; (**D**) human errors–machine errors.

latter explanation is also in line with the absence of a difference between the percent signal changes related to both moments for the human errors [$F(1,18) = 2.09$, $P = 0.17$]. Moreover, for human errors the percent signal changes represent the violation of the initial goal both for the moment of the action and for the moment of

the outcome. See Figure 2 for an overview of the percent signal changes.

Finally, we wanted to investigate whether there were other brain regions that distinguish between the observation of human errors and the observation of machine errors. Therefore, we directly

subtracted the brain activation related to the human error condition from the brain activation related to the machine error condition and vice versa. Again, we included both moments (moment of the action and moment of the outcome) in the contrasts. We found stronger activation for human than machine errors in the right and left dorsal premotor cortex (rPMC, 24, −6, 57, $z = 5.50$, lPMC, −21, −9, 60, $z = 5.63$), right superior parietal lobe (rSPL, 15, −54, 66, $z = 5.35$), left postcentral gyrus (lPCG, −36, 36, 45, $z = 6.21$) and activation in the left and right middle temporal gyrus (rMTG, 54, −69, 9, $z = 5.21$; lMTG, −42, −75, 9, $z = 6.82$). These latter clusters extended into the lateral occipitotemporal cortex (LOTC) and comprised the extrastriate body area (EBA) and the human MT+ complex (MT+) (Downing *et al.*, 2006; Weiner *et al.*, 2011). A complete list of activation related to the human error–machine error contrast is shown in Table 2. On the other hand, contrasting machine errors with human errors did not reveal any significant activation (see Figure 3 for an overview of brain activity).

DISCUSSION

To adapt our behaviour to the environment, it is not only crucial to detect our own errors but also to detect errors from others. Over the past decade, a number of studies have related MPFC to error observation processes (Shane *et al.*, 2008; de Bruijn *et al.*, 2009; Newman-Norlund *et al.*, 2009). That is, the brain area involved in error execution (for reviews see Ridderinkhof *et al.*, 2004; Ullsperger and von Cramon, 2004) is also involved in error observation. In this study, we investigated whether this shared brain activation was present in daily life contexts and whether this activation necessarily relies on simulation. In particular, we tested whether MPFC activity was only related to the detection of human errors or also to the detection of non-human errors. Further, we examined whether there were other brain areas outside the medial frontal wall that differentiated between the observation mechanisms of human and non-human errors.

Our study revealed three important results. First, our data clearly show that MPFC does not distinguish between the observation of human errors and the observation of machine errors. In other words, MPFC activation is not only related to errors that can be simulated. This highlights the general and non-social nature of the cognitive system that is responsible for the processing of observed errors. In addition, the most extensive activation in the MPFC was found when participants observed unexpected but non-erroneous events. This suggests that MPFC activation is related to a violation of expectancies of the observed events. This relates well with the fact that MPFC (and in particular pre-SMA) activity has been reported in oddball paradigms (Clark *et al.*, 2000; Ardekani *et al.*, 2002; Bubic *et al.*, 2009). Also recent studies in performance monitoring literature have indicated that MPFC might not only respond to errors or conflict but also might entail indeed a wider function by detecting salient events. For example Wessel *et al.* (2012) have shown similar MPFC activity for the execution of errors and the detection of novel events (see also Behrens *et al.*, 2007; Alexander and Brown, 2010; Jessup *et al.*, 2010; Hayden *et al.*, 2011). One can argue that even though the same brain area is involved in the observation of machine errors, human errors and unexpected events, this brain activation might have been triggered by different functional mechanisms. In other words, while our data show that motor simulation is not necessary to induce error-related brain activation in MPFC when observing errors, we cannot reject the possibility that simulation might have led to MPFC activation in the human error condition. However, one might wonder whether we need to speculate about the existence of a simulation system in human error observation, when a more general mechanism can explain the data as well.

Second, we found brain regions outside the medial prefrontal wall that distinguish between the observation of human errors and machine errors. Note that only the human action differed between these conditions (i.e. in the human error condition an incorrect action is performed whereas in the machine error condition the correct action is performed). First, subtracting human error activity from machine error activity did not reveal any significant brain activation. We can thus conclude that there are no specific brain regions involved in the processing of machine errors compared with human errors. However, when subtracting machine errors from human errors, we found activation extending in the LOTC including EBA and the human MT+ complex. These regions have been found to correlate with body-related visual perception (Downing *et al.*, 2006; Weiner *et al.*, 2011). In addition, the PMC and more specifically the frontal eye fields (FEF) were active. These areas are involved in visual attention (Donner *et al.*, 2002; Muggleton *et al.*, 2011). Finally, besides the areas involved in visual attentional and processing of complex visual information we found two sites of activation related to the action observation network (SPL and PCG). The SPL has been shown to be involved in body transformation processes and in action observation (Bonda *et al.*, 1995; Calvo-Merino *et al.*, 2005; Urgesi *et al.*, 2007). The PCG has been related to the somatosensory part of the action observation network (Keysers *et al.*, 2010; Turella *et al.*, 2011). The differential activation between human and machine errors did not elicit the classical motor simulation network (i.e. ventral premotor cortex, inferior frontal gyrus and inferior parietal lobe). However, the differential activation found in left SPL and PMC could be interpreted as evidence for reaching specific mirroring (Filimon *et al.*, 2007). Alternatively, the activation could be related to increased visual attention because they have been implicated in a dorsal attentional circuit (Corbetta and Shulman, 2002). In sum, it seems that the observation of human errors triggers additional brain regions compared with the observation of machine errors. However, further research is required to unravel the underlying cause of this activation pattern. Does the observation of a human error triggers specific simulation mechanisms compared with the observation of a machine error (as suggested by the reaching specific mirror activation) or does the observation of a human error involve more attention related processes when processing the observed behaviour compared with the observation of a machine error?

Third, we found that the observation of human errors in daily life situations evoke MPFC activity. Although there have been a number of studies investigating neural correlates of error observation, only few of these studies have addressed the observation of human errors in a daily context. Interestingly, the results obtained in these studies are not all univocal. Moreover, in contrast to earlier event related potential studies on error observation (Miltner *et al.*, 2004; van Schie *et al.*, 2004; Bates *et al.*, 2005), de Bruijn *et al.* (2007) failed to find an error related negativity component related to the observation of erroneous daily life actions. Instead, they observed a P300 component. Manthey *et al.* (2003) examined fMRI activity related to observed errors in daily situations. However, they did not report whether there was MPFC activity when comparing erroneous with correct actions. So far, only one fMRI study reported MPFC activation in relation to observed human errors in a daily context (Newman-Norlund *et al.*, 2009). Our data thus give further support for the role of MPFC in observing human errors in daily contexts.

To conclude, we found evidence for the role of the MPFC in error observation in daily life situations. However, this brain area is not only involved in the observation of human errors, but also rather in the observation of unexpected events. Further, we found an activation pattern solely dedicated to the observation of human errors.

Whether this activation reflects enhanced motor simulation or additional attentional processes is an open question.

SUPPLEMENTARY DATA

Supplementary data are available at *SCAN* online.

Conflict of Interest

None declared.

REFERENCES

Alexander, W.H., Brown, J.W. (2010). Computational models of performance monitoring and cognitive control. *Topics in Cognitive Science*, 2(4), 658–77.

Ardekani, B.A., Choi, S.J., Hossein-Zadeh, G.A., et al. (2002). Functional magnetic resonance imaging of brain activity in the visual oddball task. *Cognitive Brain Research*, 14(3), 347–56.

Bates, A.T., Patel, T.P., Liddle, P.F. (2005). External behavior monitoring mirrors internal behavior monitoring—error-related negativity for observed errors. *Journal of Psychophysiology*, 19(4), 281–8.

Behrens, T.E.J., Woolrich, M.W., Walton, M.E., Rushworth, M.F.S. (2007). Learning the value of information in an uncertain world. *Nature Neuroscience*, 10(9), 1214–21.

Bekkering, H., de Bruijn, E.R.A., Cuijpers, R.H., Newman-Norlund, R., van Schie, H.T., Meulenbroek, R. (2009). Joint action: neurocognitive mechanisms supporting human interaction. *Topics in Cognitive Science*, 1(2), 340–52.

Bonda, E., Petrides, M., Frey, S., Evans, A. (1995). Neural correlates of mental transformations of the body-in-space. *Proceedings of the National Academy of Sciences of the United States of America*, 92(24), 11180–4.

Botvinick, M., Jha, A.P., Bylsma, L.M., Fabian, S.A., Solomon, P.E., Prkachin, K.M. (2005). Viewing facial expressions of pain engages cortical areas involved in the direct experience of pain. *Neuroimage*, 25(1), 312–9.

Brett, M., Anton, J.L., Valabregue, R., Poline, J.B. (2002). Region of interest analysis using an SPM toolbox. *Abstract presented at the 8th International Conference on Functional Mapping of the Human Brain*, 2–6 June 2002, Sendai, Japan.

Bubic, A., von Cramon, D.Y., Jacobsen, T., Schroger, E., Schubotz, R.I. (2009). Violation of expectation: neural correlates reflect bases of prediction. *Journal of Cognitive Neuroscience*, 21(1), 155–68.

Calvo-Merino, B., Glaser, D.E., Grezes, J., Passingham, R.E., Haggard, P. (2005). Action observation and acquired motor skills: an fMRI study with expert dancers. *Cerebral Cortex*, 15(8), 1243–9.

Clark, V.P., Fannon, S., Lai, S., Benson, R., Bauer, L. (2000). Responses to rare visual target and distracter stimuli using event-related fMRI. *Journal of Neurophysiology*, 83(5), 3133–9.

Corbetta, M., Shulman, G.L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3(3), 201–15.

de Bruijn, E.R.A., Schubotz, R.I., Ullsperger, M. (2007). An event-related potential study on the observation of erroneous everyday actions. *Cognitive Affective & Behavioral Neuroscience*, 7(4), 278–85.

de Bruijn, E.R.A., de Lange, F.P., von Cramon, D.Y., Ullsperger, M. (2009). When errors are rewarding. *Journal of Neuroscience*, 29(39), 12183–6.

Donner, T.H., Kettermann, A., Diesch, E., Ostendorf, F., Villringer, A., Brandt, S.A. (2002). Visual feature and conjunction searches of equal difficulty engage only partially overlapping frontoparietal networks. *Neuroimage*, 15(1), 16–25.

Downing, P.E., Peelen, M.V., Wiggett, A.J., Tew, B.D. (2006). The role of the extrastriate body area in action perception. *Social Neuroscience*, 1(1), 52–62.

Duvernoy, H.M. (1999). *Human Brain Atlas* 2nd edn. Vienna, Austria: Springer-Verlag.

Filimon, F., Nelson, J.D., Hagler, D.J., Sereno, M.I. (2007). Human cortical representations for reaching: mirror neurons for execution, observation, and imagery. *Neuroimage*, 37, 1315–28.

Hayden, B.Y., Heilbronner, S.R., Pearson, J.M., Platt, M.L. (2011). Surprise signals in anterior cingulate cortex: neuronal encoding of unsigned reward prediction errors driving adjustment in behavior. *Journal of Neuroscience*, 31(11), 4178–87.

Iacoboni, M. (2005). Neural mechanisms of imitation. *Current Opinion in Neurobiology*, 15(6), 632–7.

Jessup, R.K., Busemeyer, J.R., Brown, J.W. (2010). Error effects in anterior cingulate cortex reverse when error likelihood is high. *Journal of Neuroscience*, 30(9), 3467–72.

Keysers, C., Wicker, B., Gazzola, V., Anton, J.L., Fogassi, L., Gallese, V. (2004). A touching sight: SII/PV activation during the observation and experience of touch. *Neuron*, 42(2), 335–46.

Keysers, C., Kaas, J.H., Gazzola, V. (2010). Somatosensation in social perception. *Nature Reviews Neuroscience*, 11(10), 726.

Lamm, C., Decety, J., Singer, T. (2011). Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. *Neuroimage*, 54(3), 2492–502.

Manthey, S., Schubotz, R.I., von Cramon, D.Y. (2003). Premotor cortex in observing erroneous action: an fMRI study. *Cognitive Brain Research*, 15(3), 296–307.

Miltner, W.H.R., Brauer, J., Hecht, H., Trippe, R., Coles, M.G.H. (2004). Parallel brain activity for self-generated and observed errors. In: Ullsperger, M., Falkenstein, M., editors. *Errors, Conflicts, and the Brain: Current Opinions on Performance Monitoring*. Leipzig, Germany: MPI of Cognitive Neuroscience, pp. 124–9.

Muggleton, N.G., Kalla, R., Juan, C.H., Walsh, V. (2011). Dissociating the contributions of human frontal eye fields and posterior parietal cortex to visual search. *Journal of Neurophysiology*, 105(6), 2891–6.

Newman-Norlund, R.D., Ganesh, S., van Schie, H.T., De Bruijn, E.R.A., Bekkering, H. (2009). Self-identification and empathy modulate error-related brain activity during the observation of penalty shots between friend and foe. *Social Cognitive and Affective Neuroscience*, 4(1), 10–22.

Oldfield, R.C. (1971). Assessment and analysis of handedness—Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113.

Picard, N., Strick, P.L. (1996). Motor areas of the medial wall: a review of their location and functional activation. *Cerebral Cortex*, 6, 342–53.

Ridderinkhof, K.R., Ullsperger, M., Crone, E.A., Nieuwenhuis, S. (2004). The role of the medial frontal cortex in cognitive control. *Science*, 306, 443–7.

Rizzolatti, G., Fogassi, L., Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, 2(9), 661–70.

Rizzolatti, G., Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169–92.

Shane, M.S., Stevens, M., Harenski, C.L., Kiehl, K.A. (2008). Neural correlates of the processing of another's mistakes: a possible underpinning for social and observational learning. *Neuroimage*, 42(1), 450–9.

Turella, L., Tubaldi, F., Erb, M., Grodd, W., Castiello, U. (2011). Object presence modulates activity within the somatosensory component of the action observation network. *Cerebral Cortex*, 22(3), 668–79.

Ullsperger, M., von Cramon, D.Y. (2004). Neuroimaging of performance monitoring: error detection and beyond. *Cortex*, 40, 593–604.

Urgesi, C., Calvo-Merino, B., Haggard, P., Aglioti, S.M. (2007). Transcranial magnetic stimulation reveals two cortical pathways for visual body processing. *Journal of Neuroscience*, 27(30), 8023–30.

van Schie, H.T., Mars, R.B., Coles, M.G.H., Bekkering, H. (2004). Modulation of activity in medial frontal and motor cortices during error observation. *Nature Neuroscience*, 7(5), 549–54.

Weiner, K.S., Grill-Spector, K. (2011). Not one extrastriate body area: using anatomical landmarks, hMT+, and visual field maps to parcellate limb-selective activations in human lateral occipitotemporal cortex. *Neuroimage*, 56(4), 2183–99.

Wessel, J.R., Danielmeier, C., Morton, J.B., Ullsperger, M. (2012). Surprise and error: common neuronal architecture for the processing of errors and novelty. *Journal of Neuroscience*, 32(22), 7528–37.

Wicker, B., Keysers, C., Plailly, J., Royet, J.P., Gallese, V., Rizzolatti, G. (2003). Both of us disgusted in My Insula: the common neural basis of seeing and feeling disgust. *Neuron*, 40(3), 655–64.