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Responses to irrational actions in action observation and mentalising networks of the human brain

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A B S T R A C T

By observing other people, we can often infer goals and motivations behind their actions. This study examines the role of the action observation network (AON) and the mentalising network (MZN) in the perception of rational and irrational actions. Past studies in this area report mixed results, so the present paper uses new stimuli which precisely control motion path, the social form of the actor and the rationality of the action. A cluster in medial prefrontal cortex and a large cluster in the right inferior parietal lobule extending to the temporoparietal junction distinguished observation of irrational from rational actions. Activity within the temporoparietal region also correlated on a trial-by-trial basis with each participant's judgement of action rationality. These findings demonstrate that observation of another person performing an irrational action engages both action observation and mentalising networks. Our results advance current theories of action comprehension and the roles of action observation and mentalising networks in this process.

Introduction

To understand and predict another person's behaviour, it is often helpful to observe how that person moves and to detect if they move in an unusual fashion. Many neuroimaging studies have examined the brain systems involved in understanding other people. These have identified an action observation network (AON) and a mentalising network (MZN) which are engaged by different types of social stimuli. Here we examine if and how these brain networks work together when participants view unusual actions which vary in social richness.

Many previous studies have examined brain responses during the observation of simple, goal-directed actions and have localised an action observation network (AON) (Caspers et al., 2010). This network comprises the inferior parietal lobule (IPL), the inferior frontal gyrus (IFG) and a swathe of the visual cortex from the extrastriate body area (EBA) through the middle temporal gyrus (MTG) to the superior temporal gyrus (STG). The IFG and IPL are commonly considered to be the core of the human mirror neuron system (Gallese et al., 1996; Rizzolatti and Craighero, 2004) and respond in the same way to the actions of self and other (Kilner et al., 2009; Oosterhof et al., 2010). Whilst it is clear that these brain systems are active when participants observe simple familiar actions, the role that these areas play in more complex action comprehension remains debated (Jacob and Jeannerod, 2005).

A second brain network, commonly called the mentalising network (MZN) is found in the medial prefrontal cortex (mPFC) and temporoparietal junction (TPJ) with the posterior cingulate and temporal poles also engaged (see Amodio and Frith, 2006 and Frith and Frith, 2003 for reviews). This network is robustly engaged when participants perform social tasks and think about other people's beliefs or intentions. For example, the mPFC is more engaged when participants observe social interactions between cartoon triangles (Castelli et al., 2000) and when participants play an interactive game that requires consideration of their opponents beliefs (Hampton and Bossaerts, 2008). The TPJ and adjacent superior temporal sulcus (STS) are also more active during observation of social interactions (Centelles et al., 2011) and actions with unusual intentions (Pelphrey et al., 2004; Saxe et al., 2004; Wyk et al., 2009).

Early studies reported engagement of the AON and MZN in quite different circumstances, but the extent to which the AON and MZN systems function independently and how they interact is currently debated (see Van Overwalle and Baetens (2009) for a meta-analysis). Concurrent activation of both systems is seen when the participant is asked to make 'what' or 'why' judgements about observed actions (Spunt et al., 2011) or to assess whether two figures are engaging in social interaction (Centelles et al., 2011). The mPFC and posterior STS were both engaged when participants judged the intentionality of actions with unusual goals or unusual kinematics (De Lange et al., 2008). In

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the same study, IFG responded when participants viewed actions with unusual goals, demonstrating the complementary roles of action observation and mentalising systems. However, in these studies the engagement of AON and MZN is dependent upon instructions to think about different aspects of the stimuli (see Ampe et al., 2012) and may not reflect spontaneous action understanding. Two recent studies have shown that the AON and MZN are both active during observation of simple grasping actions with social (Becchio et al., 2012) or communicative (Ciaramidaro et al., 2014) intent. These findings suggest that actions may need to be considered within a social framework to engage both systems.

Here we aim to probe the role of the AON and MZN in spontaneous action understanding using more complex stimuli. One possible way to examine both the AON and the MZN is to present participants with irrational actions. An irrational action can be defined as a goal-directed action which does not adhere to the principle of rational action (Gergely and Csibra, 2003). As such, the means by which an irrational action is achieved is inefficient, given the environmental constraints. For example, reaching up and over a pile of books to pick up the telephone is efficient when the books lie between your hand and the receiver but the same up-and-over action is inefficient when the books are not in the way. Thus the first up-and-over action is rationalised by the pile of books but the second up-and-over action is irrational because it would be more efficient to reach directly for the phone. Such actions are interesting because understanding the rationality of actions in a teleological fashion is a developmental step between basic action comprehension and theory of mind (Csibra, 2003; Gergely and Csibra, 2003). This places irrational action stimuli on the borderline between those stimuli that typically engage the AON (simple actions) and those that typically engage the MZN (theory of mind tasks). Previous studies of brain activation when participants view irrational actions have given mixed results about the engagement of either AON or MZN regions. One study reported MZN activation only (Brass et al., 2007), one study reported activation of AON regions and deactivation of MZN regions (Marsh and Hamilton, 2011) and one study reported activation of neither (Jastorff et al., 2010). Thus, one aim of the present study is to determine how the AON and MZN respond during viewing of irrational actions in a new and well-controlled stimulus set.

A second key question for both the AON and MZN in action understanding concerns the social form of the stimuli — are these systems engaged only by 'human' actors or also by animate objects? Initial reports suggested that the AON is selective only for human actions (Buccino et al., 2004; Tai et al., 2004) but more recent data suggest that observation of robotic actions (Cross et al., 2012; Gazzola et al., 2007) or moving shapes (Ramsey and Hamilton, 2010) can also engage this brain network. The MZN is activated when participants believe they are engaging with another person (Gallagher et al., 2002) even when only abstract cues are visible on the screen. Similarly, rationality or intentionality can be detected in the movements of animated shapes in adults (Castelli et al., 2000) and in infancy (Csibra et al., 1999). Eye-tracking studies suggest that participants look towards the face of an actor who performs an irrational action (Vivanti et al., 2011), but this is only possible if the actor has a human form. Thus, it remains unclear whether human form is a useful cue or modulator of the detection of rational action, in either the AON or the MZN.

To investigate these questions, we conducted an fMRI study where participants observed videos depicting rational straight, rational curved or irrational curved actions which could be implemented by a fully-visible person, a person with their face hidden or a moving ball (See Fig. 1). All stimuli depict goal-directed actions that either curve over a barrier (rational) or curve with no barrier (irrational), and all are matched for action kinematics and timing. Three different social forms will be compared: a full human (face + body), a human body only (head not visible) and a moving ball with no human present. By using these well-matched stimulus videos that precisely control the rationality of the action and the social form of the stimuli, it will be possible to define how the AON and MZN are engaged by simple observation of actions varying in rationality, and whether these responses are modulated by the social form of the stimulus.

To make predictions for possible patterns of results, it is useful to consider the three previous studies of observation of irrational actions in more detail. Brass et al. (2007) showed participants movies where an actor used an unusual effector to achieve a goal, whilst rationality of the action was defined by environmental constraints. For example, an actress turned on a light switch with her knee whilst her hands were free (irrational) or occupied by a stack of books (rational). Both the pSTS and mPFC showed greater responses to irrational actions than to rational actions. In a second study, Marsh and Hamilton (2011) showed both typical and autistic participants videos of a hand reaching for an object along a straight trajectory or a curved trajectory. Action rationality was defined by the presence or absence of a barrier. Results showed that the right IPL was more active when typical and autistic participants saw irrational actions, whilst the mPFC was less active when typical participants viewed irrational actions. In a third study of action rationality, Jastorff et al. (2010) showed participants movies of an actor reaching over a barrier to pick up an object, with a mismatch between trajectory and barrier height making some actions irrational. They report no differential MZN activity during the observation of irrational actions, but found that activity in the middle temporal gyrus (MTG) correlates with action rationality as judged by each participant after scanning.

Overall, these three studies report three different patterns of results, with the MZN activated (Brass et al., 2007), deactivated (Marsh and Hamilton, 2011) or not engaged (Jastorff et al., 2010). AON activation was also only reported in one previous study (Marsh and Hamilton, 2011). Some of the differences between these results could be accounted for by the analysis methods used. Whilst Marsh and Hamilton (2011) and Brass et al. (2007) examined responses to movies designed to be rational or irrational. Jastorff et al. (2010) correlated individual participants' ratings of action rationality with brain responses during observation. Here we will apply both methods to the same dataset. We predict that an analysis based on the categories of rational v. irrational actions will engage AON or MZN regions as found by Marsh and Hamilton (2011), and Brass et al. (2007), whilst an analysis based on individual rationality ratings will engage higher order visual cortex as found by Jastorff et al. (2010).

Our second aim is to evaluate the impact of social form on processing of action rationality. The stimuli in Brass et al. (2007) showed the actors whole body, whilst those in Jastorff et al. (2010) depicted an actor's torso, arm and face. In contrast, the stimuli in Marsh and Hamilton (2011) showed only a hand and arm with no face or body. It is possible that changes in the amount of social information available allow the observer to interpret the actions differently. The importance of social information for understanding action rationality is demonstrated in eye tracking studies which show that participants fixated the face of the actor more following their completion of an irrational action (Vivanti et al., 2011). This may be because participants seek to rationalise the actor's unusual behaviour by looking at their facial expression (Striano and Vaish, 2006) or gaze direction (see Carpenter and Call (2007) for a review). Thus, we predict that observing actions with a full human actor compared to the same object movement without an actor will lead to stronger engagement in brain regions associated with face processing. Furthermore, if facial cues matter for rationality judgement, there may be an interaction between social form and rationality in either the AON or the MZN.

Materials and methods

Participants

Twenty-five participants (19 female, mean age = 21.48, 24 right-handed) gave written informed consent before taking part. Participants

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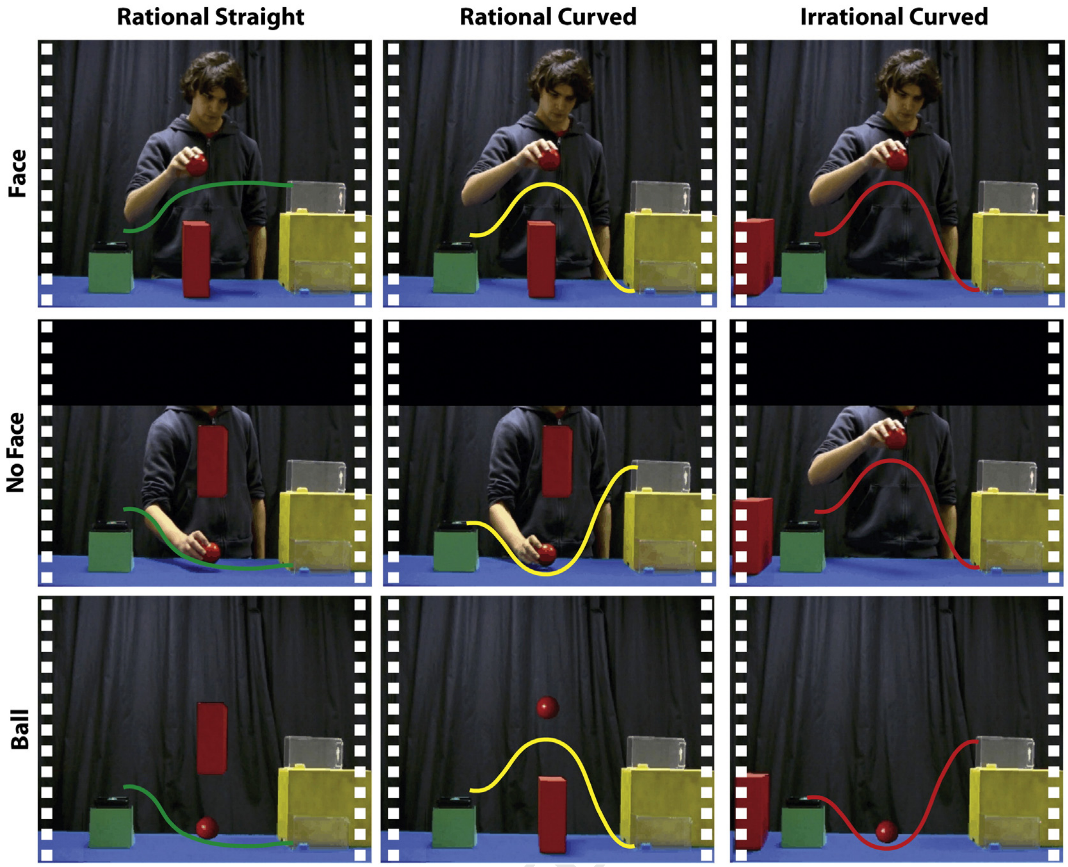

Fig. 1. The middle frame from each movie. In each movie the ball starts on the left and is placed in one of the two containers on the right. Coloured lines visualise the movement trajectory of the ball and do not appear in the movie. Rationality is constrained by the position of the barrier.

were recruited through a web-advert on the university intranet and were paid £10 for participation. The study was approved by the University of Nottingham ethics committee.

Stimulus generation

Movie clips presented during fMRI scanning are illustrated in Fig. 1. In each clip a red ball started on the left of the screen and was moved to one of the two transparent containers on the right. These containers were stacked vertically to create upper and lower action goals. The trajectory of the ball between the start point and the goal was either a straight action or a curved action. Both actions were matched for timing on a frame by frame basis such that the start and end point of the action coincided. All movies lasted 3.7 s.

To generate these movies, first a male actor was filmed moving the ball to the upper or lower container along a straight or curved trajectory (4 movies). Care was taken to match the timing of the different actions and to ensure that the trajectories to the upper and lower containers were mirror images of each other. Then, a red barrier was superimposed over each movie using VirtualDub software. Two versions of the curved action movies were created. In one version, the barrier was placed between the start point and the goal such that the action had to curve over the barrier to reach the goal, thus making the curved trajectory rational. In the second version the position of the barrier had no bearing on the action trajectory and so the action was irrational. This set of six movies (rational straight, rational curved, irrational curved, with 2 goals for each) was then edited to vary the social information available. In the human face condition, the head, torso, hand and arm of the actor were fully visible. In the human no face condition, a black strip was superimposed at the top of each movie so that the face was occluded but the torso of the actor was still visible. To generate the movies in which the ball moved independently, the coordinates of the ball were recorded for each frame of each movie. A red ball was then digitally superimposed on a still image of the background scene in the appropriate position for each frame. Video editing was completed using Matlab 6.5 and VirtualDub. The final stimulus set comprised 18 movies (three action types X two goals X three social conditions). These conditions will be referred to by codes denoting the social form of the stimuli (ball (b), face (f) and no face (n)) and the rationality of the action trajectory (rational straight (RS), rational curved (RC) and irrational curved (IC)). As the main focus of this paper is on the effects of rationality, only the responses to rational curved and irrational curved movies are included in the main analyses. Rational straight actions are included in the design to prevent the participant from expecting a curved movement trajectory on every trial but they are not included in the analyses.

fMRI procedure

During fMRI scanning participants saw movies of 3.7 second duration in an event-related design. Each run of scanning contained each of the 18 movies, repeated six times. Movies were presented in a pseudorandom order so that same movie was not repeated consecutively. A fixed 600 ms inter stimulus interval occurred between each movie. The full run of scanning lasted approximately 9 min and participants completed two runs. To maintain alertness, six catch trials were presented randomly within a run. Participants were asked to answer a simple question about the movie they had just seen, for example 'Did the actor place the ball in the top box?' Participants were required to provide 'yes' or 'no' responses with a button box. Overall accuracy for these questions was high (mean: 91.6%, standard deviation: 0.1) and there was no need to exclude any participants due to inattention. Whole brain images were collected with a 3 T Phillips Achieva MRI scanner using a 32-channel phased array head coil. 40 slices were collected per TR (3 mm thickness). TR: 2500 ms; TE: 40 ms; flip angle: 80 ; FOV: 19.2 cm; and matrix: 64 × 64. 214 brain images were collected during each of the two functional runs. High resolution anatomical scans were also collected.

Following fMRI scanning, participants were asked to watch each movie again and rate its rationality, using a battery of six statements. These items were: 'The actor was efficient at reaching the goal', 'This action seemed weird', 'The movement in this action was unusual', 'This action was unnatural', 'This action was normal' and 'I would complete this action differently'. Participants were asked whether they agreed or disagreed on a scale of one to five. The score on negative items was reversed and the total rationality score was computed for each participant for each movie (maximum score of 30 indicated most rational).

Data analysis

Data were analysed using standard procedures in SPM8. First, images were realigned, unwarped and normalised to the standard SPM EPI template with a resolution of 3 × 3 × 3 mm. Head movement characteristics were inspected for each participant and total movement never exceeded 3 mm over the course of the entire scan. Following normalisation procedures, 8 mm smoothing was applied. Two different design matrices were created for each participant. In stimuli driven design, nine regressors were generated, one for each action type (rational straight, rational curved and irrational curved) crossed with each social type (face, no face and ball) plus an additional regressor for catch trials. In the parametric design, a regressor was entered for each social category (face, no face and ball) and a further parametric regressor per social category was generated to represent the modulation of that social category by rationality. The weightings in the parametric regressors were determined by that participant's ratings of rationality for each movie. These ratings were orthogonalized automatically in SPM by setting the mean value of each predictor to zero. An example design matrix for the parametric model is included in the Supplemental information. For each design, each trial was modelled as a box-car of 3.7 second duration, convolved with the standard haemodynamic response function.

Using results from the stimulus-driven design, forward and reverse contrasts were calculated for action rationality (bRC + fRC + nRC) > (bIC + fIC + nIC), social form (ball > person and no face > face) and interactions between rationality and social form. The parametric design was used to identify brain regions which respond linearly to ratings of rationality. In these contrasts, a 1 (for the forward contrast) and −1 (for the reverse contrast) was placed over the column including the rationality ratings and a zero was placed over all other columns. All contrast images were then taken to the second level for random effects analyses. Correction for multiple comparisons was performed at the cluster level with a voxel-level threshold of $p < 0.005$ and $k = 10$ and a cluster-level threshold of $p < 0.05$ (FWE corrected). All figures are illustrated at this threshold. In social form contrasts, a small volume correction was applied to the action observation network. This mask was downloaded from www.neurosynth.org and was generated using the search term 'action observation'. The mask included the IPL, IFG and visual cortex. No additional activations were found when applying this correction.

Results

Behavioural rating of stimuli

Mean rationality ratings of each movie are presented in Fig. 2. A 3 (social) *x*2 (action) *x*2 (goal) repeated measures ANOVA revealed that rational actions were rated as more rational than irrational actions ($F(1,24) = 36.48$, $p < 0.0001$). An effect of social form showed actions performed by the ball were rated as less rational than human actions ($F(2,48) = 3.30$, $p = 0.04$). There was no effect of goal on rationality ratings ($F(1,24) = 0.04$, $p = 0.85$). A significant interaction between social form and action was found ($F(2,48) = 6.53$, $p = 0.003$), and inspection of the plots suggests the rational curved action by the ball was rated as less rational than the equivalent human actions ($F(1,24) = 36.48$, $p < 0.001$). All other interactions were not significant. Mean ratings of rationality for each movie type are presented in Table 1.

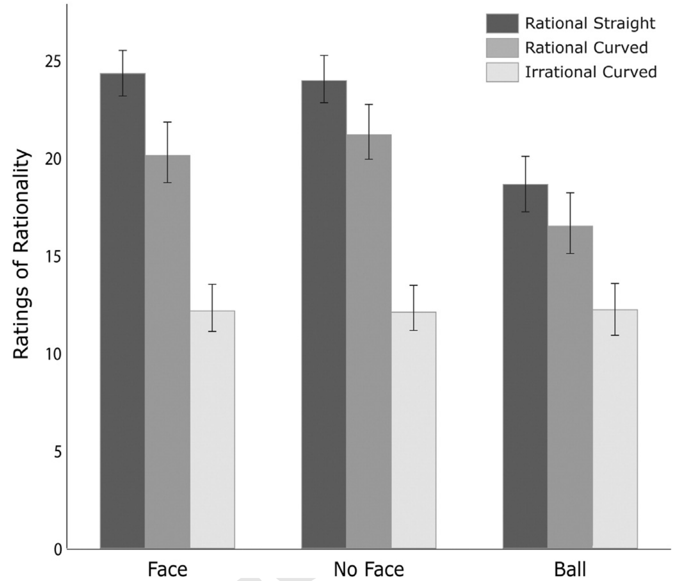

Fig. 2. Mean rationality ratings for rational straight (dark grey), rational curved (mid-grey) and irrational curved (light grey) actions by the degree of social form visible. Error bars indicate +/−1 standard error.

Brain responses to irrational actions

Brain responses whilst viewing rational actions (bRC + fRC + nRC) were contrasted with responses whilst viewing irrational actions (bIC + fIC + nIC). Three clusters responded more to irrational actions, compared to rational actions. These were identified as a diffuse cluster in the right IPL extending into the right TPJ; the right IFG; and a large area of the middle occipital cortex (Fig. 3A (blue), Table 2). In the reverse contrast, a large cluster in medial prefrontal cortex (mPFC) showed greater deactivation during irrational actions (Fig. 3B, Table 2).

Brain areas parametrically modulated by ratings of rationality

Five brain regions were parametrically modulated by individual participants' ratings of rationality. When looking for brain responses that were more active when actions were rated as most irrational, a large cluster in the right IPL extending to the TPJ was observed. This cluster is overlapping but slightly posterior to that reported in the previous analysis and the peak is centred over MTG (see Fig. 3A (green)). In addition, clusters in the middle occipital cortex, the left TPJ, the hippocampus and the cingulate were also parametrically modulated by rationality. No significant clusters were found in the reverse contrast.

Table 1
Ratings of rationality for each movie type. Values are means ± standard deviations. Q2

	Rational straight		Rational curved		Irrational curved	
Goal	Top	Bottom	Top	Bottom	Top	Bottom
Rationality ratings						
Face	21.7 ± 6.9	26.6 ± 3.2	20.0 ± 8.1	20.3 ± 7.6	13.1 ± 6.8	11.2 ± 5.1
No Face	23.1 ± 6.5	24.6 ± 5.6	20.8 ± 7.1	21.6 ± 7.0	12.0 ± 5.4	12.4 ± 6.2
Ball	16.8 ± 6.6	20.2 ± 7.3	15.8 ± 7.3	17.2 ± 8.4	13.0 ± 7.5	11.2 ± 6.5

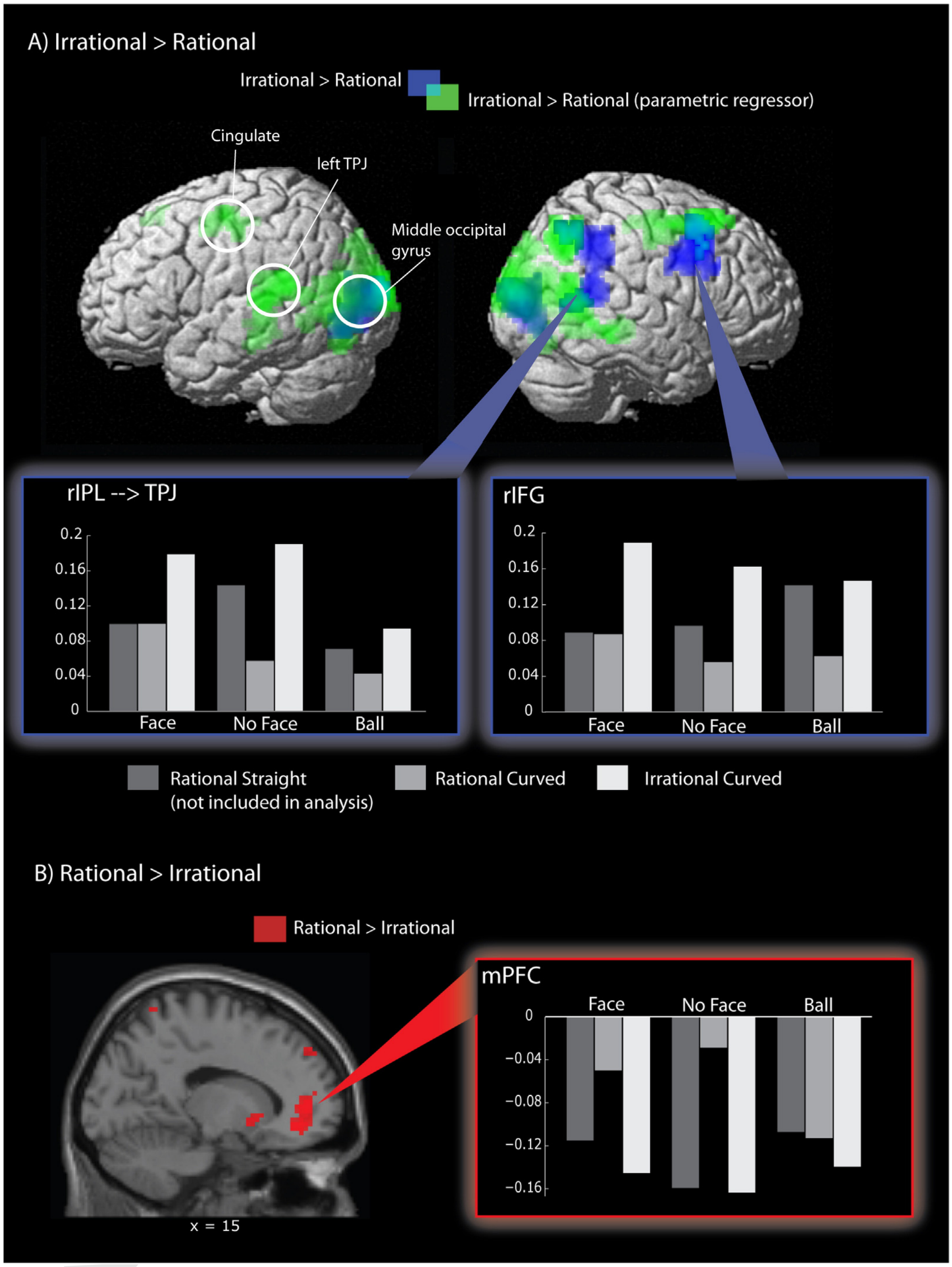

Fig. 3. A: Areas that were more active during observation of irrational curved actions compared to rational curved actions (blue), the areas that responded linearly to individual participants' ratings of action rationality (green) and the regions in which these contrasts overlap (turquoise). Parameter estimates (average SPM beta weights for the cluster) are plotted for key regions. IPL: inferior parietal lobule, IFG: inferior frontal gyrus, and TPJ: temporoparietal junction. B. Brain regions that responded more to rational curved actions, compared to irrational curved actions (red). mPFC: medial prefrontal cortex. All images are whole-brain cluster-corrected at $p < 0.05$, FWE corrected.

Brain responses to social form

The postcentral gyrus extending to the IPL and a large cluster spanning the posterior portion of the occipital cortex and extending to the STS was more active during the observation of a person acting compared to an animated ball. In the reverse contrast, a large cluster was found with peak activation over fusiform gyrus extending along the parieto-occipital fissure. In addition a small cluster in the posterior cingulate gyrus was more active when participants observed an animated ball compared to a human action. Only the lingual gyrus distinguished whether the participants observed an actor with the face visible or masked (see Fig. 4A, Table 3).

Interactions between rationality and social form

One interaction contrast yielded significant results. A large cluster in the occipital cortex, with peak activation in the fusiform gyrus responded more to irrational actions with a face and rational actions with a ball, but less to rational actions with face and irrational actions with a ball, that is: (fIC + bRC) > (fRC + bIC), see Fig. 4B and Table 4.

Table 2
Coordinates for rationality contrasts.

Location	Prob (cluster corrected p < 0.05 FWE)	Cluster size	T	MNI coords x	y	z
a) Rational > irrational						
Medial prefrontal cortex (mPFC)	0.035	197	4.49	−18	47	4
				0	35	−8
				−15	44	−8
b) Irrational > rational						
Middle occipital gyrus	0.000	491	6.06	9	−85	7
				−15	−94	10
				−9	−82	−2
Right Inferior frontal gyrus	0.004	306	4.94	36	14	34
				48	14	49
				35	5	31
Right IPL → TPJ	0.004	312	4.88	48	−40	34
				45	−45	13
				39	−61	7
c) Parametric rationality (R > I)						
No suprathreshold clusters						
d) Parametric rationality (I > R)						
Middle occipital gyrus	0.000	1454	5.97	−12	−100	10
				3	−85	13
				18	−88	10
Left TPJ	0.031	173	5.49	−51	−43	16
				−42	−49	13
				−60	−34	7
Hippocampus	0.044	159	4.67	−12	−28	−8
				−21	−31	−2
Cingulate	0.008	228	4.47	−9	−10	55
				15	−13	46
				0	−7	55
Middle temporal gyrus	0.016	200	3.81	51	−61	13
				42	−58	7
				54	−52	1

No AON or MZN regions showed an interaction between rationality and social form, even at lower thresholds.

Discussion

The present study examined how observation of irrational hand actions engages the AON and MZN in the human brain. Results demonstrate that the right inferior parietal cortex, middle temporal gyrus (both in the AON) and medial prefrontal cortex and temporoparietal junction (in the MZN) are sensitive to observed irrational actions. The parietal region was also modulated by participants' judgements of rationality. However, none of these regions were sensitive to the social form of the stimuli, and all showed similar responses to actions performed by humans and balls. We now discuss the implications of these findings in relation to previous studies and theories of rationality understanding.

Brain responses to action rationality

Four major brain systems were sensitive to action rationality: the medial prefrontal cortex, the right inferior parietal cortex extending to the temporoparietal junction, the inferior frontal gyrus and the middle temporal gyrus. These regions have traditionally been associated with different functions including mentalising, action observation and higher order visual processing. We consider each in turn.

First, the mPFC and TPJ are core components of the MZN. In our dataset, the mPFC showed a significant deactivation when watching irrational actions, whilst right TPJ showed a significant activation. Both the left and right TPJ showed correlations between participant's post-scan ratings of rationality and the BOLD signal. The deactivation of mPFC replicates the results of Marsh and Hamilton (2011), but contrasts with the results of Brass et al. (2007). However, a comparison of activation peaks (Fig. 5) shows that the activation in Brass et al. (2007) is more dorsal than the present study. As the activations from these studies are in slightly different regions, they may reflect different processes of rationality resolution. Movies used in Brass et al. (2007) involved the observation of unusual body movements in all conditions. In comparison, the movies in this study showed simple, goal directed hand actions that are much more familiar. Compare turning on a light switch with your knee to reaching in an arc for an object. In the case of the light-switch, the action is novel, whether it is rationalised by carrying books or not. However, reaching with an indirect movement path is much more familiar as we need to take environmental obstructions into account frequently. Perhaps the way we deal with action rationality when an action is novel, compared to familiar can account for the differences in findings between the two studies.

A substantial activation of higher order visual regions was found. These areas were strongly modulated by rationality ratings but were not seen in the stimulus-driven model. As Fig. 5 shows, brain areas correlating with subjective ratings were generally more posterior than those which responded in the stimulus-driven model. This is congruent with the results of Jastorff et al. (2010), who found correlations between rationality ratings and brain activation in MTG but not in more frontal areas. Furthermore, neither our study nor that of Jastorff et al found any engagement of the mPFC when using a rationality rating model. This is unlikely to be due to weak power, given the different design parameters used in each study and our positive mPFC engagement in our categorical rationality analysis.

Rather, we suggest that there may be two types of rationality perception in the brain — a continuous sensitivity to subtle kinematic features in MTG; and categorical perception of actions as either 'rational' or 'irrational' in the MZN. Research on object perception shows that early visual areas are sensitive to many individual features of an object, whilst temporal and frontal cortices can show categorical responses to object groups (Jiang et al., 2007; Van der Linden et al., 2010). Our data may reflect a similar organisation in the processing of action rationality, from kinematic features in MTG to categories of 'rational' or 'irrational' in frontal and parietal cortices.

Both the present study and Brass et al. (2007) report activation of the right TPJ during observation of irrational actions. We further add the finding that bilateral TPJ was sensitive to rationality ratings. Previous studies suggest that the right TPJ is engaged when participants see actions which violate their expectations (Pelphrey et al., 2003; Saxe et al., 2004) and when participants infer goals from non-stereotypic actions (Liepelt et al., 2008). In contrast, left TPJ was more active when participants were instructed to think about the motive of an action (Spunt and Lieberman, 2012). Together, these results demonstrate that the TPJ has a full role in responding to observed irrational actions. It is likely that this involves mentalising about why the agent performed an unusual action, or making inferences about the agents' intentions.

Activation was also found in the right IPL and right IFG, both within the AON. These regions were more active when participants saw irrational actions compared to rational actions. This result is congruent with the previous study which found stronger right IPL activity when viewing irrational actions (Marsh and Hamilton, 2011). It is also consistent with previous reports implicating right frontoparietal cortex in the comprehension of more complex actions (Hartmann et al., 2005) and their outcomes (Hamilton and Grafton, 2008). Right IFG is also engaged when participants are specifically directed to attend to the means by which an action is achieved when observing both typical (Spunt et al., 2011) and irrational actions (de Lange et al., 2008). It is possible that participants attend to the kinematic features of the action more closely when the actor violates their expectations by performing an irrational action, thus resulting in the increased IFG activation reported here. The co-activation of the right AON and the MZN during irrational action observation shows that these two networks can work together in action comprehension. We suggest that the AON identifies the complex

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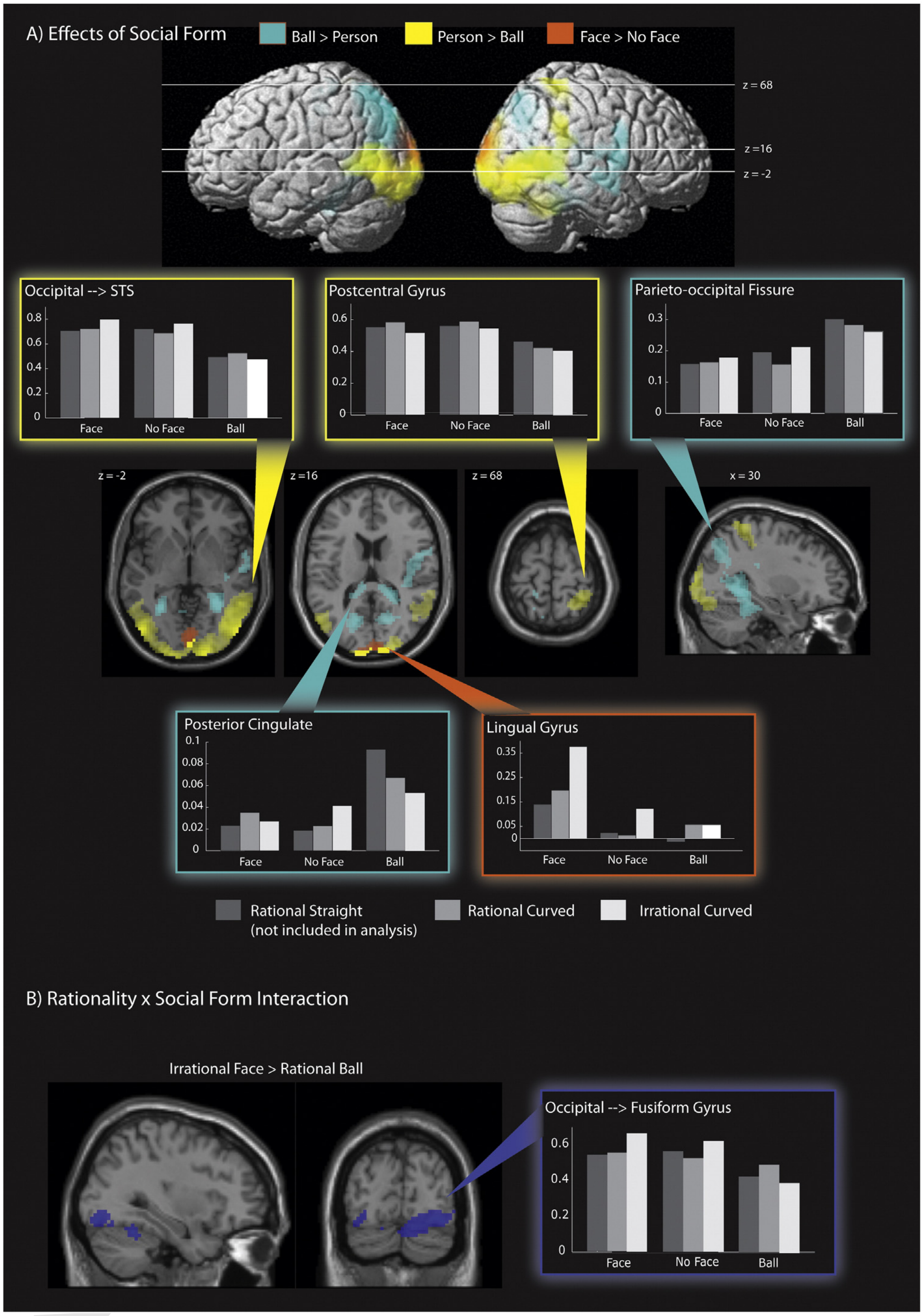

Fig. 4. A: Main effects of social form. Brain regions that responded more to moving balls compared to humans (turquoise), regions which were more responsive when observing a human actor compared to moving balls (yellow) and the region which responded more to a human when the face was visible, compared to when the face was hidden (orange). Bars indicate parameter estimates (average SPM beta weights for the cluster) for clusters of activation above threshold. B: The interaction between rationality and social form. All images are whole-brain cluster-corrected at $p < 0.05$, FWE corrected.

actions that require additional analysis, whilst the TPJ and mPFC may perform further mentalising about the actor's intentions or why they performed an unusual action is processed. This is consistent with data reported in a previous meta-analysis by Van Overwalle (2009).

All of the analyses reported in this paper have compared matched rational and irrational actions which have a curved trajectory. Rational straight actions were included in the design to prevent the observer from always expecting a curved movement and responses to these movies were never intended to be analysed. However, inspection of the parameter estimates for the rational straight actions reveals that responses to these movies are sometimes more similar to the irrational actions than the rational actions, especially in the mPFC. A possible explanation for this pattern of results could be that mPFC activity is reflecting the effort involved in rationalising behaviour. As the rational straight actions require no rationalisation and the irrational curved actions cannot be rationalised, mPFC activity is reduced. However, in the case of the rational curved actions, the observer has to evaluate the efficiency of the action against the environmental constraint in order to rationalise behaviour. This more effortful processing could be driving the increase in activity in the mPFC in only the RC actions. However, this is a post-hoc explanation and further work will be needed to determine if this really is the case.

Q4 **Table 3**
Coordinates for social contrasts.

Location	Prob (cluster corrected $p < 0.05$ FWE)	Cluster size (functional voxels)	T	MNI coords x	y	z
a) Ball > person						
Parieto-occipital fissure	0.000	3257	8.01	30	−49	−5
				60	5	10
				33	−37	−14
Posterior Cingulate	0.028	174	4.08	−12	−31	19
				−18	−31	43
				−12	−40	19
b) Person > ball						
Occipital → STS	0.000	3372	11.78	51	−79	−2
				9	−94	−11
				−48	−76	1
Postcentral Gyrus → IPL	0.011	210	6.09	21	−52	70
				30	−49	70
				33	−40	61
c) Face > no face						
Lingual Gyrus	0.000	443	5.82	9	−100	16
				−6	−103	13
				3	−82	−2
d) No face > face						
No suprathreshold clusters						

The impact of social form on rationality perception

The second aim in this study was to determine the extent to which AON and MZN responses are modulated by the social form of the actor. Only one brain region differentiated both rationality and social form. This was a large cluster in the occipital lobe, with the peak of activation found in the fusiform gyrus. This region responded more to irrational actions when the face was visible and rational ball actions, but less to rational face actions and irrational ball actions. One previous eye tracking study demonstrated that after seeing an irrational action, participants then fixate more on the face of the actor, presumably in an attempt to rationalise the observed behaviour from facial expression or eye gaze cues (Vivanti et al., 2011). If participants in our fMRI study show the same gaze behaviour, this could drive the engagement of the fusiform gyrus following observation of irrational actions with the face visible. Past studies strongly link the fusiform gyrus to face perception (Kanwisher et al., 1997) and show that this activation is modulated by covert attention to the face (Wojciulik et al., 1998).

Q6 Q5 **Table 4**
Coordinates for social × rationality interaction contrasts.

Location	Prob (cluster corr)	Cluster size (functional voxels)	T	MNI coords x	y	z
a) Face/ball						
No suprathreshold clusters						
b) Reverse face/ball						
Occipital → right fusiform gyrus	0.000	888	4.93	33	−82	−11
				−15	−49	−23
				−39	2	−38
c) No face/ball						
No suprathreshold clusters						
d) Reverse no face/ball						
No suprathreshold clusters						
e) Face/no face						
No suprathreshold clusters						
f) Reverse no face/face						
No suprathreshold clusters						

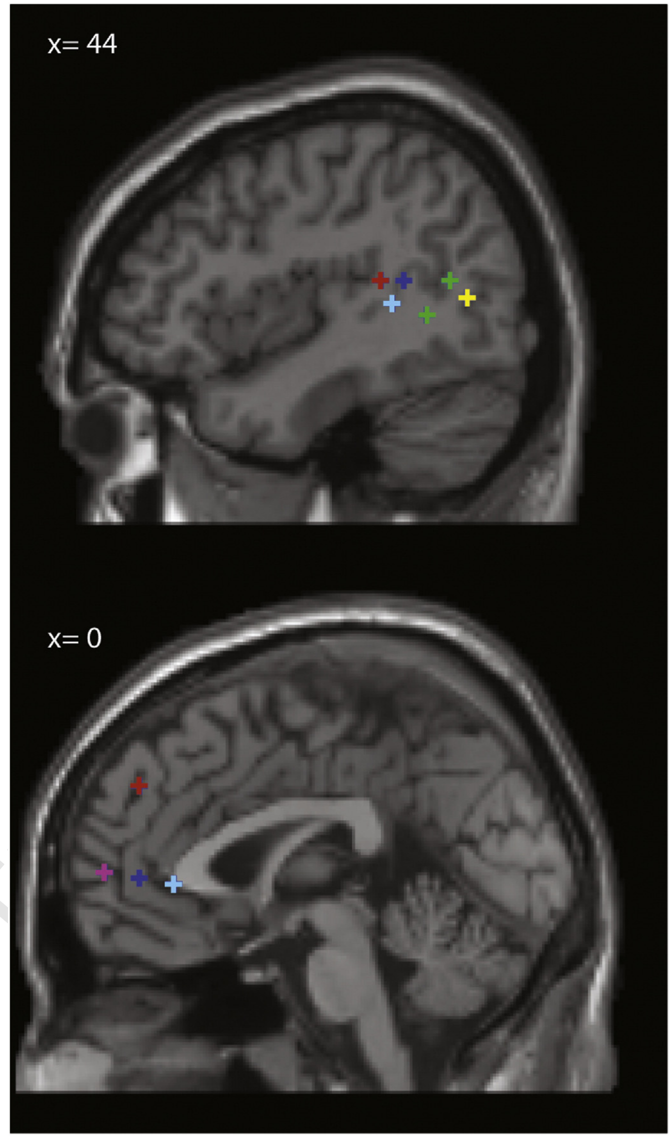

Fig. 5. A comparison of peaks of activation in TPJ, MTG and mPFC for both the stimulus driven model (dark blue) and the rationality rating model (green) from the present study and previous studies involving the observation of irrational actions (Light blue: de Lange et al., 2007; Pink: Marsh and Hamilton, 2011; Yellow: Jastorff et al., 2010; Red: Brass et al., 2007). Q1

No AON or MZN regions showed interactive responses for rationality and social form, suggesting that rationality of actions is computed, irrespective of the social form of the actor. Examining the parameter estimates for mPFC (Fig. 3B) suggests that there might be a different pattern of response to human and ball actions, with little difference between rational curved and irrational ball actions. This implies that the mPFC may be more sensitive to the rationality of human actions; however this pattern was not statistically robust. This is consistent with previous work that demonstrates that even 12 month old infants attribute rational intentions to animate blocks or balls (Csibra, 2008) and in adults, brain responses to rationality do not differentiate an animate agent from a single moving ball (Deen and Saxe, 2011).

There was no increased engagement of the IFG component of the mirror system during the observation of human actions. This is in line with an increasing body of evidence which suggests that mirror systems are not as selective for human actions as previously thought (Cross et al., Q12

2011; Gazzola et al., 2007; Ramsey and Hamilton, 2010). Instead the brain region which distinguished human from ball actions were a large, diffuse cluster in the visual cortex which is likely to reflect the increase in visual detail when the actor was present. This cluster extended to the STS, a region known to respond during perception of social stimuli (Centelles et al., 2011; Pelphrey et al., 2004; Saxe et al., 2004).

Limitations

The present study utilised a very 'dense' event-related design in which stimuli were presented with only 600 ms ISI. This design was selected to effectively minimise the 'rest' time in the scanner, allowing us to present more trials in the available time. It is possible that this dense design could reduce statistical power, particularly in regions that may have non-standard haemodynamic response functions like frontal cortex. Given the close matching between the results reported here with a dense event-related design, and those of Marsh and Hamilton (2011) which used a block design, it seems unlikely that lack of power is a major worry. Furthermore, experimental designs with short ISIs have previously been used to generate robust and replicable results when using a fully randomised trial order (Hamilton and Grafton, 2006).

In order to maintain strict experimental control over the actions presented, the same set of 18 movies was repeated throughout the entire study. Therefore, repetition suppression (the reduction in BOLD signal for repeated compared to novel stimuli (Grill-Spector et al., 2006)) may reduce the power of this study to detect positive effects. In particular, the process of rationalisation of irrational actions may diminish with repetition, leading to a reduction in selectivity for action rationality towards the end of the experiment. However, recent eye-tracking data with the same stimulus set show that gaze behaviours do not change substantially over the course of 16 repetitions, indicating that irrational actions are still viewed as 'irrational' despite becoming more familiar (Marsh, Pearson, Ropar & Hamilton, accepted for publication). The role of expectancy or predictability in processing irrational actions has yet to be formally assessed and may provide an interesting avenue for future research. Ultimately, this potential reduction in selectivity over the course of the experiment emphasises that the effects reported here are robust to decreases in experimental power.

Conclusions

This paper assesses the relative contributions of the mirror and mentalising systems for understanding irrational actions. Previous results have shown mixed results in this field due to differences in stimuli construction and analysis. The findings reported in this paper clarify some of these differences by using strictly controlled stimuli and two different analysis models. Our results show that when action rationality is altered by environmental constraints, both AON and MZN respond to this change. Therefore, we argue that AON and MZN systems are playing complimentary roles in understanding action rationality. We also demonstrate that social form has little impact on brain responses to rationality in AON and MZN regions, providing evidence that neither system is selective for human action, as previously thought.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2014.09.020.

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