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

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ABSTRACT

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 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; Vander 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 the 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