

COGNITIVE NEUROSCIENCE

Reputation in an economic game modulates premotor cortex activity during action observation

Harry Farmer,^{1,*} Matthew Apps^{1,2} and Manos Tsakiris¹¹Department of Psychology, Royal Holloway, University of London, Egham, Surrey TW20 0EX, UK²Department of Experimental Psychology, University of Oxford, Oxford, UK**Keywords:** functional MRI, mirror neurons, motor system, social decision making, trust

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Abstract

Our interactions with other people – and our processing of their actions – are shaped by their reputation. Research has identified an Action Observation Network (AON) which is engaged when observing other people's actions. Yet, little is known about how the processing of others' actions is influenced by another's reputation. Is the response of the AON modulated by the reputation of the actor? We developed a variant of the ultimatum game in which participants watched either the visible or occluded actions of two 'proposers'. These actions were tied to decisions of how to split a pot of money although the proposers' decisions on each trial were not known to participants when observing the actions. One proposer made fair offers on the majority of trials, establishing a positive reputation, whereas the other made predominantly, unfair offers resulting in a negative reputation. We found significant activations in two regions of the left dorsal premotor cortex (dPMC). The first of these showed a main effect of reputation with greater activation for the negative reputation proposer than the positive reputation proposer. Furthermore individual differences in trust ratings of the two proposers covaried with activation in the right primary motor cortex (M1). The second showed an interaction between visibility and reputation driven by a greater effect of reputation when participants were observing an occluded action. Our findings show that the processing of others' actions in the AON is modulated by an actor's reputation, and suggest a predictive role for the PMC during action observation.

Introduction

The observation of the actions of others leads to the activation of a network of neural regions, centred on the premotor and inferior parietal cortices (for recent reviews see: (Bonini *et al.*, 2013; Molenberghs *et al.*, 2012)). The existence of this Action Observation Network (AON) offers a link between perceiving other's actions and the performing our own and has been hypothesized to be involved in a number of social cognitive processes including imitation, empathy and mind reading (Oberman & Ramachandran, 2007; Hurley, 2008; Gallese, 2009; Iacoboni, 2009; Bonini *et al.*, 2013). However, very little is known about how the reputation of the person performing an action, influences the processing of the action in the AON.

Several recent studies have shown that the AON response is modulated by social context. EEG studies have shown that mu suppression, which has been linked to action observation (Cochin *et al.*, 1998; Muthukumaraswamy & Johnson, 2004; Lepage & Théoret, 2007), increases with the social relevance of the observed actions (Kilner *et al.*, 2006; Oberman *et al.*, 2007a,b; Kourtis *et al.*, 2010;

Meyer *et al.*, 2011; Perry *et al.*, 2011; Gutsell & Inzlicht, 2013). In addition research measuring corticospinal (CS) excitability using transcranial magnetic stimulation (TMS) has demonstrated that the AON is sensitive to the communicative value of gestures (Möttönen *et al.*, 2010, 2016) and to the amount of social interaction the participant has had prior to observing actions (Hogeveen & Obhi, 2012).

Neuroimaging studies have also demonstrated that the social identity of an observed actor can modulate activation in the inferior parietal lobe (IPL) and premotor cortex (PMC). Gutsell & Inzlicht (2010) found greater mu suppression for a racial in-group compared to a racial out-group during the observation of simple actions. Similar results have also been found using TMS (Déry & Théoret, 2007; Molnar-Szakacs *et al.*, 2007) and fMRI (Liew *et al.*, 2011). Two recent studies have demonstrated that the effects of such modulations are not merely due to the physical differences between the actor and observer. Molenberghs *et al.* (2013) found that observing a stranger who had randomly been assigned to the same team as the participant led to a preferential activation of the IPL, compared to observing someone assigned to another team. Sobhani *et al.* (2012) used an MVPA classifier to identify a region of the right ventral premotor cortex that distinguished between when Jewish participants were observing the actions of a likeable group (tolerant people) compared to a dislikeable group (neo-Nazis).

Correspondence: Harry Farmer, as above.
E-mail: h.farmer@ucl.ac.uk

*Present address: Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London, WC1N 3AR, UK.

While previous studies have investigated the effects of group membership on the response of the AON, they tell us little about how the reputation of an individual, as formed during real-time social interaction, modulates AON response. We often observe the actions of another without knowing its consequences. Instead we must infer the intentions of another's actions from their reputation established during our past interactions with them. Previous research has shown that the AON is sensitive to the reward value of observed actions (Cheng *et al.*, 2007; Brown *et al.*, 2013) but how does the reputation of an actor influence the AON response?

Another key factor of interest for the current is whether the visibility of an observed action interacts with the reputation of the actor. There is now considerable evidence that the AON is activated not only when the actual execution of an action is observed but also when an action is known to have been carried out but its visual properties are unobserved. Single-unit recordings in the Macaque dorsal premotor cortex (dPMC) have found neurons that preferentially respond when the goal of another's action is known but the action it's self is occluded (Umiltà *et al.*, 2001).

In humans, studies using behavioural (Tausche *et al.*, 2010; Orgs *et al.*, 2011; Springer *et al.*, 2011; Mattiassi *et al.*, 2014) and neuroimaging methods (Ramnani & Miall, 2004; Stadler *et al.*, 2011, 2012; Cross *et al.*, 2013; Jacquet & Avenanti, 2015; Valchev *et al.*, 2015) have demonstrated that the human AON is also sensitive to occluded actions. Indeed Ramnani & Miall (2004) found that merely informing participants that another person was acting via the presentation of an abstract symbol was sufficient to activate the AON. These findings have helped to shed light on the possible functional role of the AON with a number of researchers positing that AON activation to unseen actions represents the motor system attempting to infer the action based on limited sensory information (Avenanti & Urgesi, 2011; Friston, Mattout, & Kilner, 2011; Mattiassi *et al.*, 2014; Orgs *et al.*, 2011; Thioux & Keysers, 2015). In this study, we were particularly interested in how action visibility affected activations in AON regions modulated by reputation as this would allow for the distinction between different functional roles for this modulation with activation to occluded actions, suggesting that these areas played a role in the prediction of the other's actions rather than mere simulation of the observed action.

To address these questions we developed a variant of the ultimatum game (UG) (Güth *et al.*, 1982; Bolton & Zwick, 1995) which incorporated the lack of certain information about the outcome faced by trustors in the investment game (IG) (Berg *et al.*, 1995; Charness *et al.*, 2011). During the experiment, one proposer made fair offers on the majority of trials, whereas the other made unfair offers, leading to either a positive or negative reputation being formed of each proposer. To examine the effects of reputation and action visibility on the AON, at the beginning of each trial, participants observed the proposer indicate their choice by making either a visible action, by grasping a light, or an occluded action, by pushing a button which turned on a light. We examined activity time locked to these events and tested the hypothesis that activity in the AON would be modulated by both whether an action was covertly or overtly observed and the reputation of the proposer making the action.

Methods

Design

In this study, we used a 2×2 factorial design to examine activity in the AON when participants observed the actions of one of two players ('proposers') prior to each round of an economic game. The

first factor was the visibility of the action. This could be either visible, where participants observed a reaching movement or occluded where they observed a light being switched on by the proposer pressing a button under the table. The second factor was the reputation of the proposer. This could be either positive, when observing the actions of the proposer who made fair offers on 80% of the trials, or negative, when observing the actions of the proposer who made unfair offers on 80% of the trials.

Participants

Twenty-one participants took part in this study that was approved by the Departmental Ethics Committee, Royal Holloway, University of London. All gave their informed consent to participate and were paid for their participation. All participants were right-handed and were screened for neurological disorders. Three participants were excluded from the analyses, two due to a high level of movement artefacts and one due to a technical problem that led to a loss of their data. This left a total of eighteen participants (mean age \pm SD: 21.1 ± 2.4 , 4 male).

Procedure

Experimental task

The main task in this study was a variant of the UG but played under conditions of imperfect information (Weber *et al.*, 2004). As in the UG each trial involved a proposer who chose how to split a pot of £10 and a receiver who had the choice to either accept the amount offered in which case both the receiver and proposer were given their share of the pot or reject the offer in which case neither party would receive any money. Throughout this task participants took the role of a receiver while two different interaction partners took the role of the proposer. However, participants were ignorant of how their interaction partners had decided to split the pot on each trial until after they had made their decision. This setup meant that participants had to base their decision on their past experience of how each proposer had split the pot i.e. their reputation. This study used prerecorded videos of the interaction partners but, to ensure that participants felt that their decisions mattered, they were informed that both they and each proposer would be paid based on the results of a randomly selected trial. Therefore participants believed they could still influence the reward each proposer received by either accepting or rejecting their offers, but were aware this was not a reciprocal interaction such as in the work of Xiang *et al.* (2013). To avoid any effects of gender, proposers were gender matched to the participant.

Trial structure

Each trial was divided into four different periods (see Fig. 1). In the *observation* period participants observed a 2 s video in which the proposer was seated behind a desk with their hands hidden from view and a lamp on either side of them. In each trial the proposer indicated their decision on how to split the pot by either using their right hand to grasp the left or right lamp with a power grip (visible condition) or using a hidden remote to turn on the left or right lamp (occluded condition). Note that this meant that the proposer was always making some kind of motor action, but in one case the action was visible and in the other it was occluded. Participants were informed that the video in each trial depicted the proposer as they were making a choice on how to split the pot and that in each

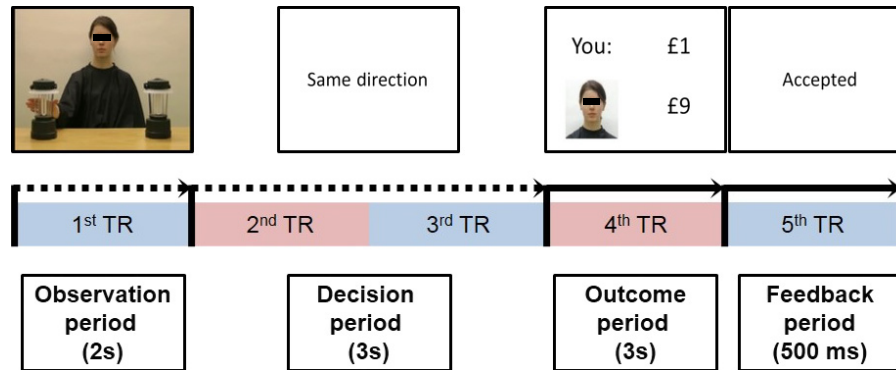


FIG. 1. Structure of experimental trials (dotted lines indicate varied onsets for observation and decision periods. In the observation period, (onset varied across the 1st temporal resolution (TR) participants saw the proposer either gasp one of the lights (visible) or turn on one of the lights by pressing a hidden button (occluded). We examined activity time locked to these videos. In the decision period (onset varied across the 2nd and 3rd TRs) participants decided whether to accept or reject the proposers offer. In the outcome period, they discovered what offer the proposer had made and in the feedback period they were informed of their choice for that trial.

case the proposer was able to see, on an off-screen sign hidden to the participant, whether the action (or light) they were choosing corresponded to a fair or unfair decision. In addition, videos were counterbalanced such that there was no relationship between the lamp chosen by the proposer and the fairness of the split, although this fact was not made explicit to our participants.

In fact the proposers were confederates and decisions attributed to them were manipulated by the experimenter to ensure that one of the proposers (positive) usually made a fair division, offering either 40%, 50% or 60% of the pot to the participant, whereas the other proposer (negative) usually made an unfair division, offering either 5%, 10% or 15% of the pot to the participant. To ensure that participants did not become too habituated to the correspondence between the fair and unfair splits and the identity of the proposers, there were also six catch trials in which the proposers made offers of the opposite fairness from the offer they usually made. This ensured that participants treated their decision on each trial as being of equal importance. To allow participants to fully learn the correspondence between the fairness of the split and the identity of the proposer, the catch trials only appeared after the first ten trials.

During the *decision* period, participants had 3 s to decide whether they wanted to accept or reject the division of the pot that the proposer had made in the *observation* period, using one of the two direction buttons as detailed above. In this period of the trial participants saw a screen with either the word 'same' or 'different' on it, which indicated whether they had to press the button corresponding to the same side of the screen the proposer had indicated or to the opposite side to accept the offer. Participants were told to respond using an egocentric reference frame rather than the reference frame of the proposer. For example if in a 'same' trial if the proposer chose the lamp on their left, the participant would have to press the right button to agree. Importantly, participants only discovered whether each trial required them to use the same or opposite button to indicate accept after they had finished observing the video for that trial. This ensured that on each trial, the subject could not prepare a motor response at the time of the actions of the proposer. Crucially, this meant that observed activation in the motor system was not due to motor preparation but must instead have been due to action observation. In addition the fact that participant's ability to make their desired response was dependent on their knowledge of the proposers' previous action ensured that participants attended to the proposer's actions throughout the study.

During the *outcome* period, participants saw the face of the proposer and how they had decided to split the pot of money between themselves and the participant. The outcome screen was present for 3 s and ensured that participants had a chance to learn the difference between the positive and negative proposer in terms of how they split the pot of money.

Finally, during the *feedback* period participants received feedback on what their decision had been in the form of either the word 'accepted' or 'rejected' or, in cases where participants failed to press either button before the end of the 'decision' screen, the word 'missed'. Feedback was displayed for 500 ms. The purpose of the *feedback* period was to ensure that participants understood how to use the buttons to correctly express their decisions and also to provide them with an additional prompt to make sure they responded to the *decision* period within the 3 s.

Scanning session

Participants attended a training session to ensure to ensure that all scanned participants understood the nature of the task and were influenced by reputation when making their response judgments (see Data S1). Those who successfully learnt the reputations of the two proposers were then asked to return within 14 days for the main scanning session. In this session, participants were reminded of the details of the game and were then positioned in the scanner. As our question in this experiment was not about how people learn the reputation of other people, subjects first carried out a training block of ten trials of the game to give them time to learn the association between the two proposers and their likely responses (i.e. fair or unfair). To ensure that participants learnt the association there were no catch trials in this session (i.e. one proposer always made fair offer, and the other always made unfair offers). During this practice session a high resolution T1-weighted structural image was acquired for the purposes of normalization (see below) and displaying results.

Following the completion of the practice block and anatomical scan participants then began the main experimental task. The game consisted of 140 trials, which were equally distributed between the four experimental conditions (35 positive visible, 35 negative visible, 35 positive occluded and 35 negative occluded). Events in each trial took place across five TRs (Temporal Resolutions) (0–15 s; TR = 3 s). The interval between scan onset and *observation* period

onset was varied over the first TR from trial-to-trial and the interval between the *observation* period and the *decision* period was varied across the second and third TRs from trial-to-trial. This achieved an effective temporal sampling resolution much finer than one TR for the conditions of interest. These intervals were uniformly distributed for each condition, ensuring that Evoked Haemodynamic responses (EHRs) time locked to the events were sampled evenly across the time period following each *observation* or *decision* period.

Participants then rated the faces of the two proposers and 18 distractor faces for attractiveness and trustworthiness. They had previously rated the face during the training session prior to any interaction with them. During this phase and magnitude, maps were collected using a GRE field map sequence. Finally participants were removed from the scanner and were debriefed as to the true nature of the study. Participants were informed that they would be paid £15 plus the money they had previously earned in the training session (see Data S1).

Image acquisition and data analysis

Functional images were acquired using a Siemens 3.0 Tesla Trio scanner at Royal Holloway, University of London. Stimuli were projected onto a screen behind the participant and viewed in a mirror positioned over the participant's head and participants responded using a 4 button response box. Presentation software (Neurobehavioural Systems, 2012) was used for the presentation of stimulus and the collection of participants' responses. Behavioural data analysis was performed offline, and event timings were prepared for subsequent general linear model (GLM) analyses of fMRI data. Analyses of fMRI data were conducted in SPM8.

720 EPI scans were acquired from each participant. In each scan 38 slices were acquired in an ascending manner, at an oblique angle ($\approx 15^\circ$) to the AC-PC line to decrease the impact of susceptibility artefacts in the orbitofrontal cortex (Deichmann *et al.*, 2003). A voxel size of $3 \times 3 \times 3$ mm (20% slice gap, 0.6 mm) was used; TR = 3 s, TE = 32, flip angle = 85° . Prior to the functional sequence high resolution T1-weighted structural images were acquired at a resolution of $1 \times 1 \times 1$ mm using an MPAGE sequence. Immediately following the functional sequence, phase and magnitude maps were collected using a GRE field map sequence (TE₁ = 5.19 ms, TE₂ = 7.65 ms).

Data were processed and analysed using SPM8 (www.fil.ion.ucl.ac.uk/spm). The EPI images from each participant were corrected for distortions using the FieldMap toolbox (Andersson *et al.*, 2001). The B0 field map acquired after the EPI sequence was used to calculate static distortion and the EPI images were then realigned, and coregistered to the participant's anatomical image. The structural image was processed using a unified segmentation procedure combining segmentation, bias correction, and spatial normalization to the MNI template (Ashburner & Friston, 2005). The same normalization parameters were then used to normalize the EPI images. Finally, the images were spatially smoothed to conform to the assumptions of the GLM implemented in SPM8 by applying a Gaussian kernel of 8 mm FWHM.

A first-level GLM was created for factorial analyses. The four conditions (positive visible, negative visible, positive occluded and negative occluded) were modelled as separate regressors and an additional regressor modelled activity during the *decision* period (regardless of the condition the period was in). Residual effects of head motion were modelled as covariates of no interest in the analysis by including the six head motion parameters estimated during realignment.

Random effects analyses (Full-Factorial ANOVAS) were applied to determine voxels significantly different at the group level. SPM{t} contrast images from all participants at the first-level were input into second-level full factorial design matrices. *T*-contrasts were conducted in the second-level random effects analyses for visibility (visible vs. occluded) and reputation (positive vs. negative). An *F*-contrast was conducted in the second-level random effects analyses for the interaction of the first GLM. To give a complete picture of our data, we present all results above a whole-brain threshold of $P < 0.001$ with a cluster size threshold of 10.

To test the anatomically specific hypotheses we used a small volume correction approach that ensured were appropriately corrected for multiple comparisons and that any significant voxels were in the same region as those identified in the AON meta-analysis by Molenberghs *et al.* (2012). Note that these findings would have been upheld had we used the most common cluster-wise corrections for multiple comparisons (Woo *et al.*, 2014), however, such an approach does not provide the anatomical specificity to the results that was required to meet the aims of this study. As this study investigated action observation the three coordinates were taken from Molenberghs *et al.*'s analysis of a subset of studies that examined mirroring during action observation, rather than auditory, somatotopic or emotional mirroring. From those coordinates we restricted ourselves to activations in the left hemisphere because all of the observed actions were carried out with the right hand and previous research on the AON (Aziz-Zadeh *et al.*, 2002) indicates that each hemisphere shows stronger activation when viewing actions conducted by the contralateral hand. We further restricted our coordinates to include only those areas that fall into the classical AON regions of the IPL and the premotor cortex. This left us with one coordinate centred on the left precentral gyrus (MNI: -51, 1, 46), one centred on the left middle frontal gyrus (MNI: -28, -11, 55) and one centred on the left IPL (MNI: -53, -32, 38). All coordinates from Molenberghs *et al.* (2012) were converted from Talairach to MNI using the MNI to Talairach Coordinate Converter (Lacadie *et al.*, 2008).

Results

Behavioural results

Ratings of proposers' faces

Paired sample *t*-tests were carried out on the ratings given to the proposers faces in the training session. There was no significant differences in ratings of attractiveness ($t(17) = -0.62$, $P = 0.55$) or trustworthiness ($t(17) = -0.69$, $P = 0.50$). To examine whether the experimental manipulation of reputation had been successful, analyses of covariance were carried out on the attractiveness and trust ratings. In each, the dependent variable was the postscanning ratings, the independent variable was the reputation of the proposer and the covariate was the prescanning ratings. The ANCOVA for attractiveness revealed no significant effect of the experimental manipulation, $F(1, 20.29) = 0.9$, $P > 0.05$. However, the ANCOVA for trustworthiness found a significant effect, $F(1, 16.4) = 5.183$, $P < 0.05$, with participants judging the positive reputation proposer as being more trustworthy ($M = 4.83$, $SD = 4.79$) than the negative proposer ($M = 1.5$, $SD = 5.94$).

Participants' choices in the decision period

To investigate how well participants had learnt the proposers' reputations we calculated the proportion of results accepted out of all

decisions made (excluding missed trials) for each of the four conditions. A 2×2 repeated measures ANOVA was carried out on the number of decisions made with reputation (positive/negative) and visibility (visible/occluded) as the independent variables. A main effect of reputation was found $F(1,17) = 123.7$, $P < 0.001$ but there was no main effect of visibility and no significant interaction. This was due to the fact that participant accepted a more trails for the positive proposer ($M = 0.895$, $SD = 0.128$) than for the negative proposer ($M = 0.193$, $SD = 0.22$) (see Fig. 2).

To further explore the question of whether participants were still learning or adapting behaviour based on the reputations of the proposers by start of the scanning sessions we split the trials for each proposer into seven blocks of ten trials each and calculated the proportions of responses accepted in each block. A 2×7 repeated measures ANOVA of block and reputation. This analysis revealed a

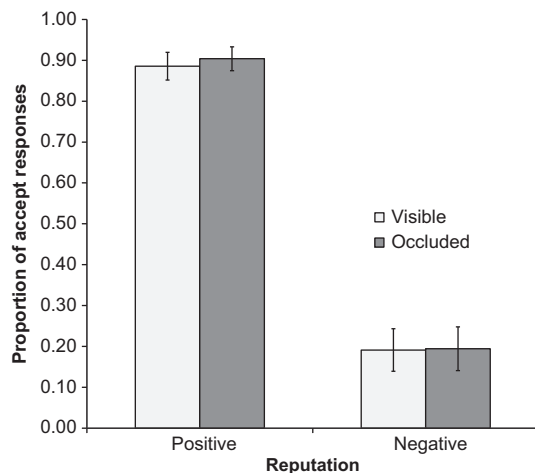


FIG. 2. Proportion of trials accepted by reputation of proposer and visibility of action. Error bars represent SEM.

main effect of reputation $F(1,17) = 124.18$, $P < 0.001$. However, there was no significant effect of block, $F(6, 102) = 0.45$, $P = 0.847$ and no significant interaction between reputation and block, $F(6,120) = 0.2$, $P = 0.993$, suggesting that participants had indeed learnt the proposer's reputations and the appropriate response prior to the start of the scanning task.

Participants' reaction times in the decision period

A $2 \times 2 \times 2$ repeated measures Mixed Models analysis was conducted on participants reaction times (RTs), with RT as the dependent variable and response (accept, reject), visibility (visible/occluded) and reputation (positive/negative) as fixed effects (see Fig. 3). A mixed models approach was used due to the fact that 11 of our participants did not have any trials in at least one of the conditions. There were no significant main effects but there was a significant interaction between reputation and response, $F(11.1,63.35) = 104.5$, $P = 0.001$. Planned comparisons revealed that this interaction was driven by the fact that participants were faster significantly to accept offers from the fair proposer ($M = 1137.03$, $SD = 276.31$), compared to the unfair proposer ($M = 1239.69$, $SD = 300.55$), $t(17) = -5.07$, $P < 0.001$, and marginally significantly faster to reject offers from the unfair proposer ($M = 1269.49$, $SD = 261.53$), than from the fair proposer ($M = 1455.57$, $SD = 451.99$), $t(14) = 1.93$, $P = 0.074$.

Functional imaging results

Interaction between action and reputation in the premotor cortex

The F contrast carried out on the interaction between visibility and reputation revealed a cluster centred on the left occipital gyrus and extending into the left lingual gyrus which was significant at $P = 0.05$ after false-discovery rate (FDR) correction for multiple comparisons (see Table 1). SVC revealed a significant activation in

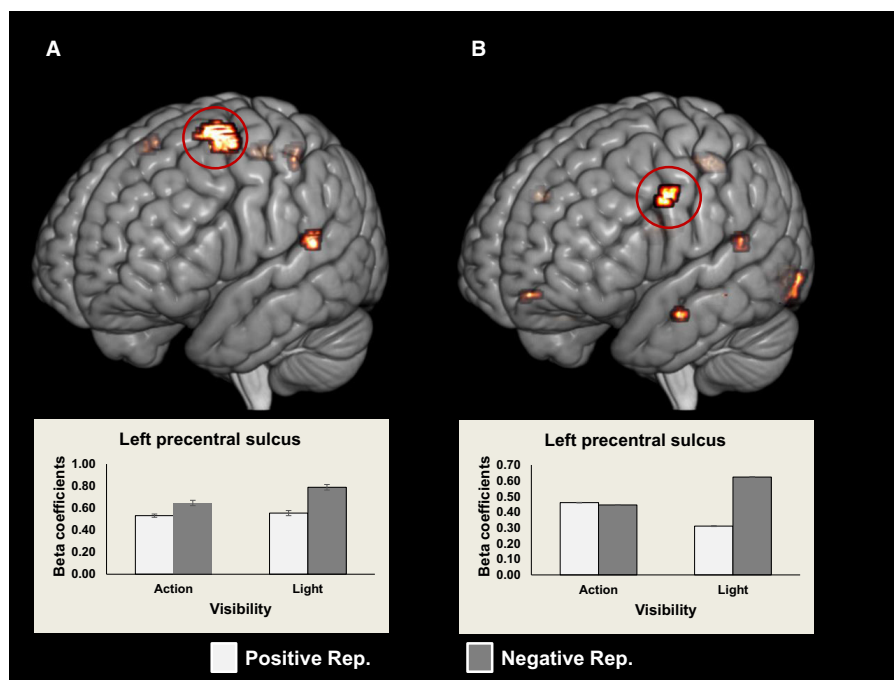


FIG. 3. (A) Brain areas showing a main effect of reputation. (B) Brain areas showing an interaction between action and reputation. Threshold set at $P < 0.001$ uncorrected. $k = 10$ voxels. Beta coefficients averaged across whole cluster using MarsBar (Brett et al., 2002). Error bars represent SEM. Circles indicate regions significant after small volume correction.

TABLE 1. Whole-brain peak voxel coordinates in MNI space and *z*-values for data time locked to indicator period. Activations thresholded at $P > 0.001$ uncorrected and $k = 10$ voxels

Region (BA)	H	X	Y	Z	Z-Score	k
Reputation X Visibility						
Lateral Occipital Gyrus (18)*	L	-18	-92	-10	4.43	153
Precuneus Gyrus (7)	R	6	-62	46	4.14	47
Posterior Thalamic Radiation	R	34	-54	10	3.92	69
Fusiform Gyrus (20)	L	-40	-12	-24	3.91	11
Lateral Occipital Gyrus (18)	R	30	-86	-20	3.85	43
Orbital Sulcus (11)	R	18	36	-14	3.79	12
Precentral Sulcus (6)	L	-54	8	38	3.76	43
Inferior Frontal Sulcus (6)	L	-48	2	38	3.24	
Inferior Frontal Sulcus (44)	R	44	6	32	3.67	19
Inferior Temporal Gyrus (20)	R	56	-14	-30	3.57	12
Posterior Thalamic Radiation	L	-32	-56	12	3.56	10
Unfair > Fair						
Precentral Sulcus (6)†	L	-26	-4	66	4.65	133
Intraparietal Sulcus (7)	R	30	-48	52	3.77	17
Precuneus Gyrus (7)	L	-8	-62	54	3.64	27
Superior Temporal Sulcus (41)	L	-42	-46	12	3.54	24
Precuneus Gyrus (5)	R	12	-58	52	3.44	22
Precentral Sulcus (6)	R	30	-4	58	3.27	12
Visible > Occluded						
Inferior Temporal Gyrus (37)***	R	48	-60	0	5.44	1597
Lateral Occipital Gyrus (19)	R	38	-80	6	4.47	
Lateral Occipital Gyrus (19)***	L	-50	-78	4	5.40	1445
Middle Temporal Gyrus (37)	L	-46	-60	10	4.88	
Inferior Temporal Gyrus (37)	L	-42	-64	4	4.70	
Superior Frontal Gyrus (10)	L	-12	66	10	3.89	124
Medial Orbitofrontal Gyrus (10)	L	-10	62	0	3.49	
Medial Superior Frontal Gyrus (10)	R	6	56	24	3.47	
Superior Frontal Sulcus (9)	L	-18	32	44	3.54	10
Occluded > Visible						
Cingulate Sulcus (32)	L	-10	10	46	3.66	40
Precentral Sulcus (6)	R	54	6	40	3.35	20

†, *, ** and *** indicate activations significant at FDR cluster corrected $P > 0.1$, 0.05, 0.01 and 0.001 respectively. H, hemisphere; k, cluster size. Concurrent shading indicates distinct regions in the same cluster.

the left precentral gyrus (see Table 2 and Fig. 3). Analysis of the parameter estimates from the peak voxel found that this interaction was driven by significantly greater activation for: positive visible ($M = 0.34$, $SD = 0.51$) than positive occluded ($M = 0.17$, $SD = 0.56$), $t(17) = 2.85$, $P < 0.05$; negative occluded ($M = 0.49$, $SD = 0.48$) than negative visible ($M = 0.31$, $SD = 0.43$), $t(17) = -2.53$, $P < 0.05$; and negative occluded than positive occluded, $t(17) = -4.18$, $P = 0.001$.

Main effect of reputation in a separate premotor region

Neither whole brain nor SVC corrected analysis revealed any significant clusters for the positive > negative *t*-contrast. For the

TABLE 2. Small volume corrected peak voxel coordinates in MNI space and *z*-values for data time locked to indicator period. H, hemisphere, k, cluster size

Region (BA)	H	X	Y	Z	Z-Score	k
Reputation X Visibility						
Precentral Sulcus (6)	L	-54	6	40	3.37	7
Unfair > Fair						
Precentral Sulcus (6)	L	-30	-6	62	3.70	16

negative > positive *t*-contrast there were no activations survived whole-brain cluster wide FDR correction. However, SVC revealed increased activity for the negative proposer in a separate region of the left precentral gyrus to that found in the interaction contrast (see Table 2 and Fig. 3).

Areas showing a main effect of visibility

The visible > occluded *t*-contrast revealed significant FDR corrected activation in bilateral occipital and temporal regions extending across the middle temporal gyrus and middle occipital gyrus and encompassing the left STS (see Table 1). SVC did not reveal any significant activation for either contrast in the hypothesized regions.

Areas showing covariance with individual differences in trustworthiness ratings

To analyse individual differences in the effect of reputation on BOLD response during action observation we first calculated the change between pre and postscan trust ratings for each proposer and then subtracted the change in the negative proposer from that of the positive proposer. This measure of distinction between the trustworthiness of two proposers was entered as a positive covariate into three analyses of covariance, one for the positive > negative *t*-contrast, one for the negative > positive *t*-contrast and one for the interaction *F*-contrast. The positive > negative ANCOVA revealed significant FDR corrected bilateral activation of the thalamic nucleus, which the negative > positive ANCOVA revealed a significant FDR corrected activation centred on the right paracentral gyrus (primary motor cortex: M1). No FDR corrected clusters were found for the interaction ANCOVA (see Table 3, Fig. 4).

TABLE 3. Whole-brain peak voxel coordinates in MNI space and *z*-values for areas with activation showing positive covariance with trust ratings. Activations thresholded at $P > 0.001$ uncorrected and $k = 10$

Region (BA)	H	X	Y	Z	Z-Score	k
Reputation X Visibility						
Anterior Corona Radiata	L	-22	42	8	4.08	33
Paracentral Gyrus (4)	R	4	-32	70	3.73	15
Paracentral Gyrus (4)	L	-4	-36	72	3.66	
Frontal Inferior Gyrus Pars	R	60	22	24	3.53	30
Triangularis (44)						
Frontal Inferior Gyrus Pars	R	60	28	18	3.48	
Triangularis (45)						
Cerebellum 7b	R	44	-60	-50	3.36	20
Nucleus Putamen (48)	L	-22	4	-4	3.34	13
Fair > Unfair						
Thalamic Nucleus***	L	-6	-28	16	4.45	160
Thalamic Nucleus	R	6	-30	16	3.98	
Cerebellar Crus1 (19)	L	-36	-74	-24	3.83	26
Precuneus gyrus (7)	L	-8	-68	46	3.47	19
Cerebellum_6 (37)	L	-36	-58	-22	3.35	10
Unfair > Fair						
Paracentral Gyrus (4)***	R	6	-20	56	4.59	1260
Cingulate Sulcus	R	8	-36	56	4.35	
Anterior Cingulate Gyrus (11)	L	-4	30	-4	3.81	11
Rolandic Sulcus (4)	L	-18	-32	70	3.64	25
Paracentral Gyrus (4)	L	-14	-24	70	3.35	
Anterior Rostral Sulcus (10)	R	8	58	4	3.39	18
Anterior Cingulate Gyrus (32)	R	8	38	12	3.30	10

†, *, ** and *** indicate activations significant at FDR cluster corrected $P > 0.1$, 0.05, 0.01 and 0.001 respectively. H, hemisphere, k, cluster size. Concurrent shading indicates distinct regions in the same cluster.

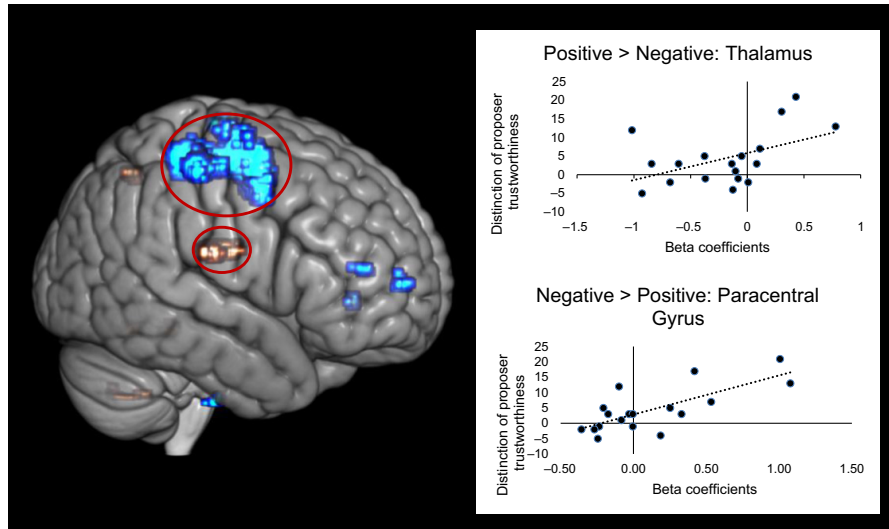


FIG. 4. Brain Areas showing covariance with individual differences in trustworthiness ratings. Red indicates positive correlation with positive > negative contrast. Blue indicates positive correlation with negative > positive contrast. Beta coefficients averaged across whole cluster using MarsBar (Brett et al., 2002). Circles indicate regions significant after FDR correction.

Discussion

The aim of this study was to investigate whether the AON was modulated by the reputation of an individual performing an act. In line with our hypothesis, we found significant activations in two regions of the left dorsal premotor cortex (dPMC). The first of these showed a main effect of reputation with greater activation for the negative reputation proposer than the positive reputation proposer. The second showed an interaction between visibility and reputation which was driven by a greater effect of reputation when participants were observing choices relayed by an occluded action. Furthermore individual differences in trust ratings of the two proposers covaried with activation in right M1, providing further evidence for the modulating effect of reputation on motor system activation during action observation. As our motivation for conducting this study was to examine the effects of reputation on the AON we will focus our discussion on the activations we found within the AON. We discuss these findings in relation to recent accounts which suggest the AON processes predictive information about others' actions.

Negative reputation leads to greater AON activity

Broadly speaking this study supports recent evidence showing that activation in the AON, and particularly the dPMC, is modulated by the social context in which actions are observed. Activity in the AON has been found to differ depending on whether the action is performed by an in-group or out group member (Molenberghs *et al.*, 2013), or whether the actions are by a member of a liked or disliked group (Sobhani *et al.*, 2012). However, in both previous studies the direction of the modulation was the reverse of that in this study with greater activation for the actions of in-group members or liked others. In this study the left dPMC showed greater activation for the proposer with a negative reputation and the increased right M1 activation for the negative compared to positive proposer positively covaried with how much more untrustworthy the negative reputation proposer was perceived compared to the positive reputation proposer.

The difference between our study and previous ones may be due to the fact that in those studies the observed actions had no

consequences for the observer and thus activity may have been driven by differences in the level of attention or personal relevance of the actor. In our study, the actions of both the positive and the negative proposer had consequences for the participants, who could potentially lose money, or treat the proposer unjustly, if they did not attend to both the identity of the proposer and the direction of the proposers' actions. The actions of both proposers needed to be attended to in order that participants could optimize their decision making on the task. Thus, our study provides evidence that the AON is engaged when observing the actions of others during strategic social interactions.

The finding in our study of greater activation in the AON when observing the actions of the proposer with a negative reputation ties into previous results suggesting that the AON shows a bias towards interpreting actions with a threatening or negative outcome. Lotze *et al.* (2006) found that activation in the right STS was positively correlated with the negative valence of observed expressive valence. Gutsell & Inzlicht (2013) showed that reduced mu-suppression for the observation of out-group actions was abolished when those actions had a threatening component. Similarly Losin *et al.* (Losin *et al.*, 2012, 2014, 2015) have shown that actively imitating a member of a negatively perceived racial or political group leads to greater recruitment of the AON than does imitating members of a positively perceived group. Sinke *et al.* (2010) also reported greater activation in the left dPMC when participants observed another person making threatening, as opposed to teasing, gestures to a third party. Thus this study's finding of increased activation in the dPMC during the observation of a disreputable person's actions adds to the evidence that this region is sensitive to the potentially negative consequences of others' actions, i.e. receiving an unfair offer.

The increased AON activation for the negative reputation proposer also ties in with research showing a general processing bias towards those with poor reputations. Several EEG studies have found increased ERPs for untrustworthy faces in components related to face processing and attention (Yang *et al.*, 2011; Dzhelyova *et al.*, 2012; Marzi *et al.*, 2014). In addition, studies that manipulated trustworthiness with verbal descriptions (Rule *et al.*, 2012) or economic games (Vanneste *et al.*, 2007) have demonstrated biases

towards disreputable others in memory (Rule *et al.*, 2012) and attention (Vanneste *et al.*, 2007). Overall these findings indicate a rapid attentional bias towards those perceived as disreputable which might explain the increased AON activation seen in this study.

A key aspect of this study was that differentially attending to the actions of the two different proposers was orthogonal to any subsequent response of the participant. That is, there was no benefit to processing the actions of the two other proposers differently. So why did the premotor cortex respond differentially to the actions of the two different proposers? Notably, many have argued that the processing of others' actions in the PMC is largely automatic (Press *et al.*, 2008). We process actions and often imitate them even when there is no intention to do so. It is therefore clear that the goals of others' actions could be processed automatically without the necessity of such processing to be either conscious or even beneficial. However, whilst PMC processing of others' goals may be automatic, there is considerable evidence that processing others' actions needs to differ depending on the context. For example we may need to attend to others' actions differently when learning through observation (Cross *et al.*, 2009b; Burke *et al.*, 2010; Wade & Hammond, 2015), when tracking or learning about the motivational value of actions for another (Suzuki *et al.*, 2012; Apps *et al.*, 2015, 2016), and when processing the insufficiency of actions for meeting goals (Casile *et al.*, 2010; Maffei *et al.*, 2015). Here, our results suggest that reputation may influence the automatic processing of others' actions. This reputational effect may be driven by the fact that fairness is considered as a social norm (Tabibnia *et al.*, 2008; Rand *et al.*, 2013). Most participants expect other people to make fair rather than unfair offers in the ultimatum game. As a result, unfair offers are potentially more salient (Gabay *et al.*, 2014). Thus, it is plausible that the automatic processing of others' actions is modulated when the other individual has a negative reputation formed by the consistent violation of social norms. Future research should examine whether such consistent violations lead to modulations of attention due to the potentially increased salience of actions of individuals with negative reputations.

Interaction between reputation and visibility in the dPMC

In addition to the main effect of reputation another region of the left dPMC showed an interaction between action and reputation. Intriguingly this interaction was driven by a difference between the positive and negative proposers in the occluded action condition. Whilst the finding of greater AON activation for occluded compared to visible actions may initially seem counterintuitive as we outlined in the introduction there is considerable evidence that the AON, and specifically the dPMC, is activated when the goal of an action is known but the actual kinematics are unobservable. Notably neurons in the Maacque dPMC are known to fire preferentially to occluded actions (Umiltà *et al.*, 2001). In humans neuroimaging studies have shown that the dPMC is engaged when predicting the outcome of others' actions (Ramnani & Miall, 2004; Stadler *et al.*, 2011; Cross *et al.*, 2013), when specifying the desired end state of an action (Majdandžić *et al.*, 2009), when detecting errors in the actions of others (Desmet *et al.*, 2014) and when predicting the sensory consequences of an action (Kilner, 2011). Furthermore Stadler *et al.* (2012) demonstrated that TMS induced disruption of the dPMC led participants to make more errors when predicting the outcomes of occluded actions indicating that it plays a functional role in the prediction of occluded actions.

The above findings have motivated several predictive accounts of the AON (Kilner *et al.*, 2007; Schütz-Bosbach & Prinz, 2007;

Keysers & Gazzola, 2009; Avenanti & Urgesi, 2011; Friston *et al.*, 2011; Schippers & Keysers, 2011). On such accounts the role of the premotor cortex during action observation is to solve that computational challenges that result from ambiguous perceptual information about an action (Avenanti & Urgesi, 2011; Avenanti *et al.*, 2013). These accounts predict that decreasing the amount of sensory information regarding the trajectory of an action will lead to an increase in the amount of activity in the AON. In support of this claim Avenanti *et al.* (2013) showed that disrupting areas involved in the visual processing of action with TMS led to greater CS excitability suggesting greater neural activity within the motor system. Another recent study revealed greater BOLD activation the dPMC when participants observed hand movements towards an occluded object compared to a visible object (Thioux & Keysers, 2015).

In our study, participants were aware that in the light condition the proposer was performing an occluded action. Thus predictive accounts of the AON would expect an increase in activity in the motor regions due to the greater need to generate an internal rather than perceptually driven model of the other's action. We therefore suggest that the interaction found in this study can best be explained as a result of this greater computational burden on the premotor cortex, combined with a greater motivation to predict the outcome of actions performed by the negative proposer compared to those performed by the positive proposer.

Role of dPMC activation in action inference

One important question for the predictive account of the dPMC activations found in this study is the issue of exactly what feature of the proposers' action is being predicted within the dPMC in this situation. Research in action processing has suggested the existence of a network of hierarchically organized action representations within the brain (Wolpert & Kawato, 1998; Grafton & Hamilton, 2007; Hamilton & Grafton, 2007; Badre & D'Esposito, 2009; Cross *et al.*, 2009a; Kilner, 2011). This hierarchy is formed of several distinct levels. The lowest is the kinematic level which represents features such as reach trajectory and grip type. Next is the motor level which represents the sequences of muscle activity needed to bring about particular kinematics. These sequences are determined by the action goal level which represents the immediate purpose of an action, such as the location of a object to be interacted with. Finally there is the level of the distal intention behind that action (Kilner, 2011). Several researchers (Grafton & Hamilton, 2007; Hamilton & Grafton, 2007; Kilner, 2011) have suggested that action observation utilizes the same hierarchical network.

Within such a framework, the PMC is believed to process more abstract information about the goals of another's actions. Research on action execution has implicated the dPMC in the motor planning (Badre & D'Esposito, 2009; Pearce & Moran, 2012; Hartwigsen & Siebner, 2015; Nakayama *et al.*, 2016). Research in macaques using single-cell recordings has demonstrated that neurons in the dPMC are active both when specifying the action required to meet a behavioural goal and when executing that action (Nakayama *et al.*, 2016). It has also been shown that neural populations in the dPMC represent information about the spatial goal of an action as action planning becomes more complex (Pearce & Moran, 2012). In humans the left dPMC has been implicated in the transformation of object-related information into motor programs (Gallivan *et al.*, 2011; Monaco *et al.*, 2011; Gallivan & Culham, 2015) and in the rapid switching between motor plans (Hartwigsen & Siebner, 2015). In the domain of action observation, Majdandžić *et al.* (2009) used a repetition suppression paradigm while participants observed

actions that could differ in either their grip type, trajectory or final placement. They found that the dPMC showed adaptation effects for repetition of final placement but not grip type or trajectory. Given these findings we tentatively suggest that the dPMC activation in this study is likely to reflect predictive processing of the action-goal (i.e. which light participants were reaching to/turning on) rather than lower level detail of the kinematics used to achieve that goal.

Conclusion

In conclusion, the current experiment sought to investigate the ability of reputation to modulate activity in the human AON. We show that two separate regions of the dPMC – a key region of the AON – are sensitive to the reputation of the person performing an actor with the activation in one of these areas being modulated by the visibility of the action performed. In addition, the difference in BOLD response between the positive and negative proposers in right M1 correlated with participant's difference in their ratings of trustworthiness for the proposers showing some further evidence that the motor system is sensitive to the effects of reputation when observing others actions. We suggest these findings can be interpreted within predictive accounts of the AON, in which the dPMC is engaged when making inferences about the other's action. This study shows for the first time the influence of reputation, formed during an economic game, on the neural systems involved in perceiving another's actions. Such findings pave the way for understanding more about how social factors influence the processing of others' actions. Future research should examine the extent to which reputation modulates the AON interact with other personality traits, racial effects and gender.

Supporting Information

Additional supporting information can be found in the online version of this article:

Data S1. fMRI study.

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Abbreviations

AON, action observation network; dPMC, dorsal premotor cortex; EHRs, evoked haemodynamic responses; FDR, false-discovery rate; GLM, general linear model; IPL, inferior parietal lobe; PMC, premotor cortex; TMS, transcranial magnetic stimulation.

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