UNDERSTANDING ACTION RATIONALITY: STUDIES OF NEUROTYPICAL AND AUTISTIC POPULATIONS

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ABSTRACT

A remarkable feature of human behaviour is that it is possible to extrapolate a large amount of information about what a person thinks or believes, purely by observing their behaviour. There are separate systems in the brain that decode *what* action is being performed and *why* that action is performed. Independently, these systems are reasonably well understood but the way in which they interact is still an open question. In this thesis I investigate how we come to understand others actions, particularly if they are unusual or irrational. Irrational actions provide a special test case for examining this question because full comprehension requires an understanding of what an agent is trying to achieve as well as an understanding of why they are performing the action in an unusual way.

The first study in this thesis uses fMRI to identify the neural networks that differentiate rational and irrational actions. It also examines the extent to which activity within these networks is dependent upon the presence of a human agent. I report that both the action observation network and the mentalizing network are sensitive to the rationality of actions but neither system differentiates the social form of the agent. In the second study, I aimed to further this knowledge by examining the cognitive processes that underpin rationality comprehension. I used eye tracking to identify how participants direct their attention and predict action goals during observation of rational and irrational actions. A number of eye tracking markers which reflect rationality detection were identified.

A second major aim of this thesis was to examine whether individuals with autism spectrum condition (ASC) have a specific impairment in rationality comprehension. Previously neural differences during irrational action observation have been reported but the cognitive reasons for this difference have not been specified. In study three participants with ASC observed rational and irrational hand actions during eye tracking. The rationality detection markers identified in the previous study were present in individuals with ASC suggesting that the cognitive mechanisms for rationality understanding are intact. However, subtle group differences emerged when considering social components of the task. I hypothesised that these differences would be larger in an interactive rationality comprehension task.

In study five I evaluate the use of an overimitation paradigm in typically developing children. I conclude that imitation behaviour is dependent upon social responsiveness and rationality comprehension. Furthermore, these aspects of imitation behaviour can dissociate when comparing explicit judgements of rationality and implicit imitative responses. In the final study I therefore use this task to examine rationality comprehension and social responsiveness in children with ASC. I report that children with ASC have the capacity to understand action rationality but may have difficulty with social modulation of their responses.

I conclude this thesis with a new model of rationality comprehension which links brain, cognition and behaviour. I also propose why individuals with ASC may have difficulty with the social component of action comprehension tasks.

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CHAPTER 1. GENERAL INTRODUCTION

1.1 ACTION UNDERSTANDING AND MENTALIZING IN ADULTS

By observing the people around us, we are able to make sense of their actions in terms of what they are doing and why. For example, walking around a busy shopping area, we can anticipate each person's movement path to avoid bumping into them, make inferences about what they are buying and the beliefs or desires that are attached to their actions. Thus, action understanding is fast, automatic and can afford complex interactions between individuals. By watching the lady at the greengrocers reaching for the plums, we can see from the shape of her hand and the subtle movements of her muscles that she is squeezing the fruits. Extrapolating this information and combining it with the action context, we may infer that she is trying to select the ripe fruit. Perhaps she is going to make a plum crumble for pudding. If on the other hand, the lady starts to prod the plums with her elbow instead, this action is much harder to understand. We may need to make more elaborate inferences about her beliefs, knowledge or intentions in order to fully rationalise her behaviour.

The way in which we understand and interpret others' behaviour is a core topic for social cognition and one that this thesis aims to advance. In particular, I focus on how we respond to actions that seem irrational as these are the cases in which interpretation and inference are also needed for understanding. First, I briefly introduce the cognitive theories that attempt to explain how we move from the visual perception of an action to an understanding of what the agent is doing and why. I will then outline the case for studying irrational actions and why they are important for action understanding. Following this I describe some of the tools that we can use to examine the mechanisms of action understanding and review previous studies which have contributed to our understanding of this topic. Finally, I identify the key questions that this aims to thesis address and summarise the experiments that will be reported.

1.1.1 A HIERARCHY OF ACTION UNDERSTANDING

When observing an action, we can understand it at a number of different levels (Hamilton & Grafton, 2007). In a bottom-up framework, basic action understanding starts with perceptual input. Beyond this, we can extract kinematic features of actions such as muscle contractions, hand posturing and the trajectory of the movements. Our perceptions here are of a stream of movements which we need to segment into discrete units of meaningful action in order to gain understanding (Heider, 1958). Adults are able to parse movement sequences into a series of actions and are consistent in their boundary demarcations (Newtson, 1973). These demarcations are understood in terms of action goals (Newtson & Engquist, 1976) or outcomes (Hommel, Müsseler, Aschersleben, & Prinz, 2001) and are organised hierarchically (Baldwin & Baird, 2001). Thus, we can represent an action in terms of its immediate goals, like grasping a plum, or in terms of higher order goals like checking the plum is ripe. Judgements about future intentions can also be made: she is going to make a plum crumble (Vallacher & Wegner, 1987). The key to this view of action understanding is the fact that actions are represented in terms of goals and sub-goals in a hierarchical structure.

This structure of action is revealed when we consider studies of imitation in which participants observed an action and were subsequently asked to copy it (Wohlschläger, Gattis, & Bekkering, 2003). Children copy the goal of an action (touching a particular object) but will ignore the means by which the action was achieved (whether the experimenter used their left or right hand), indicating that touching the object was the dominant goal whereas using the left hand was a subordinate goal that was not imitated. This pattern of results changed when the objects were absent and the experimenter touched a particular location on the table with their left or right hand. In this case children faithfully imitated the hand used, presumably because the children now perceived the goal of the action to be using the correct hand (Bekkering, Wohlschläger & Gattis, 2000). A similar pattern of results show that adults also organise actions into a hierarchy of goals. They are more likely to imitate an action goal and object treatment but rely on their own motor programs for movement kinematics and effector choice (Wohlschläger & Bekkering, 2002).

Action goals are therefore central for action understanding. However, the precise definition of a 'goal' differs between researchers. The goal of an action can be defined as a physical object that is to be grasped or manipulated (Gattis, Bekkering, & Wohlschlaeger, 2002). In this view, a goal-directed action is an action that targets or manipulates a particular object. Alternatively, the term goal has also been used to describe the desired end state of an action and a goal-directed action under this view describes an action that changes the state of world to match the desired end state (Travis, 1997). The experiments in this thesis use this second definition, examining simple goal-directed hand actions in which the goal of the action is to move or retrieve an object to and from a particular location. In the next section I review theories of how we identify and understand the goal of an observed action.

1.1.2 COGNITIVE MECHANISMS OF ACTION UNDERSTANDING: UNDERSTANDING THE 'WHAT' OF AN ACTION

The dominant view of how we understand others' action goals is through embodiment. The theory of embodiment proposes that we apply the knowledge of our own bodies onto others in order to understand their action goals. One such influential theory was pioneered by Marc Jeannerod. It is based on the idea that during action execution we have a covert representation of the actions that we will produce. This covert representation (or s-state) is a motoric representation that has not yet been potentiated. When observing someone else performing an action, this s-state may also be active in the observer. In this way, the observer is performing a simulation of the action that they are witnessing within their own motor system. It is argued that this motor simulation grants the observer access to the actor's goals and intentions by 'placing themselves in the actors shoes' (Jeannerod, 1995). Evidence for this account comes from studies which demonstrate a functional relationship between action production and the mental simulation of that action.

This relationship has been established between the time it takes to perform and action and the simulated performance time (Decety, Jeannerod, & Prablanc, 1989). This time also increases to the same degree when task difficulty of the actual or the imagined action increased (Decety & Lindgren, 1991). Physiological responses to performed and simulated actions are also similarly altered by task difficulty. This has been demonstrated using electromyographic (EMG) recordings from the active (or imagined to be active) muscle (Bonnet, Decety, Jeannerod, & Requin, 1997) and in recordings of heart rate (Decety & Jeannerod, 1993). Finally, mental rehearsal of actions in athletes also improves actual action performance as much as physical practice of that action (Vogt, 1995).

As simulation theory emphasises embodiment of actions in order to access understanding, it predicts that understanding should relate to ability to perform these actions. Superior action understanding performance has been demonstrated for individuals that have related motor expertise (Aglioti, Cesari, Romani, & Urgesi, 2008) while poorer gesture comprehension relates to gesture production ability in patients with limb apraxia (Buxbaum, Kyle, & Menon, 2005). Developmental studies also report that motor ability and action comprehension are tightly coupled (Carpenter, Nagell, & Tomasello, 1998; Gredebäck & Kochukhova, 2010).

Studies of brain function also support this embodied approach to action understanding. The involvement of the motor system during action observation tasks is frequently reported and the recent discovery of mirror neurons provides physiological evidence in support of action simulation (Gallese, Fadiga, Fogassi, &

Rizzolatti, 1996; Rizzolatti, Fogassi, & Gallese, 2001). Furthermore, involvement of the motor system during action comprehension tasks is demonstrated by interference studies in which performing an incongruent action during an understanding task impairs performance (Kilner, Paulignan, & Blakemore, 2003). Further discussion of the brain systems recruited during action understanding is reported in Section 1.2 of this introduction.

While simulation theory has gained a large amount of support, there is also evidence which does not fit with this account of action understanding. A point of contention for simulation theory is at what level of action does simulation occur (De Vignemont & Haggard, 2008)? As previously mentioned, actions can be considered as a stream of fluid muscle expansions and contractions, of movements and joint angles. Do we represent each of these aspects of an observed action motorically? Or do we simulate actions more generally in terms of their abstract goals? The direct-matching account argues that we represent actions at a kinematic level of description (Iacoboni et al., 1999; Rizzolatti et al., 2001). Through this bottom-up matching, we are able to represent an actor's goal by covertly representing the motoric components of actions and therefore understand what it is that we would be doing if it were us performing the action (Gallese, Keysers, & Rizzolatti, 2004).

Problems with this account lie with the problem that direct matching is not always possible. For example, children are able to understand actions that are performed by adults but their limbs are much shorter and their hands much smaller. As such, they are unable to perform an adult's actions in an identical way

(Wohlschläger et al., 2003). Furthermore, the precise kinematics used to perform even a simple action is not always directly observable and understanding the exact means by which an action is achieved is not as important as understanding the action goal in many cases. Recent studies also suggest that action simulation can be modulated by the observer's perception of the actor's intention (Liepelt, Cramon, & Brass, 2008) and through social interaction (Kourtis, Sebanz, & Knoblich, 2010). Therefore, a simple, bottom-up matching approach does not encompass the flexibility within the action understanding system.

Additionally, if we consider how best to respond to observed action, it is not always useful to represent the actor's own motor plan as we do not always wish to perform an imitative response. Rather a complementary action which helps to achieve the agents' goal would be more useful. For example helping someone to move a table, one person must walk forwards whilst the other walks backwards. Yet the movements still need to be coordinated to successfully work together. In this situation, a representation of the actor's motor plan would interfere with your own, making joint action much less successful than is (Sebanz, Bekkering, & Knoblich, 2006).

A further problem with a simulation account of action understanding is that many of the same motor acts are used to achieve different action goals. For example reaching to grasp a wine bottle and reaching to grasp a dumbbell could have exactly the same kinematics but the goals of these actions are patently different. If simulation of an action's motor properties allows the observer access to these goals, how can it distinguish between these two motorically similar actions?

More recently theories regarding the role of the motor system during action observation have moved towards a predictive account (Csibra, 2004; Kilner, Friston, & Frith, 2007). Csibra argues that the activation of the motor system during action observation is the result of predictive action monitoring. Under this theory, interpretations about the goals of actions are completed outside of the motor system. Once an action goal has been predicted, the motor system then reconstructs the motor programme required to achieve that goal. Thus, this account places emphasis on top-down propagation of goal information to the motor system rather than a bottom-up matching approach. In essence, the observer is able to make predictions about the goal that an actor may have using Bayesian inference. From these predictions, an observer can then access a motor code that they can use to achieve that goal. As an action ensues, the observer can then compare their action prediction with the one that is occurring and update their prediction of the action goal accordingly. Emerging evidence for this model comes from computer simulations (Friston, Mattout, & Kilner, 2011) and electroencephalograpy (EEG) data which show predictive rather than reactive neural responses to observed actions (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004).

This predictive account also resolves a number of the problems raised against the simulation theory. For example, the level of ascription used by the motor system is selected by the observer, based on their interpretation of the action goal. Translation between adult and child actions is no longer a problem if the motor programme is generated within the observers' motor repertoire and based on the perceived goal. Finally, top-down modulation of the motor system can be based on goal inference in the context of the observed actions (see Csibra (2004) for a full account).

In summary, this section reviews theories for how it is that we can represent what others' goals are. It may be a process of simulation or of predictive inference but it is commonly accepted that the motor system is used to understand the goals of others. Another important aspect of action understanding is being able to interpret why a particular goal-directed action was performed and what the actor was intending, given the action context. In the next section I focus on the theories which try to explain how we make inferences about the 'why' of actions.

1.1.3 INFERENTIAL PROCESSES AND THEORY OF MIND: UNDERSTANDING THE 'WHY' OF AN ACTION

Understanding why someone has performed a particular action requires the observer to make a mental state judgement about the actor. For example, the lady at the green grocers now selects some brussels sprouts. From her behaviour we may guess that she likes the taste of sprouts or that she believes that eating sprouts is good for your health. This representation of others beliefs, desires or intentions is termed Theory of Mind (Premack & Woodruff, 1978) or mentalizing (Frith & Frith, 2003). Originally, when theory of mind was first described, it involved the representation of anothers' intentions (Premack & Woodruff, 1978). However, the investigation of how mental states are represented has been dominated by tasks requiring an understanding of beliefs. This is probably because the false-belief task provides a clear-cut assessment of theory of mind abilities (Dennett, 1978).

In the original study by (Wimmer & Perner, 1983) participants were told a story in which an agent (Maxi) holds a false belief about the location of some chocolate. When asked where Maxi will look for his chocolate, the participant needs to inhibit their own knowledge of the location of the chocolate and separately represent Maxi's false belief in order to correctly predict his behaviour. An extensive number of studies conclude that children start to pass this false belief task from around the age of 4 years and up (see Wellman, Cross, & Watson (2001) for a review) so it is commonly reported that mentalizing abilities start to develop throughout early school years. However, recent evidence from implicit mentalizing tasks with infants suggests that this ability starts to appear much younger (see section 1.5.2 for a review of the development of mentalizing abilities).

It is widely acknowledged that adults are very adept at mentalizing (Apperly, Samson, & Humphreys, 2009) but the question of how we mentalize is largely a philosophical debate (Goldman, 1993; Gopnik, 1993). Empirical studies assess the quality of adult mentalizing using tasks that involve reading social stories and answering questions that require the reader to represent the mental state of one of the characters (Happé, 1994) or labelling the interactions of cartoon shapes that are interacting in a socially meaningful way (Castelli, Happé, Frith, & Frith, 2000a;

Heider & Simmel, 1944). Most adult studies of mentalizing use brain imaging techniques to identify the neural mechanisms that are engaged during mentalizing tasks. These studies are reviewed in section 1.2.2.

1.1.4 ACTION RATIONALITY

Whilst the separate topics of how we understand basic actions and how we mentalize about others' behaviour have been extensively studied, the complete picture of how we link action comprehension and mentalizing to create a full understanding of what someone has done and why is less studied. This thesis contributes to this gap in the literature by studying responses to irrational actions. Rationality understanding provides an important bridge between action understanding and mentalizing as it may require a combination of basic action comprehension and inferential processing simultaneously (Brass, Schmitt, Spengler, & Gergely, 2007). If this is the case then examination of responses to irrational actions can provide us with information about how the processes of action understanding and mentalizing work together. In this section I start by providing a working definition of action rationality and review a cognitive theory which suggests that understanding irrational actions requires basic action understanding processes as well as mentalizing.

The principle of rational action states that an agent will act in the most efficient manner possible, considering the environmental constraints that have an impact on their action (Dennett, 1987). Therefore, within this thesis I use the term ‘irrational’ to describe an action that is inefficient or uses unusual means to achieve a particular goal. Critically for this view, the action context or the environment does not provide an explanation for the unusual behaviour displayed. Therefore, the action cannot be understood in terms of the physical context. Instead, the observer needs to give mentalistic explanations for why the actor performed the action in an unusual or inefficient manner (Heider & Simmel, 1944).

A teleological account of action understanding provides a cognitive framework that can explain how we understand basic actions, but it also provides an account for how we understand actions that violate the principle of rationality (Gergely & Csibra, 2003). This theory proposes that actions are understood in terms of their outcomes or goals and the means by which this action was achieved is explained with respect to the environmental context. For example, a child running towards her mother leaps over a box that is in the way. We understand her goal is to get to her mother and the leaping action is necessary to avoid the box. In this way, her actions are explained in terms of contextual reality and there is no need to represent her mental states such as the desire to reach her mother or her belief about the solidity of the box. Csibra and Gergely (1998) refer to this form understanding as taking a ‘teleological stance’ and argue that it is a developmental precursor to mentalizing. In the case of an irrational action, the girl still makes a leap towards her mother but this time the box is not in the way. Taking a teleological stance is not sufficient to explain this behaviour because the physical context does not constrain and rationalise her action. Instead we need to invoke an alternative mentalistic action explanation with which we can understand her behaviour. Perhaps she is trying to impress her mother or perhaps she believes there is a hole under the grass that she needs to leap over. Here, both real and fictional factors are incorporated into our explanation of her behaviour. Thus the action goal can be represented as a desire (wanting to reach her mother) and the physical constraints are actually her beliefs (there is a hole under the grass). Csibra and Gergely argue that when an action is rational, basic teleological reasoning is used to understand it. However, when an action is irrational it is necessary to switch to the more computationally demanding strategy of mentalizing. Thus it seems that in cases where actions are irrational, the full consort of action understanding is required (see Figure 1.1).

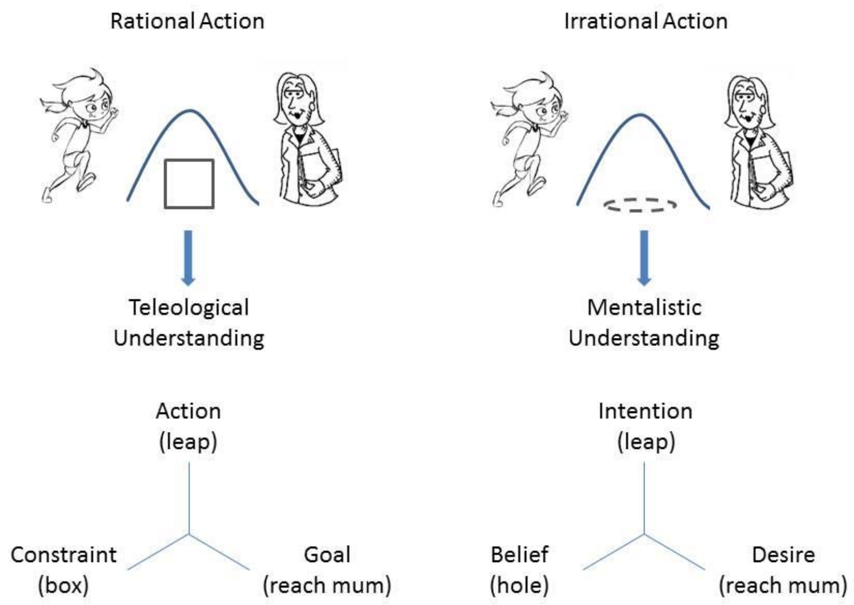

Figure 1.1. Teleological and mentalistic representations of rational and irrational actions.

Previous studies have examined a number of different types of irrational actions. Some irrational actions used an unusual effector such as the use of a knee or forehead to operate a switch that could be easily operated by a hand (Brass et al., 2007; Gergely, Bekkering, & Király, 2002; Vivanti et al., 2011). Alternatively, actions were completed using an inefficient movement path when a more direct route was available (Gergely & Csibra, 2003; Jastorff, Clavagnier, Gergely, & Orban, 2011; Marsh & Hamilton, 2011). Finally, other studies engineered a mismatch between the stereotypical use of an object and the action performed with that object to generate irrational actions (de Lange, Spronk, Willems, Toni, & Bekkering, 2008). Within this thesis, I refer to all of these actions as irrational and treat them similarly although differences between these types of irrational actions may exist. This is discussed in more detail in Chapter 7, Section 7.3.

Having established that irrational actions may be an important tool to investigate how action understanding and mentalizing processes are combined, I now review the different methods that have been used to measure action understanding. In particular I focus on whether action understanding and mentalizing dissociate in the brain, in eye gaze, in people with autism spectrum condition and in typical child development. First I consider our knowledge of how the brain processes actions and mental states.

1.2 BRAIN NETWORKS FOR ACTION UNDERSTANDING

There are two brain networks that are commonly reported as being engaged during action understanding tasks. These are the action observation network (AON) and the mentalizing network (MZN). Early studies reported engagement of the AON and MZN in quite different circumstances, but the extent to which the AON and MZN function independently and how they interact is currently debated (see Van Overwalle and Baetens (2009) for a meta-analysis). In the following sections, I review current knowledge of the action observation network and mentalizing networks respectively. Following this, I address the question of how independent these networks are and discuss the circumstances in which both networks are simultaneously engaged.

1.2.1 THE ACTION OBSERVATION NETWORK

Many previous studies have examined brain responses during the observation of simple, goal-directed actions and have localised an action observation network (AON, Caspers, Zilles, Laird, & Eickhoff, 2010). This network comprises the inferior parietal lobule (IPL), the inferior frontal gyrus (IFG) and a swathe of visual cortex from extrastriate body area (EBA) through middle temporal gyrus (MTG) to superior temporal gyrus (STG). The IFG and IPL are commonly considered to be the core of the human mirror neuron system (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti & Craighero, 2004).

Mirror neurons are defined as single cells which respond when an individual performs an action and observes an equivalent action. Such neurons have been recorded in the premotor and parietal cortex of the macaque monkey (Fogassi et al., 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). Though individual mirror neurons have not been studied in the same regions in the human brain, neuroimaging evidence suggests that equivalent systems can be found (Van Overwalle, 2009; Caspers et al., 2010). The controversy (Hickok, 2009) over whether the mirror neuron system in monkeys is the same as the system identified in humans has largely been resolved by two recent fMRI studies. The first demonstrated matching fine-scale patterns of activity in parietal cortex during performance and observation of finger and hand actions, which implies that very similar neuronal populations are engaged in each task as predicted by the mirror neuron hypothesis (Oosterhof, Wiggett, Diedrichsen, Tipper, & Downing, 2010). Second, Kilner et al., (2009) asked participants to alternately perform and observe hand actions during fMRI. Suppression of the BOLD signal in inferior frontal gyrus was found when the action performed matched the previous observed action and when the action observed matched the previous performed action. The best explanation for this pattern of activity is that performed and observed actions both engage the same population of neurons, as required by the mirror neuron hypothesis. Throughout this thesis, I use the term ‘mirror systems’ as a compact way to describe the human mirror neuron system without requiring the presence of mirror neurons themselves, and I use the term 'mirroring' to refer to activity within classic mirror system regions which is assumed to link representations of performed and observed actions.

Since the discovery of human mirror systems, a number of claims have been made concerning their function. The mirror system seems to match observed actions onto the observer's own motor system, so it has been claimed that this system allows action comprehension and imitation 'from the inside' (Rizzolatti & Sinigaglia 2010) using processes of simulation (see section 1.1.2). Other claims suggested that the extended mirror system plays a role in emotional contagion (Singer et al., 2004; Wicker et al., 2003), or that it provides a mechanism for empathy (Gallese, 2003), language (Rizzolatti & Arbib 1998) and mentalizing abilities (Gallese & Goldman 1998). Therefore, the mirror system could provide a unifying basis for social cognition (Gallese, Keysers & Rizzolatti 2004). However, the evidence for some of these claims remains weak.

In this section, I focus on the claim that the mirror system provides the brain basis for understanding other people's actions, goals and intentions. Multiple studies have reported that the core human mirror system regions of IPL and premotor cortex are engaged when typical individuals observe another person acting (reviewed in Caspers et al. 2010). But can we go further and consider what cognitive processes might take place in these regions? As described in section 1.1.1, we can represent an observed action in multiple ways. It is possible to encode the shape of the actor's hand (a kinematic feature), the object they reach towards (a goal feature) and the actor's overall intention. The human brain likely represents all these features simultaneously, but can we distinguish how and where these are encoded?

Recent work suggests that kinematic and goal features of observed actions engage slightly different components within the human mirror system. Studies examining kinematic processing in the human brain indicate involvement of both higher order visual systems and IFG. For example, if you see a person lift a box, you can normally infer the weight of the box based on kinematic factors such as the velocity of the actor's lifting action (Hamilton et al. 2007). However, this ability is disrupted if repetitive transcranial magnetic stimulation is used to create a 'virtual lesion' (Pascual-Leone, Walsh, & Rothwell, 2000) of the IFG (Pobric & Hamilton 2006). BOLD responses in IFG are also sensitive to different hand apertures during grasping actions (Hamilton and Grafton, 2008) and to different grasp types for example, ring pull vs precision grip (Kilner et al., 2009). Evidence from single cell recordings in macaque monkeys also provides support for the idea that kinematic analysis occurs in area F5 (the monkey homologue of human IFG) as different types of grasp elicit different neuronal firing rates (Bonini et al., 2011; Spinks, Kraskov, Brochier, Umilta, & Lemon, 2008).

In contrast, studies of goal processing suggest that the parietal mirror system, in particular anterior intraparietal sulcus (aIPS), is sensitive to action goals, independent of the kinematics that were used to achieve that goal. Hamilton and Grafton (2006) used a repetition suppression task in which participants watched movies of a hand reaching for a food item or tool during fMRI scanning. Data analysis compared trials where the goal of the action was the same as the previous trial (e.g. take-cookie followed by take-cookie) compared to trials where the goal of the action was different to the previous trial (e.g. take-disk followed by take-cookie). The results show that BOLD signal in just one cortical region, the left aIPS, was suppressed when participants saw a repeated action-goal regardless of the hand trajectory used. This pattern of response is predicted only in brain regions which contain neuronal populations that are sensitive to the manipulated features of the movies (taking a cookie versus a disk) (Grill-Spector, Henson, & Martin, 2006). This means that aIPS contains neuronal populations which are sensitive to action goals. Oosterhof et al. (2010) also found evidence for the encoding of action goals in aIPS using multi-voxel pattern analysis. Further studies found that the IPL also encodes action outcomes, regardless of the action kinematics (Hamilton & Grafton, 2009). In this study the same object was acted upon, only the means by which the goal was achieved was manipulated. Action outcome resulted in differential BOLD responses in the IPL regardless of the action kinematics. Data from monkeys is also compatible with this position, with reports of single neurons which differentiate reach-to-eat and reach-to-place actions in the IPL (Fogassi et al. 2005). Note that goal here is defined very simply in terms of the identity of the object a person grasps, for example, taking a cookie compared to taking a computer disk. More complex action sequences and their goals might be represented elsewhere.

Together, these studies demonstrate that the human mirror system responds selectively to observed actions, and that different types of action processes depend more on different components of the mirror system. In particular, kinematic features of an action are encoded in the frontal mirror system, while goal features are encoded in the parietal mirror system. However, these mirror systems are not necessarily the only brain regions with a role in action understanding. As detailed in the next section, some action comprehension tasks also engage brain areas associated with mentalizing.

1.2.2 THE MENTALIZING NETWORK

Multiple studies have identified a mentalizing network in the brain, comprising medial prefrontal cortex (mPFC) and temporoparietal junction (TPJ). Temporal poles and precuneus are also sometimes found (see Gallagher & Frith, 2003; Amodio & Frith, 2006; Saxe & Kanwisher, 2003 for reviews). These regions are engaged when reading stories which require mental state attributions (Saxe & Powell, 2006; Young, Dodell-Feder, & Saxe, 2010) or when considering the beliefs and future actions of others in interactive games (Fletcher et al., 1995). For example, playing rock-paper-scissors encourages participants to think ("he thinks I'll do rock, but I'll do scissors and trick him"), and computational models can track this type of belief inference occurring in mPFC and TPJ (Hampton & Bossaerts, 2008; Yoshida, Seymour, Friston, & Dolan, 2010). However, the mentalizing network is not only engaged in tasks requiring explicit verbal belief inference. I focus here on the increasing number of studies which report engagement of this network during non-verbal or minimally verbal tasks in which participants spontaneously attribute intentions or consider the longer term motivations underlying an action.

One of the earliest nonverbal mentalizing studies recorded brain activity while participants viewed animated triangles moving on the screen (Castelli, Happé, Frith, & Frith, 2000). For some of these animations, typical individuals spontaneously describe the action in terms of the mental states of the triangles (e.g. *the big triangle is coaxing the little triangle*), while for others the action of the triangles is purposeless. Observation of the mentalizing triangles results in activation of mPFC and TPJ, despite the lack of verbal stimuli or instructions.

More recently, spontaneous activation of mentalizing systems during action observation was reported by Brass et al. (2007). In this study Brass and colleagues showed participants movies of unusual actions (e.g. turning on a light with your knee). In some cases, the context made the action rational (e.g. turning on a light with your knee because your hands are fully occupied) but in other movies the same action was judged as irrational (turning on the light with your knee when your hands are free). Brass et al report greater activation in the mentalizing network including TPJ and mPFC when participants viewed irrational actions compared to rational ones. Critically, this activation was not related to the unfamiliarity of the actions because all actions were unusual. Rather, the engagement of TPJ and mPFC reflected the rationality of the actions. This study shows that observation of human actions without instructions to mentalize can engage brain regions associated with mentalizing if the observed actions are hard to interpret.

1.2.3 SIMULTANEOUS ENGAGEMENT OF THE AON AND MZN

From the evidence reviewed in the previous sections, it seems logical that the action observation network and mentalizing networks should play complementary roles in understanding observed actions. The action observation network processes ‘what’ and the mentalizing network processes ‘why’. However, one review has claimed that these networks function independently and are rarely active concurrently (van Overwalle & Baetens, 2009). Since this review was published however, there have been a number of studies which refute this claim. This section reviews the evidence for simultaneous engagement of the AON and MZN during action understanding tasks and assesses the validity of the claim that these networks play complementary roles in action understanding. Concurrent activation of both systems is seen when the participant is asked to make ‘what’ or ‘why’ judgements about observed actions (Spunt, Satpute, & Lieberman, 2011). In their fMRI study, participants showed increased BOLD responses in IPL and IFG regions during action observation when participants were asked to think about *how* the actions were being performed. In the same subjects and with the same action stimuli, mPFC and TPJ were more active when participants were asked to think about *why* the actions were being performed. This study shows a nice dissociation between levels of action processing in the brain. It seems that the mirror systems are recruited for kinematic analysis of actions such as ‘they are gripping a tin can’ but the mentalizing system is recruited for long-term intentionality judgments such as ‘they are recycling the can to save the environment’. However, in this study the engagement of AON and MZN is dependent upon instructions to think about different aspects of the stimuli (see Ampe, Ma, Hoeck, Vandekerckhove, & Overwalle, in press) and may not reflect spontaneous action understanding.

Further studies have refined our knowledge of when action understanding engages mentalizing brain systems. de Lange et al. (2008) showed participants images of ordinary actions, actions which had an unusual intention and actions which had unusual kinematic features. This study found that while participants watched actions with an unusual intention, there was greater activity in the STS and mPFC, whereas actions with unusual kinematic features activated the IFG more. This study suggests that both mirror and mentalizing systems are complimentary systems which both contribute to action understanding. The additional recruitment of the mentalizing system for action understanding in social contexts is also reported in a study by Ramsey & Hamilton (2010). In this study, participants watched short movies of a toy animal hiding in one of two locations. Following the hiding phase, an actor came out from behind a curtain, surveyed the possible locations and reached into one to find the toy. Similar to the previously mentioned studies, the results showed complimentary activation of both mirror and mentalizing systems; the IFG was sensitive to action trajectory while the mPFC and right temporal pole were sensitive to successful search behaviour. The design of these studies does not allow strong conclusions about whether participants were attributing beliefs to the actor or only considering intentions, but both studies show that tasks focused on intentions with no explicit belief component are processed differently from tasks that focus on simple goals.

A different way to probe the interaction of the AON and the MZN is to record brain responses during observation of irrational actions. As previously argued in section 1.1.4, understanding the rationality of actions in a teleological fashion is a developmental step between basic action comprehension and theory of mind (Csibra, 2003; Gergely & Csibra, 2003). This means that tasks involving implicit rationality judgement may provide a link between AON and MZN systems. Three previous studies have examined brain responses during passive observation of irrational actions. First, Brass et al. (2007) as previously described in section 1.1.4, found that both pSTS and mPFC showed greater responses to irrational actions than to rational actions. Brass et al. (2007) suggest that these results support an inference based model of action understanding in which observed irrational actions are 'rationalised' in the MZN. This is consistent with claim that teleological reasoning about action is a precursor to mentalizing (Csibra, 2003; Gergely & Csibra, 2003). Differential AON activity was not reported in this study, possibly because these regions respond most robustly to familiar goal-directed hand actions.

In a second study, Marsh and Hamilton (2011) showed both typical and autistic participants videos of rational and irrational hand actions during fMRI. Every movie showed a simple goal-directed hand action with a straight or curved trajectory; action rationality was defined by the presence or absence of a barrier. In a rational action, the arm reached for an object in a straight, efficient trajectory or in a curved trajectory over a barrier. Matched irrational actions were those that took either the same curved trajectory with no barrier or the straight trajectory where the hand appears to pass through the barrier. In the irrational movies, the unusual means by which the action was performed might prompt the observer to engage in inference or mentalizing. Results showed that right IPL was more active when typical and autistic participants saw irrational actions, while mPFC was less active when viewing irrational actions in the typically developing participants only. These results provide an important distinction between typical and autistic responses to action rationality. However, there is an inconsistency in the finding of a decrease in mPFC activity in Marsh and Hamilton (2011), compared to the increase in mPFC activity reported by Brass et al. (2007).

A third study of observation of irrational actions reports a different pattern of results again. Jastorff, Clavagnier, Gergely, and Orban (2010) showed participants movies of an actor reaching over a barrier to pick up an object. Actions varied in terms of trajectory height and barrier height, and movies with a mismatch were more 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. Responses in this region were also sensitive to barrier height and arm trajectory.

Overall, three papers have been published on observation of irrational actions and all three report different effects. There might be an increase in mPFC activation for irrational actions (Brass et al., 2007) a decrease in mPFC (Marsh & Hamilton, 2011) or no change (Jastorff et al., 2010). These mixed results make it hard to develop theories or models concerning the interaction of the AON and the MZN during the processing of complex action stimuli. The first study in this thesis will seek to clarify these mixed results by examining the differences between previous studies. I aim to replicate the finding that action rationality does indeed engage both action observation and mentalizing systems simultaneously (see Chapter 2). If this is the case, then examining the cognitive processes involved in understanding irrational actions may be the key to understanding how the action observation and mentalizing networks interact. I now review other methods that can be used to examine the cognitive processes involved in action understanding.

1.3 EYE GAZE

Eye-tracking can be used as a natural, implicit and dynamic measure of action understanding. For example, the finding that adults and children anticipate action outcomes by looking towards the action goal before the action is complete has been used to assess action understanding (Falck-Ytter, Gredebäck & von Hofsten, 2006; Flanagan & Johansson, 2003; Gredeback, Stasiewicz, Falck-Ytter, Rosander, & Hofsten, 2009). The seminal study by Flanagan and Johansson was the first to demonstrate this effect. They asked participants to complete a block stacking task and to watch someone else complete the same task while their eye movements were recorded. A comparison of eye movements during the observation and execution tasks revealed some remarkable similarities. Specifically, they reported robust anticipation of both observed and performed actions such that participants reliably fixated the end point of an action, prior to it being completed. In contrast, action anticipation was not present in a condition in which the blocks moved independently.

Since the discovery of anticipatory eye movements, much research has been conducted to identify the cognitive processes that they reflect. Due to the tight coupling between eye movements for observation and execution tasks, Flanagan and Johansson proposed this as evidence for a direct-matching or simulation approach to action understanding (see section 1.1.2).

Several studies provide support for the idea that anticipatory eye movements during observation reflect motor system activity. Gredebäck & Kochukhova (2010) demonstrate a positive relationship between manual ability to perform a simple puzzle task and faster anticipation of actions during observation of the same task in 25 month old infants, suggesting the development of motor skills is linked to the development of predictive eye movements. Ambrosini, Sinigaglia and Costantini (2011) demonstrated that restricting an observers' capacity to perform the observed action inhibits predictive eye movements, showing that capacity for action is also reflected in this measure. Further evidence of the involvement of the motor system during action observation comes from an interference paradigm (Cannon & Woodward, 2006). Adults watched goal-directed hand actions whilst performing a simple motor task, a working memory task, or no task. Anticipatory looking was reduced only when participants were concurrently performing the motor task compared to all other conditions. This interference effect demonstrates the involvement of the motor system in generating predictive eye movements.

Although the motor system is implicated in generating predictive eye movements, emerging evidence suggests that predictive eye movements are not identical to those produced during action execution. This is contrary to the predictions of the direct matching hypothesis. For example, Rotman, Troje, Johansson, & Flanagan (2006) showed action anticipation for unpredictable actions was slower than for predictable actions but that latency of prediction was linked to the time at which the goal of the action became apparent. Eshuis, Coventry, & Vulchanova (2009) also argue that anticipatory looking is driven by the goal of the action. They report that participants only demonstrated anticipations for goals that had an end effect (sounds/movement at the goal location). Therefore, they suggest that predictive eye movements are driven by the intention of an agent to achieve a goal and the desirability of the goal end state. They also found that observation of human motion was not necessary for anticipatory looking, and therefore conclude that the human mirror system cannot be driving this process (but see Ramsey and Hamilton (2010) for evidence that self-propelled shapes can also activate the human mirror system).

Only two previous studies have investigated action rationality with eye tracking. The first measured predictive eye movements and found that action anticipation was slower when an action was irrational (Gredebäck & Melinder, 2009). This finding is consistent with Rotman et al. (2006), suggesting that predictive eye movements are driven by goal understanding. However, this study failed to control for goal salience and action kinematics between rational and irrational actions and this may impact the results (this is discussed in more detail in Chapter 3, section 3.2.1). The second study to measure responses to irrational actions found that participants looked longer at the face following an irrational action, in comparison to a matched rational action (Vivanti et al., 2011). It was argued that this measure reflected children's tendency to seek an explanation for the irrational action. Both of these studies investigate only one cognitive component of irrational action understanding, using one eye tracking measure. Understanding rationality may include many cognitive processes such as action monitoring, goal prediction, evaluation of the environmental constraints and detection of rationality.

On the whole, action understanding research that employs eye-tracking has been dominated by the analysis of predictive eye movements. However, the research reviewed in this thesis has demonstrated that predictive eye movements can be modulated by motor ability, goal type, action predictability and environmental features (Gredebäck, Stasiewicz, Falck-Ytter, von Hofsten, & Rosander, 2009). In addition, speed of anticipation is very sensitive to the way in which the stimuli is constructed (Rotman et al., 2006) and so it is very difficult to compare across studies. It seems that this simple measure alone is not able to reflect the multiple cognitive processes that underpin action understanding, especially when actions are more complex. The experiment presented in Chapter 3 aims to identify the eye tracking measures that can allude to the cognitive processes involved in the observation of irrational actions. It also tests the hypothesis that predictive eye movements are generated by the motor system by comparing predictive eye movements for rational and irrational actions. It seems that observation of irrational actions may require additional engagement of the mentalizing network whereas observation of rational actions relies on the action observation network. If predictive eye movements are modulated by action rationality, then they cannot be a product of the motor system alone.

1.4 AUTISM

Typically, we automatically attribute goals and intentions to the agents that we observe. However, individuals with autism may not make these same attributions. Currently there are two competing theories that claim that people with autism have difficulty understanding goals and intentions of others. These are the 'mentalizing theory' and the 'broken mirror theory'. Each of these theories proposes that one of the two reviewed action understanding networks function atypically in autism. In the mentalizing theory, it is proposed that only mentalizing network is atypical, while at least basic processing in the mirror system is normal. In contrast, the broken mirror theory proposes that a core deficit in mirroring leads to difficulties with mentalizing. In this section, I examine each of these theories and then consider the evidence from each, looking at traditional behavioural tasks, implicit measures such as eye tracking and EMG, and neuroimaging measures.

1.4.1 MENTALIZING THEORY

There is little disputing the repeated finding that many children and adults with autism have particular difficulties with false belief tasks (Baron-Cohen et al., 1985; Frith, 2001). Brain activity in mentalizing regions when participants with autism watch the animated triangles movies is also abnormal (Castelli, Frith, Happé,

& Frith, 2002). The mentalizing theory proposes that difficulties with false belief tasks are the result of an inability to represent other people's mental states (Frith, Morton, & Leslie, 1991), or to represent the mental states of others independently of what they know to be true (Leslie, 1987). Within this field, there is an important distinction between implicit and explicit mentalizing (Apperly & Butterfill, 2009).

Explicit theory of mind is measured with traditional false-belief tasks such as Maxi's chocolate (described in section 1.1.3, Wimmer & Perner, 1983). Typical children under around 4.5 years old often fail this task, and autistic individuals with a verbal mental age below 9.2 years also tend to fail (Happé, 1995). However, more able individuals with autism often pass false-belief tasks, and may even pass more complex second order tasks (Happé, 1994). Thus, there is a dissociation between the time course of explicit false belief development in typical children (emerging at around 4.5 years and complete by 8 years) and the time course of autism (emerging between 1 and 2 years of age and lasting throughout the lifespan). This has led to a search for precursors to mentalizing and to the investigation of other theories of autism.

In contrast to the late development of explicit mentalizing, implicit mentalizing seems to be present from early infancy (Kovacs, Teglas, Endress, Téglás, & Endress, 2010; Onishi & Baillargeon, 2005) and is measured by recording gaze durations and eye movements when participants view movies in which an actor has a false belief (see section 1.5.2 for details of the typical development of mentalizing). Recent data demonstrate that even high functioning adults with

Aspergers syndrome who pass verbal false belief tasks fail to show implicit mentalizing in an eye tracking task (Senju, Southgate, White, & Frith, 2009). It is now argued that failure of implicit mentalizing is the core difficulty in autism (Frith, 2012). This resolves the difficulties over the time course of mentalizing failure, because implicit mentalizing develops over the first two years of life at the same time that autism emerges, and implicit mentalizing remains impaired in high-functioning adults with autism. Brain imaging data on implicit mentalizing in autism is not yet available, but it is possible that current tasks such as describing the behaviour of animated triangles tap into implicit mentalizing resources. Brain activation in this task is atypical in high functioning adults with autism, despite their good explicit theory of mind skills (Castelli et al., 2002).

Research on implicit mentalizing and the precise difference between implicit and explicit tasks is on-going, and further developments in understanding the role of implicit theory of mind in autism are likely. For present purposes, I contrast a pure mentalizing theory of autism with a broken mirror theory. The pure mentalizing theory predicts that mentalizing is a single, core deficit in autism and that other social brain systems are unaffected or secondarily affected. For example, basic goal understanding processes should be intact in autism under the mentalizing theory because these do not require the mentalizing network. However, there is still debate over whether difficulties with mentalizing are a single, core deficit in autism or whether these are a consequence of atypical processing in other social brain systems, for example the mirror system. I consider this question in the next section.

1.4.2 BROKEN MIRROR THEORY

The broken mirror theory claims that developmental failure of the mirror system is the primary social difficulty in autism, and a cause of poor mentalizing. Under this theory, deficits in understanding the kinematic and goal features of an action would lead to further difficulties in understanding emotions and mental states. Initial evidence in support of this theory came primarily from studies of imitation. When typical adults imitate hand actions, the mirror system is activated (Buccino, Binkofski, & Riggio, 2004; Decety, Chaminade, Grèzes, & Meltzoff, 2002; Iacoboni, 1999) and damage to the mirror system in adults causes imitation difficulties (Heilman, Rothi, & Valenstein, 1982). It is often reported that autistic children have specific difficulties with imitation (see Williams, Whiten, and Singh (2004) for a review) and this difficulty may have cascading effects into the social domain, leading to difficulty in understanding the intentions or emotions of others (Iacoboni & Dapretto, 2006; Ramachandran & Oberman, 2006; Williams, Whiten, Suddendorf, & Perrett, 2001).

Evidence for atypical mirror system functioning in autism comes from studies which report atypical brain responses during action observation (Nishitani, Avikainen, & Hari, 2004; Oberman et al., 2005), or during a facial imitation task (Dapretto et al., 2006). A more recent variant of the broken mirror theory focuses not on comprehension of individual goal directed actions, but on the prediction of actions in a sequence. The account is based on the finding that mirror neurons in parietal cortex encode actions as part of a sequence (Fogassi et al., 2005). For example, some mirror neurons in the IPL respond selectively when the monkey brings food to his mouth or sees someone bring food to their mouth, but not when bringing a small object towards the shoulder or seeing someone bring an object to their shoulder. They suggest these mirror neurons allow an observer to chain actions together and represent intentions. Building on this work, Cattaneo et al., (2007) measured electromyographic (EMG) recordings from a jaw-opening muscle (mylohyoid MH) in children when they were performing simple reach-to-eat and reach-to-place actions. In typical children, MH activity increased during the reach phase of a reach-to-eat action but not of a reach-to-place action, and similar results were found for observation of actions. Thus, typical children chain together the reach and mouth-open actions of an eating sequence, and show similar predictive mouth opening when observing others. In contrast, matched children with autism did not show this anticipatory mouth opening, during either performance or observation. Based on these data, Rizzolatti and Fabbri-Destro (2010) put forward an action-chaining hypothesis of autism. They suggest that predicting actions and inferring intentions in this way is a precursor to mentalizing and belief inference skills. If this is true, then a deficit in action chaining could lead to the social deficits we see in autism (Rizzolatti, Fabbri-Destro, & Cattaneo, 2009).

In the next section, I evaluate the claims that either the whole mirror system or the ability to chain actions in a sequence is abnormal in autism. I focus mainly on recent studies which use implicit (eye tracking or EMG) measures of action comprehension, and neuroimaging studies.

1.4.3 BEHAVIOURAL STUDIES OF ACTION UNDERSTANDING IN AUTISM

The extent to which there is a global imitation impairment in individuals with autism remains a subject of contention. There have been multiple studies that report reduced imitation in children with autism on a number of different imitation tasks, including imitation of meaningless actions, mimicry of facial expressions and the spatial perspective taking component of imitation. These results have led to the claim that imitation is globally impaired in individuals with autism (Williams et al., 2004). However, there are also a number of studies which lead us to question this claim. By varying the nature of the task and the clarity of the instructions, it is possible to improve imitation performance in children with ASC. For example, it has been demonstrated that children with autism are capable of imitating both hand actions and facial expressions when they are explicitly instructed to do so (Beadle-Brown, 2004; McIntosh, Reichmann-Decker, Winkielman, & Wilbarger, 2006). They also perform better when the imitation task is well structured and doesn't require spontaneous imitation (Hepburn & Stone, 2006).

Some imitation tasks can separate imitation of action goals from imitation of the means by which the goal was achieved. This is an interesting distinction because we know from neuroimaging findings that these action features are represented in different brain regions and fall at different levels of the action hierarchy. The use of one such task elegantly demonstrated that children with autism were able to imitate action goals but failed to spontaneously copy the action style (Hobson & Lee, 1999; Hobson & Hobson, 2008). Intact goal-directed imitation in children with autism has also been seen in a simple hand movement task. Autistic children and controls matched for verbal mental age were tested on Bekkering's goal directed imitation task described in section 1.1.1 (Bekkering et al., 2000). Both groups of children accurately imitated the action goal, i.e. they touched the appropriate dot on the table. Interestingly however, both groups of children made systematic hand errors in which they failed to make contralateral movements across their body when this action was demonstrated. Instead they tended to make the more efficient, ipsilateral movement to touch the correct dot (Hamilton et al., 2007). This pattern of behaviour is indicative of goal-directed imitation as children are representing the action goal but using their own motor programs to generate an action that will achieve their goal (Bekkering et al., 2000). Therefore, this study provides evidence that individuals with ASC do represent action goals in a hierarchy and are able to imitate these goals.

Further evidence for good goal understanding in children with ASC is demonstrated in a study where children observed an adult attempting and failing to dismantle a dumb-bell. Both typically developing and autistic children were able to complete this action, despite never actually witnessing a successful attempt (Aldridge, Stone, Sweeney, & Bower, 2000; Carpenter, Pennington, & Rogers, 2001). This demonstrates that children with autism are able to represent an actors' intended goal without needing to see it physically performed. In summary, it seems that autistic children are able to imitate goal-directed actions, when given clear and explicit instructions to do so. The behavioural evidence reviewed here suggests that simple goal representation is intact in autism, contrary to the predictions of the broken mirror hypothesis.

However there is mixed evidence for individuals with autism being able to understand more complex goals or sequences of actions. In a picture ordering task, children with autism were able to correctly sequence a series of pictures that depicted goal-directed actions (Baron-Cohen, Leslie, & Frith, 1986) but in a comparable task, adolescents with autism were less able to order object-directed action sequences (Zalla, Labruyere, & Georgieff, 2006).

More recently, a study by Boria et al. (2009) demonstrated poorer understanding of subsequent actions in children with autism. In this study, children were shown static images of a hand either touching an object, grasping-to-use it or grasping-to-place it. Children were asked what the actor was doing and why. Children with autism were able to distinguish touching and grasping actions. They were also able to identify subsequent use of the object as well as typically developing children in the grasp-to-use condition. However, their performance was substantially poorer when identifying the grasp-to-place actions, with object-use dominating their responses, despite the grasp type rendering this action implausible. Boria and colleagues argue that children with autism are unable to use the motor information to make an inference about the subsequent action, providing evidence for the action chaining theory. However, in their second similar experiment, children with autism were able to identify grasp-to-place actions if an image of the end goal was also present. Boria argues that this evidence corroborates their initial finding and children with autism are not just making stereotyped, object-use responses. An alternative explanation for this improved ability in the second experiment could be that the imagination demands are reduced as the action end point is visible. A better test of this effect should test different, dynamic grasps with the possible end points visible. This will reduce the imagination demand of the task and will require correct analysis of the motor properties of the grasp to infer the subsequent action.

1.4.4 IMPLICIT MEASURES OF ACTION UNDERSTANDING IN AUTISM

Eye tracking studies of action observation have also been used to assess mirror neuron function in autistic children. Typically, eye movements during action observation and action execution are predictive of the actions that they are monitoring. It has been suggested that these predictive eye movements are reflective of mirror neuron function as eye movements during action observation mirror those during action execution (see section 1.3 for a full review of the evidence for this claim). In a study of autistic five-year olds, (Falck-Ytter, 2010) demonstrated that infants with autism were able to anticipate actions to the same degree as typical infants and adults. This finding suggests that even young children with autism are able to predict the actions of others and provides evidence against impaired action chaining in autism.

However, other studies of action chaining in autism do suggest difficulties. Cattaneo et al (2007), as described earlier, showed that children with autism failed to produce predictive MH muscle activation during the performance or observation of a reach-to-eat action, in contrast to typical control children. They argue that this indicates a failure of action chaining in participants with autism. One limitation in this study is the failure to exclude dyspraxia in the autistic sample of participants; dyspraxia is often comorbid with autism (Ming, Brimacombe, & Wagner, 2007) and impacts on motor control but it is not linked to mentalizing.

Further evidence for impaired action chaining in autism comes from a study by Fabbri-Destro et al. (2009) who used a similar methodology to that of Johnson-Frey et al. (2004). In this study, children with and without autism were asked to pick up a block and move it to either a small or large container whilst their movement time was measured. Throughout the experiment, the task demands of the reach action remained constant. However, manipulating the size of the container increased the task demands of the place action. Despite the controlled demands of the reach action across conditions, typically developing children modified the speed of the initial reach action such that they were slower when the following action was harder and faster when the following action was easier. This bias is thought to reflect future planning of the second action in the sequence. In children with autism, the speed of the reach action was not biased by the difficulty of the following action, indicating a lack of action planning. Overall, the evidence for impaired action chaining in autism is mixed. Eye-tracking studies show that online action prediction is functioning typically in autistic children. Studies that use more complex action sequences do reveal differences between typical and autistic children although they fail to control for motor ability in their tasks. Further research is needed to assess the action chaining account of the broken mirror hypothesis.

1.4.5 NEUROIMAGING STUDIES OF ACTION UNDERSTANDING IN AUTISM

Neuroimaging techniques provide the most rigorous tests of the integrity of the mirror system in autism. A number of early studies report differences between typical and autistic participants. For example, Oberman et al. (2005) report reduced mu wave suppression during observation and execution of hand actions in typical participants but mu suppression only occurred during execution tasks in the autistic participants. In addition, Théoret et al. (2005) demonstrated that motor evoked potentials, induced by transcranial magnetic stimulation during action observation were reduced for autistic participants. However, no group differences in magneto-encephalographic recordings were found between typical and autistic participants during the observation of hand actions (Avikainen, Kulomäki, & Hari, 1999). It is important to note that all of these studies used measures with very limited localisation of effects and participant numbers were low.

fMRI studies provide evidence with better spatial resolution and can identify specific brain abnormalities in a more convincing way. Dapretto et al. (2006) conducted the first study to provide evidence for the broken mirror hypothesis with fMRI. In their study, participants were asked to observe and imitate emotional facial expressions during fMRI scanning. They report reduced activation in the IFG component of the mirror system during observation and imitation in autistic participants. Furthermore, the amount of activation significantly correlated with autistic symptom severity. However, imitation of emotional facial expressions is not a goal-directed action task and it is very different from the original hand-grasping studies that were used to study the mirror neuron system in monkeys (Gallese et al., 1996). Therefore, this study provides only weak evidence for the broken mirror hypothesis.

In a more comparable study of hand actions, Dinstein et al. (2010) asked participants to perform and observe sequences of simple hand postures during fMRI scanning. They report no group differences between autistic and typical participants during observation or execution of hand postures in mirror neuron regions. In addition, autistic participants demonstrated normal movement selectivity for repeated hand postures in left anterior intraparietal sulcus (aIPS) and ventral premotor cortex (vPM) in both observation and execution conditions. This study provides the first robust evidence against mirror system dysfunction in autism.

Only one study has tried to assess the integrity of both mirror and mentalizing systems in autism in the same study (Marsh & Hamilton, 2011). Manipulation of action rationality was used as a tool to engage the mentalizing system. As previously reported, Brass et al. (2007) demonstrated that irrational actions automatically activate the mentalizing system in the typical observer, even with no prior instruction to mentalize. By using matched rational and irrational action stimuli Marsh and Hamilton were able to dissociate mirroring and mentalizing systems in the autistic brain in a non-verbal, action observation task.

Eighteen adults with autism and 19 age and IQ-matched typical adults completed the experiment. They watched movies of simple, goal-directed reach actions to either a piece of food or a tool during fMRI scanning. Some actions were rational while in others the hand took an irrational route to reach the target object. Control movies depicting a shape drifting across the screen were also shown. The results showed that both typical and autistic participants engage mirror regions, in particular left aIPS when observing hand actions. In addition, this area was also sensitive to action goals in both participant groups. As the left aIPS is the established goal processing region of the mirror system as defined in Hamilton and Grafton (2006) and Hamilton and Grafton (2008), this result provides evidence against a global mirror neuron deficit in autism and corroborates behavioural evidence that suggests that goal understanding is intact in autism.

In contrast, differences between the typical and autistic participants emerged when regions outside the mirror system were examined, and when action rationality was considered. In both typical and autistic participants, the right aIPS was activated for irrational actions compared to rational actions. However, in the mPFC, only typical participants differentiate irrational from rational actions. mPFC activity in the autistic participants remained the same regardless of the rationality of the observed action. These results demonstrate that, within the same group of participants, responses in the mirror system to observed actions can be normal while responses in the mentalizing system are abnormal.

1.4.6 SUMMARY

Evidence for the integrity of mirroring and mentalizing brain systems in autism has been reviewed above. In typical individuals, the mirror system encodes action kinematics and goals while the mentalizing system plays a role in making inferences about the actors' beliefs and intentions. Evidence for poor mentalizing in autism is clear cut, but there is much less support for the proposal that this social difficulty originates in failure of mirror systems. Many studies have demonstrated good goal understanding in autism, together with normal brain responses in mirror systems. Few studies have directly tested the integrity of mentalizing systems in relation to action understanding in autism but initial reports suggest that this may be functioning atypically. Action rationality is a new tool that can tap in to both mirror and mentalizing systems and studies comparing rational and irrational actions may be able to provide us with a better understanding of the interactions between mirroring and mentalizing. However, a better understanding of what action rationality is and why irrational actions engage the mentalizing system is also needed. Implicit measures, such as eye-tracking, give us insight into the fast, automatic processing of actions and can allude to subtle differences in perception in autism. This is the subject of the experiment reported in Chapter 4.

1.5 DEVELOPMENTAL STUDIES

Investigating the emergence of action understanding and mentalizing skills throughout development can also provide us with information about the nature of these processes and how they are linked. Does one skill develop before the other or do they both develop simultaneously? In this section I briefly review the developmental work that contributes to our understanding of the development of action understanding and mentalizing. Finally, I consider the development of rationality understanding and when this skill emerges.

1.5.1 THE DEVELOPMENT OF ACTION UNDERSTANDING

It seems that the first year of life is crucial in the development of many abilities that relate to action understanding. In a longitudinal study, Carpenter et al. (1998) document the emergence of gaze and point following, imitation of actions and gestures and production of communicative gestures. All of these abilities emerged within the first year in a progressive sequence. Interestingly, the authors note that production of actions like pointing commonly preceded comprehension of others' pointing behaviour, implying that motor ability is a precursor to action comprehension. The coupling between action comprehension and motor ability was also demonstrated when 18-to 25-month-old infants were given a puzzle to solve or asked to watch someone else perform the same puzzle while their eye movements were recorded. Infants who were able to complete the puzzle also made predictive saccades to the next puzzle piece during observation of another person completing the puzzle. However, those infants who did not have the manual ability to complete the puzzle also failed to make these predictive eye movements during the observation task (Gredebäck & Kochukhova, 2010). Both of these studies provide evidence that is consistent with an embodied approach to action understanding and imply that action production is an important precursor for action understanding.

Goal attribution is also thought to develop in the first year of life. This was first demonstrated in a study in which 6-month-old infants were habituated to a reach action in which an actor repeatedly picked up one of two objects. At test, the object locations were switched but infants looked longer when the actor reached to the new object at the old location. This indicates that the infants expected the actor to maintain their goal (the object that they previously reached for), despite the objects switching locations (Woodward, 1998). Further variations of this task have demonstrated that this goal attribution is aided by manual experience of the same actions prior to observation (Sommerville, Woodward, & Needham, 2005) and it is related to the causal consequences of the actions (Woodward & Sommerville, 2000). Therefore, it seems that basic action comprehension skills develop early in life and resemble the sophisticated goal hierarchy that has been identified in adults.

There is also evidence that 18-month-old infants understand the intentions of others, even if they do not witness a completed goal-directed action. This was demonstrated in a study in which infants observed an actor attempting but failing to pull a dumbbell apart. When given the dumbbell themselves, infants subsequently completed the action indicating that they were able to represent the failed intention of the actor (Meltzoff, 1995).

In sum, it seems that action understanding abilities are extremely well developed from an early age. Sophisticated processes of goal attribution and intention understanding are intact by the end of the first year and may mature alongside the development of motor capabilities. In contrast, explicit mentalizing skills are commonly thought to develop much later.

1.5.2 THE DEVELOPMENT OF MENTALIZING

As briefly summarised in section 1.1.3 mentalizing ability was traditionally assessed using a false-belief task. The developmental stage at which children are able to track beliefs and understand that another agent holds a false belief has been the topic of much debate. Originally it was proposed that children start to represent others knowledge and track beliefs from the age of 4.5 years (Wimmer & Perner, 1983) but more recent evidence shows that if you simplify the task children as young as 3 years can pass (Rubio-Fernández & Geurts, 2013). Debate about how best to assess mentalizing and what skills are required to pass the false belief task is on-going (see (Wellman et al., 2001) for a meta-analysis). Individual differences in mentalizing development were assessed in a longitudinal study of 45 children who were assessed during infancy and again at 4 years of age (Wellman, Lopez-Duran, LaBounty, & Hamilton, 2008). This study demonstrated that early attention to actions can predict later mentalizing abilities, again implying that action understanding and mentalizing are linked in some way.

More recent studies have advanced our knowledge of the developmental trajectory of mentalizing by assessing false-belief attribution in infants using eye tracking (Kovacs, Téglás, & Endress, 2010; Onishi & Baillargeon, 2005; Southgate, Senju, & Csibra, 2007). In these studies, the classic false belief paradigm is acted out non-verbally on screen whilst the participants' eye movements are recorded. At test, when the protagonist who holds a false belief reappears on screen, infants made predictive eye movements to false belief location rather than the true object location, indicating they are anticipating that the protagonist will behave in accordance with their false belief. Using this implicit measure of belief tracking, mentalizing has been identified in infants as young as 7-months old (Kovacs, Téglás, et al., 2010).

The difference in developmental time-course between implicit and explicit measures of mentalizing has led to dual process explanations (Apperly & Butterfill, 2009). Apperly and Butterfill (2009) propose that implicit mentalizing reflects a fast and automatic process which develops early in life but is limited in its flexibility. In contrast explicit mentalizing is incredibly flexible and can undertake complex cognitive processes but it is slow and cognitively demanding.

The distinction between implicit and explicit processes and the degree of automaticity involved in these processes is interesting, especially when we consider that adults with ASC who are able to pass explicit false belief tasks like 'Maxi's chocolate' actually fail a similar task when the response is measured implicitly using eye-tracking (Senju et al., 2010). The distinction between implicit and explicit processes emerges as a theme throughout this thesis. The studies I present here use both implicit and explicit measures of rationality understanding in an attempt to examine inconsistencies between them.

1.5.3 THE DEVELOPMENT OF RATIONALITY UNDERSTANDING

Infants are sensitive to the rationality of actions from as early as 6-months of age (Gergely Csibra, 2008; Gredebäck & Melinder, 2010). This sensitivity has been measured using implicit measures of looking time and predictive eye movements (see section 1.3). Another way to investigate rationality understanding is to examine responses to irrational actions in imitation tasks. In a striking study of rational imitation, it was demonstrated that 14-month old infants may modulate their imitation behaviour based on action rationality (Gergely et al., 2002). Infants were shown a demonstration of an actor turning on a light box with her forehead. In one condition, the demonstrator was unable to use her hands to touch the light because she was holding in a blanket around her shoulders. Due to the constraint of holding the blanket, one can argue that using her forehead was the most rational way to turn on the light. In a second condition, the actress did not hold the blanket around her shoulders but instead demonstrated that her hands were free by placing them on the table next to the light. Results showed that infants were significantly more likely imitate and to turn on the light with their forehead in the condition in which the actors' hands were not constrained. The authors proposed that the infants are evaluating the rationality of actions with respect to the goal and the constraints that act upon the actor when making decisions about what to imitate. If an action can be rationalised by the environmental constraints, infants will imitate selectively but if it is not possible to rationalise the action, infants faithfully imitate.

However, a series of recent studies argue that it may be the infants' ability to perform the head-touch action in the hands free condition which drives faithful imitation, rather than rationality evaluation. The head-touch action is easier for infants to perform when they can put their hands on the table next to the light box (as in the hands free condition) compared to across their chest (in the hands constrained condition). Therefore, infants have greater motor resonance for the hands-free action and imitate it faithfully (Paulus, Hunnius, & Bekkering, 2012; Paulus, Hunnius, Vissers, & Bekkering, 2011a, 2011b).

Despite the mixed evidence for faithful and selective imitation in infancy, studies of 2-to-8-year old children also display an apparent paradox in imitation behaviour (Over & Carpenter, 2012), on some occasions choosing to faithfully imitate and on others, to be selective. The differences in imitation behaviour cannot be explained by developmental changes as both selective and faithful imitation co-occurs throughout development. This is introduced in more detail in section 5.2 of this thesis. In Chapters 5 and 6 of this thesis, I investigate some of the social cues which may modulate imitation of irrational actions.

1.6 CONCLUSIONS

By examining the mechanisms through which irrational actions are understood, I hope to advance our knowledge of how we understand others' complex behaviour. Within this question I assess brain, cognition and behavioural responses to irrational actions so that we can really tease apart the mechanisms through which action understanding is achieved at all levels of ascription. I place specific emphasis on the comparison between implicit and explicit measures of understanding as interesting inconsistencies between these measures have arisen in the past.

A second important question that this thesis also addresses is the extent to which irrational action understanding is impaired in individuals with autism. A previous neuroimaging study has highlighted different neural responses to irrational actions in people with autism (Marsh & Hamilton, 2011) but an understanding of what this difference means for cognition and behaviour is still required. Therefore, each of the tasks that I develop for use in the typically developing population will be applied to people with autism to establish which action understanding mechanisms are intact and which are impaired in autism.

1.7 SUMMARY OF STUDIES

Study 1: Here I aimed to replicate the finding that observation of irrational actions does simultaneously engage the mirror and mentalizing networks in typically developing adults. In addition, I question the extent to which this engagement is reliant on a human agent performing these actions. Participants watched movies of matched rational and irrational hand actions during fMRI scanning. Movies also varied with respect to how visible the agent was (fully visible, face occluded or invisible). Participants were asked to rate the rationality of each movie after scanning. Results supported the previous finding that observation of irrational actions engages the mirror system (IPL, IFG) and the mentalizing system (mPFC, TPJ) simultaneously. Activity within these regions also correlated with participants individual judgements of action rationality. The amount of social information available to the observer did not impact upon this engagement. This suggests that rationality is computed for human agents and inanimate objects alike and also that both mirror and mentalizing systems are not as selective for human action as previously thought.

Study 2: Here I investigate the cognitive processes that underpin rationality understanding using eye tracking. Previous eye tracking studies of action understanding use a variety of measures and it is not clear which is best. This study aimed to assess the suitability of different measures that may reflect irrational action understanding and to develop a principled analysis protocol that can be applied to an autism sample (study 3). We ran several analyses on looking time to various areas of interest, scan paths and goal fixation latency. From these analyses we identified the measures that reflect action rationality, social form or interactions between rationality and social form in typical adults. These were looking times to the action goals, the hand, the barrier and the face; a scan path analysis in which we identified the origin of the first saccade to the action goal; and predictive goal fixation time when the goal saccade originated at the hand. These measures are now used in study 3.

Study 3: This builds on study two using an adult ASC sample and a second typically developing sample matched for age and IQ. Using the measures identified from study two, I was able to assess the similarities and differences between typical and ASC eye movements during irrational action observation. Results showed that typical eye movement patterns replicated those from study two. Additionally, participants with ASC showed very similar patterns of eye movements to the typically developing group, reflecting the rationality and social form of the action. The main difference between groups was that the ASC group showed reduced visual attention to the actions, looking less at the action goals and the hand and making less predictive saccades from the hand to the goal. However, when these predictive saccades were present, ASC participants were just as fast to predict the actions as typically developing individuals. This pattern of results is indicative of intact action understanding mechanisms in ASC but the reduction in attention to actions may reflect poor social modulation of behaviour.

Study 4: As study three did not show different eye movements between groups for rational and irrational actions, I decided to investigate rationality understanding in a more social, interactive environment. Overimitation is a phenomenon in which typically developing children copy the actions of other with high fidelity, even when they are visibly unnecessary or irrational. It is not clear if this is due to a failure of causal reasoning or a social drive to affiliate. To test these theories, I gave typically developing children an overimitation task, using simple and familiar objects. In this task, children saw a demonstrator produce three actions on a box in order to retrieve a toy; one of these actions was irrational (e.g. tapping the lid of the box twice). I then measured whether the child completed the unnecessary action when given the box. Overall, the propensity to overimitate increased with age and with understanding of the objects. These results support the hypothesis that overimitation is a socially driven behaviour that also reflects rationality understanding. I therefore predict that children with ASC will not overimitate to the same degree as typically developing children.

Study 5: In the final study of this thesis, I tested children with ASC and matched typically developing children on the overimitation task developed in study four. While ASC children were able to complete all of the goal-directed, rational actions in this task, they show a significant reduction in overimitation behaviour as well as a reduced understanding of action rationality. This leads me to conclude that overimitation is a socially driven phenomenon that may reflect a desire to affiliate with the demonstrator or to conform to the normative behaviour demonstrated. In either case, children with ASC are immune to this drive.

CHAPTER 2. RESPONSES TO IRRATIONAL ACTIONS IN ACTION OBSERVATION AND MENTALIZING NETWORKS OF THE HUMAN BRAIN

2.1 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 mentalizing network (MZN) in the perception of rational and irrational actions. Past studies in this area report mixed results, so the present chapter 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 right inferior parietal lobule extending to the temporoparietal junction was more active during observation of irrational, compared to 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 mentalizing networks. These results advance current theories of action comprehension and the roles of action observation and mentalizing networks in this process.

2.2 INTRODUCTION

Chapter 1 made the case that irrational actions may be used as an important tool to investigate the interaction of the action observation (AON) and mentalizing (MZN) networks. This is a theoretically interesting question as it can help us understand how we move from understanding what someone is doing to why. However, previous studies report mixed results with respect to the simultaneous engagement of the AON and the MZN during irrational action observation. As reported in section 1.2.3, Brass and colleagues (2007) report an increase in activity in the mPFC during observation of irrational actions, whilst Marsh & Hamilton (2011) report a decrease. However Jastorff and colleagues (2011) report no change. The aim of the present chapter is to re-examine brain responses during irrational action observation using new and well controlled stimuli. To optimise my experiment, I first consider some possible explanations for the differences between the reported results.

One difference between the studies was the analysis method used. While 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 the difference in perceived rationality between conditions was subtle, so detecting rationality might require a fine grained analysis of action kinematics, thus engaging MTG. A second important difference is in the precise stimuli used. Brass et al. (2007) used novel whole-body actions which were rationalised by the environmental constraints. Marsh and Hamilton (2011) used simple goal-directed hand actions, as did Jastorff et al. (2010). These stimuli differ in the amount of social information available to the observer in each study, from the whole body (Brass et al, 2007), the torso, arm and face (Jastorff et al, 2010) or the hand and arm alone (Marsh and Hamilton, 2011). 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 & Vaish, 2006) or gaze direction (see Carpenter & Call (2007) for a review) .

Conversely, studies suggest that even young infants can distinguish action rationality for objects with no social form, for example a moving ball or block (Csibra, 2008). In adults, perceived rationality of a chain of moving dots modulated activity in the pSTS (Deen & Saxe, 2011). This suggests that social form is not necessary for rationality discrimination. However it remains to be seen whether activity in AON and MZN during irrational action observation is modulated by the social form of the actor.

To address these differences, the present study will use well-matched stimulus videos which precisely control the rationality of the action and the social form of the actor. All stimuli will 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. Finally, the data analysis will consider both the effects of rationality as defined by the movie categories and the relationship between brain activity and individual participants' subjective ratings of rationality. These novel and well controlled stimuli will allow me to define the relationship between the AON and MZN during complex action understanding.

Due to the inconsistent results reported in previous studies, I do not make strong predictions about the direction of the effect in mPFC but I do predict its involvement. I also consider the connectivity of the mPFC using psychophysiological interactions (PPI).

2.3 MATERIALS AND METHODS

2.3.1 PARTICIPANTS

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

2.3.2 STIMULUS GENERATION

Movie clips presented during fMRI scanning are illustrated in Figure 2.1. In each clip a red ball started on the left of the screen and was moved to one of two containers on the right. 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 seconds.

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) were 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 stimulius 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.

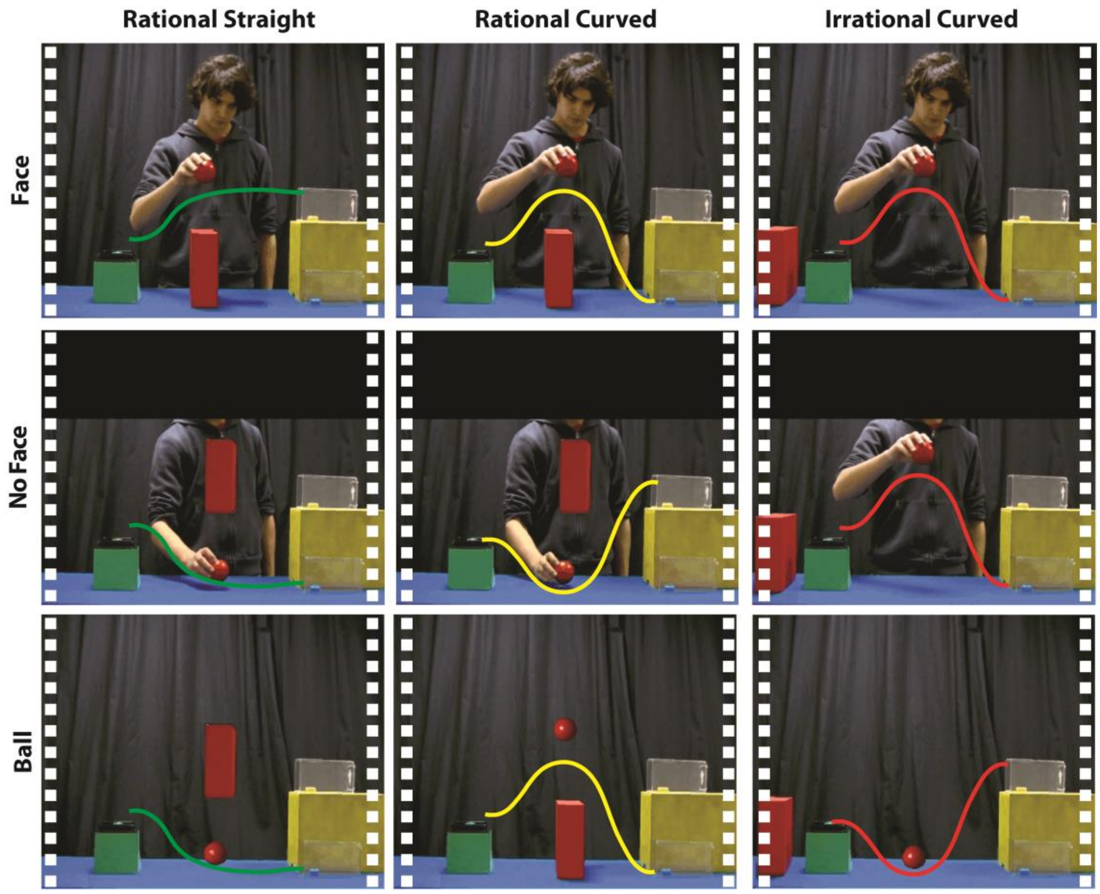

Figure 2.1.The middle frame from each movie. In each movie the ball starts on the left and is placed in one of two containers on the right. Coloured lines visualise the movement trajectory of the ball and do not appear in the movie. Rationality is constrained by the position of the barrier.

2.3.3 fMRI PROCEDURE

During fMRI scanning participants saw movies of 3.7 seconds duration in an event-related design with a 600ms ISI. One run of scanning contained each of the 18 movies, repeated six times in a pseudorandom order. Care was taken so that same movie was not repeated consecutively. Each run of scanning lasted approximately 9 minutes 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 answered questions with a button response, these responses were not analysed. Whole brain images were collected with a 3T Phillips Achieva MRI scanner using a 32-channel phased array head coil. 40 slices were collected per TR (3mm thickness). TR:2500ms; TE:40ms; flip angle:80° ; FOV:19.2cm; matrix: 64x64. 214 brain images were collected during each of 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'. Additionally, participants rated movies for likeability, using a battery of four statements. Participants were asked whether they agreed or disagreed on a scale of one to five. The score on negative items was reversed and a total rationality and likeability scores were computed for each participant for each movie (maximum score of 30 indicated most rational and a maximum score of 20 indicated most likeable).

2.3.4 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 2x2x2mm. After normalisation, 8mm 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 two further parameteric regressors per social category were generated to represent the modulation of that social category by rationality and by likeability. The weightings in the parametric regressors were determined by that participant's ratings of rationality and likeability for each movie. For each design, each trial was modelled as a box-car of 3.7 seconds 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 and likeability. 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 IPL, IFG and visual cortex. No additional activations were found when applying this correction.

To investigate the functional connectivity between the AON and the MZN, we also used psychophysiological interactions (PPIs). The mPFC was selected as a seed region based on the rational > irrational contrast and consisted of 197 voxels (see Figure 2.3). A PPI regressor was then calculated by extracting the BOLD signal from this region in individual participants. This signal was deconvolved to estimate the underlying neural activation and multiplied by a contrast vector which differentiates rational from irrational actions. This PPI regressor was entered into a third general linear model. Five additional regressors were entered but not analysed. These consisted of the extracted BOLD signal from the mPFC, a contrast vector for rational > irrational movies and a regressor for each of the three social form categories. All PPI analyses were performed using the SPM8 PPI toolbox. Forward and reverse contrasts were calculated for rational PPI > irrational PPI.

2.4 RESULTS

2.4.1 BEHAVIOURAL RATING OF STIMULI

Mean rationality ratings of each movie are presented in Figure 2.2. A 3 (social) x2 (action) x2 (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. Participants reported liking rational actions more than irrational actions ($F(1,24)=7.29$, $p=0.01$) but an interaction between action type and social form shows that this effect is stronger in the face and ball conditions compared to the no face condition ($F(2,48)=6.39$, $p=0.003$). Mean ratings of rationality and likeability for each movie type are presented in Table 2.1.

	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
Likeability Ratings						
Face	12.2 ± 2.9	13.7 ± 2.6	13.0 ±3.6	12.8 ± 3.5	11.0 ± 3.6	10.7 ± 4.1
No Face	12.6 ± 3.2	13.4 ± 3.0	12.2 ± 4.1	13.0 ± 3.3	12..3 ±3.5	12.6 ± 3.5
Ball	13.3 ± 4.0	14.4 ± 3.9	13.4 ± 4.1	11.7 ± 3.2	12.5 ± 4.0	12.6 ± 4.1

Table 2.1 Ratings of rationality and likeability for each movie type. Values are means ± standard deviations.

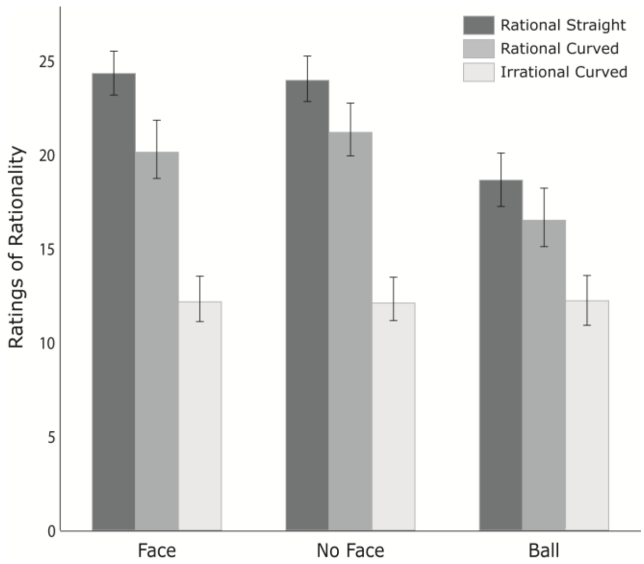

Figure 2.2. Mean rationality ratings for rational straight (dark grey), rational curved (mid-grey) and irrational curved (light grey) actions as a function of social form. Error bars indicate ± 1 standard error of the mean.

2.4.2 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 right IPL extending into right TPJ; right IFG; and a large area of middle occipital cortex (Figure 2.3A (blue), Table 2.2). In the reverse contrast, a large cluster in medial prefrontal cortex (mPFC) showed greater deactivation during irrational actions (Figure 2.3B, Table 2.2).

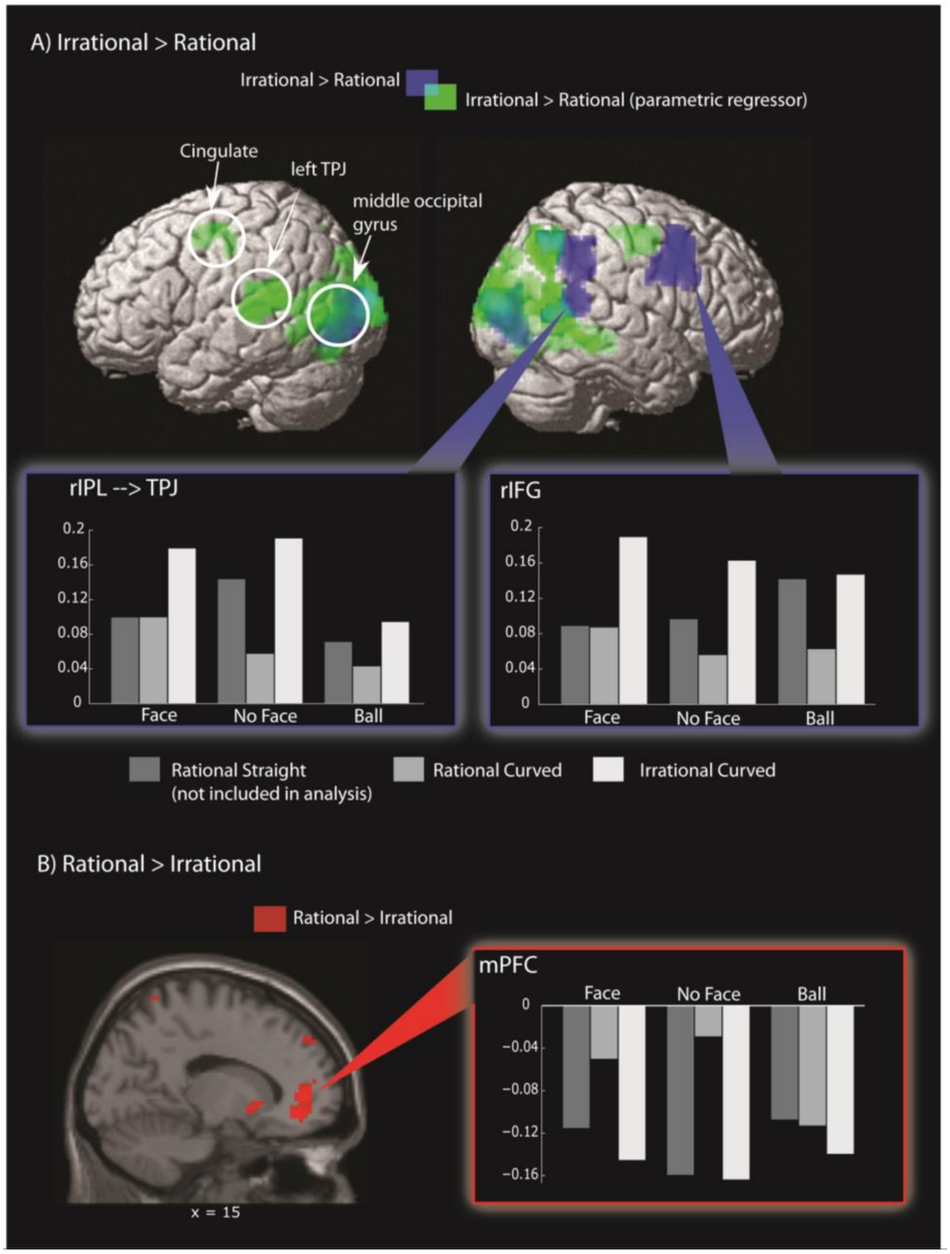

Figure 2.3 Brain areas that are sensitive to action rationality. Panel A: Areas that were more active during observation of irrational curved actions compared to rational curved actions (blue), the areas that responded linearly to individual participants' ratings of action rationality (green) and the 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, TPJ: temporoparietal junction. Panel 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.

Table 2.2. Coordinates for rationality contrasts.

Location	**Prob (cluster corrected p<0.05 FWE)**	**Cluster size**	**T**	**MNI co-ords 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	1619	6.00	-12	-100	10
				3	-85	13
				18	-88	10
Left TPJ	0.022	190	5.81	-51	-43	16
				-42	-49	13
				-60	-34	7
Cingulate	0.019	197	4.64	-9	-10	55
				15	-13	46
				0	-10	55
Right IPL → TPJ	0.000	398	4.50	42	-64	46
				54	-52	1
				51	-61	13

2.4.3 BRAIN AREAS PARAMETRICALLY MODULATED BY RATINGS OF RATIONALITY

Four 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 right IPL extending to TPJ was observed. This cluster is overlapping but slightly posterior to that reported in the previous analysis and includes MTG (see Figure 2.3A (green), Table 2.2). In addition, clusters in middle occipital cortex, left STS and the cingulate were also parametrically modulated by rationality. No significant clusters were found in the reverse contrast. No regions of the brain were parametrically modulated by how much participants reported liking the actions.

2.4.4 FUNCTIONAL CONNECTIVITY MODULATED BY ACTION RATIONALITY

I also explored the functional connectivity of the mPFC using a PPI analysis. There were no regions showing different functional correlations with the mPFC during rational compared to irrational actions at a voxel-level threshold of $p<0.005$ and $k=10$ and a cluster-level threshold of $p<0.05$ (FWE corrected).

2.4.5 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 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 Figure 2.4A and Table 2.3).

Table 2.3. Coordinates for social contrasts

Location	Prob (cluster corrected p<0.05 FWE)	Cluster size	T	MNI co-ords		
				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						

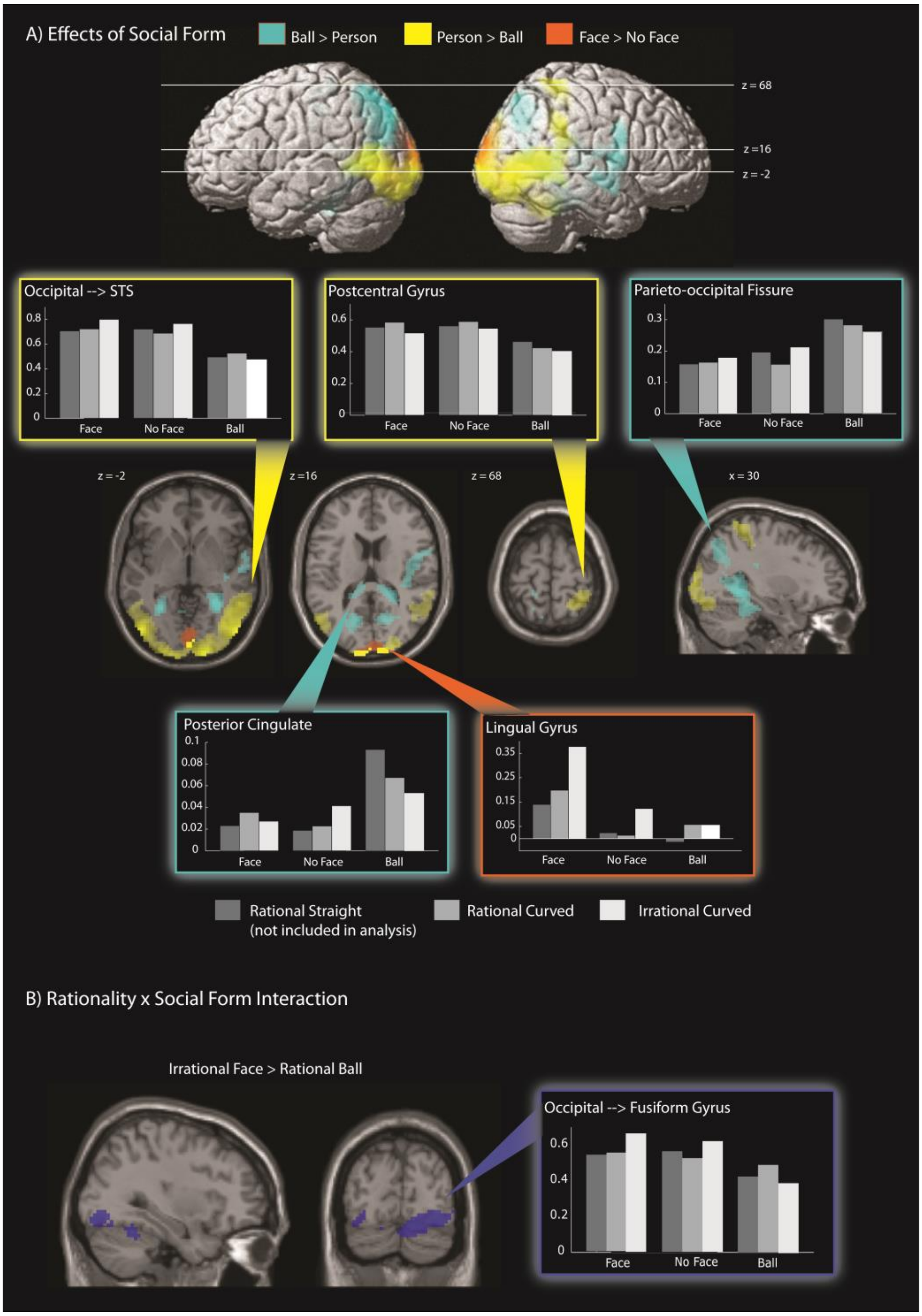

Figure 2.4. Brain regions sensitive to social form. Panel A: Main effects of social form. Brain regions that responded more to moving balls compared to humans (turquoise), regions which were more responsive when observing a human actor compared to moving balls (yellow) and the region which responded 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. Panel B: The interaction between rationality and social form. All images are whole-brain cluster-corrected at $p<0.05$, FWE corrected.

2.4.6 INTERACTIONS BETWEEN RATIONALITY AND SOCIAL FORM

One interaction contrast yielded significant results. A large cluster in 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 Figure 2.4B and Table 2.4. No AON or MZN regions showed an interaction between rationality and social form, even at lower thresholds.

Table 2.4. Coordinates for social x rationality interaction contrasts

Location	Prob (cluster corrected p<0.05 FWE)	Cluster size	T	MNI co-ords 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						

2.5 Discussion

The present study examined how observation of irrational hand actions engages the AON and MZN in the human brain. Results demonstrate that 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. I now discuss the implications of these findings in relation to previous studies and theories of rationality understanding.

2.5.1 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 temporoparietal junction, the inferior frontal gyrus and the middle temporal gyrus. These regions have traditionally been associated with different functions including mentalizing, action observation and higher order visual processing. I now consider each in turn.

First, mPFC and TPJ are core components of the MZN. In my dataset, mPFC showed a significant deactivation when watching irrational actions, while right TPJ showed a significant activation. Both 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 (Figure 2.5) 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. Crucially, the differential response to action rationality in mPFC was not detected in the rationality rating model. This could explain why Jastorff et al. (2010) do not find this frontal activation in their study which used rationality ratings.

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

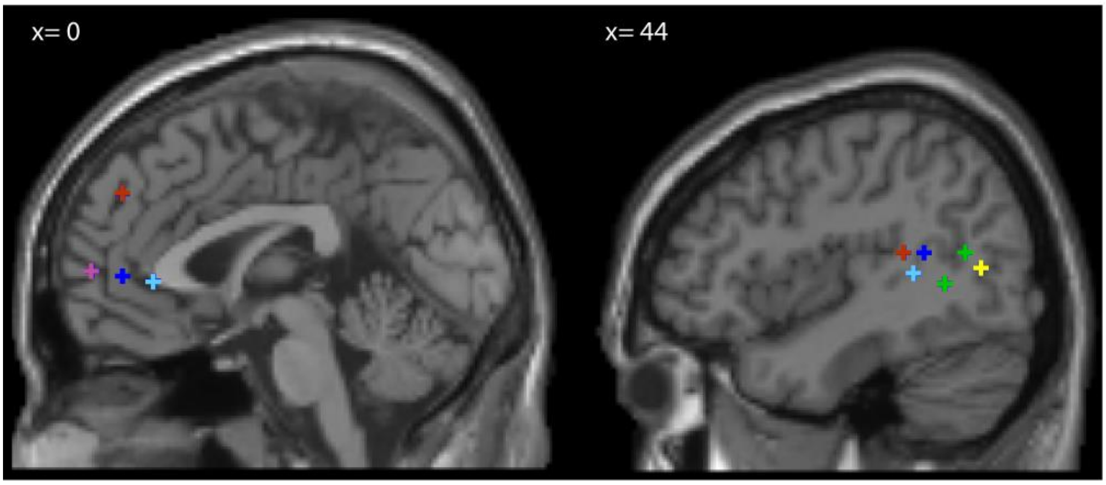

Figure 2.5. A comparison of peaks of activation in TPJ, MTG and mPFC. Crosses represent the peaks of activation in the stimulus driven model (dark blue) and the rationality rating model (green) from the present study and previous studies involving the observation of irrational actions (Light Blue: de Lange et al., 2007; Pink: Marsh & Hamilton, 2011; Yellow: Jastorff et al., 2010; Red: Brass et al., 2007).

Activation was also found in 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 & Hamilton, 2011). It is also consistent with previous reports implicating right frontoparietal cortex in the comprehension of more complex actions (Hartmann, Goldenberg, Daumüller, &

Hermsdörfer, 2005) and their outcomes (Hamilton & 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. I suggest that the AON identifies the complex action goals that require additional analysis, while the TPJ and mPFC may perform further mentalizing about the actor's intentions or why they performed an unusual action. This is consistent with data reported a previous meta-analysis by Van Overwalle (2009).

Finally, 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 Figure 2.3A 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. I suggest this pattern may reflect the difference between sensitivity to subtle kinematic features in MTG, and categorical perception of rationality in the AON and MZN. Work on object perception shows that early visual areas are sensitive to many individual features of an object, while temporal and frontal cortex can show categorical responses to object groups (Jiang et al., 2007; van der Linden, van Turennout, & Indefrey, 2010). These data may reflect a similar hierarchy in the processing of action rationality, from kinematic features in MTG to categories of 'rational 'or 'irrational' in parietal cortex.

This study found no evidence for action rationality modulating the connectivity of the mPFC. This gives the preliminary indication that that the connectivity between the AON and the MZN is similar during the observation of rational and irrational actions. However, these results should be treated cautiously as the design of this study was not optimised for PPI analyses and further work should investigate this more rigorously.

All of the analyses reported in this chapter 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 mPFC in only the rational curved actions. However, this is a post-hoc explanation and further work will be needed to determine if this really is the case.

2.5.2 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 to rationality 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 rationalize 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 fusiform gyrus following observation of irrational actions with the face visible. Past studies strongly link fusiform gyrus to face perception (Kanwisher, McDermott, & Chun, 1997) and show that this activation is modulated by covert attention to the face (Wojciulik, Kanwisher, & Driver, 1998).

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 (Figure 2.3B) 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 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 & 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., 2011; Gazzola, Rizzolatti, Wicker, & Keysers, 2007; Ramsey & Hamilton, 2010). Instead the brain region which distinguished human from ball actions were a large, diffuse cluster in 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).

2.5.3 CONCLUSIONS

This chapter assesses the relative contributions of the mirror and mentalizing 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 chapter clarify some of these differences by using strictly controlled stimuli and two different analysis models. My results show that when action rationality is altered by environmental constraints, both AON and MZN respond to this change. Therefore, I argue that AON and MZN systems are playing complimentary roles in understanding action rationality. I 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.

CHAPTER 3. IDENTIFYING ROBUST EYE TRACKING MEASURES OF ACTION COMPREHENSION IN TYPICALLY DEVELOPING ADULTS

3.1 ABSTRACT

Observing irrational actions engages both the action observation and mentalizing networks of the brain. However, little is known about the cognitive processes that underpin the comprehension of irrational actions. The experiment reported in this chapter aims to use eye tracking to identify some of these processes by examining a number of measures which may reflect rationality comprehension. Twenty typically developing adults watched movies of rational and irrational hand actions while their eye movements were recorded. Measures of looking time, scan path and saccade latency were calculated. Results showed that looking time measures such as the amount of time spent looking at the hand or the action goals reflected the rationality of the actions. Conversely, the latency analysis was more sensitive to the kinematic features of actions, regardless of action rationality. I conclude that the measures used in this paradigm can successfully differentiate basic action comprehension such as goal prediction and more complex action understanding such as rationality detection.

3.2 INTRODUCTION

The experiment presented in Chapter 2 clearly demonstrates that irrational actions provide a special test case to investigate the interplay between the action observation network and the mentalizing network. The discussion in Chapter 2 also makes a number of hypotheses about the perception of irrational actions and where participants are attending during action observation. For example, I propose that participants closely attend to the action kinematics during observation of irrational actions and this may be driving the increased activation in IFG. This hypothesis is supported by data suggesting that when participants are asked to attend to the way in which an action is performed, IFG is activated (de Lange et al., 2008; Spunt et al., 2011). In addition, I proposed that the interaction between rationality and social form in the occipital cortex may be due to increased fixations on the face of the actor during irrational actions. This pattern of results has been reported previously (Vivanti et al., 2011) and it would be useful to replicate this finding within my own stimuli. The first aim of the present study is to test these claims about attention and perception during irrational action observation in typically developing adults using eye-tracking.

As reviewed in Chapter 1, section 1.3, eye tracking can provide a potentially excellent method to study action observation in an implicit and natural way. In this exploratory study I also aim to identify the eye tracking measures which can be used as markers for the cognitive processes that support rationality comprehension. In doing so, I hope to develop a clear measure of rationality comprehension that can be used to assess understanding in individuals with autism. I start by reviewing some important methodological issues.

3.2.1 METHODOLOGICAL CONSIDERATIONS

There are many important methodological issues with eye tracking data. One such issue arises from the rich data that eye tracking produces. There are many measures that can be taken from eye tracking data yet there is little consensus on which is the most appropriate to use. A further issue in using eye tracking to study rationality understanding is that most previous studies on this topic have studied infant and child eye movements. It is unclear whether reported gaze patterns are stable across time and that these measures are valid for adult eye tracking. In this section I review the findings from the child and infant studies of action observation, with a focus on the measures that have been selected and the cognitive processes that they are thought to reflect.

Looking time measures have been used to assess rationality understanding in typically developing infants (Elsner, Pfeifer, Parker, & Hauf, 2013). Modelled actions were either irrational (the model turned on a light with her forehead) or rationalised by an environmental constraint (a blanket wrapped around the models' shoulders prevented her from using her hands). An analysis of looking times revealed that infants looked longer at the rationalized actions in which an environmental constraint impacted upon the action, although looking times to the specific action and constraint areas of the movie did not differ in the majority of trials. The authors interpret this increased looking time during constrained actions to mean that the infants detected action rationality and spent time evaluating the environmental constraints imposed upon the actions.

Looking time was also used as a measure of rationality understanding in participants with ASC (Vivanti et al., 2011). In their study, Vivanti et al. (2011) showed ASC and typically developing children movies of irrational actions in which an actor performed an action with an unusual body-part (for example, closing a drawer with her shoulder) and matched rational actions in which the actor completed the same action but had her hands occupied. Results showed that both groups of participants looked longer at the face of the actor during irrational actions. Vivanti et al. (2011) propose that increased time looking at the face of the actor indicates the participants' attempt to rationalize the actors bahaviour by seeking more information about the actor and their intention. However, it is not possible to tell from these results whether participants in the ASC group actually use this information to make inferences about behaviour.

In a study of prospective looking, infants were habituated to an action in which a hand reached and grasped one of two objects. Following habituation, a test trial in which the two objects switched location was presented. At test, infants made more predicitve first looks to the previoulsy grasped object, not the previously grasped objects' location (Cannon & Woodward, 2012). Thus measures of first-goal-look and looking time to the different goal locations can indicate the degree of goal prediction used by the participant.

Predicitive gaze has also been reported as an index of goal prediction during both action execution and action observation (Flanagan & Johansson, 2003). In their study Flanagan and Johansson (2003) asked participants to move three blocks in series from one location to another whilst their eye movements were recorded. During action execution, participants fixated start and end points of each action but made very few fixations between these locations. Furthermore, their eye movements were predicitive of their actions as they fixated the end point of their action 150ms prior to reaching it. Similarly, when participants observed movies of someone else performing the task, their eye movements were also predictive. Therefore, Flanagan and Johansson (2003) argue that predictive eye movements during action observation can be used as an index of goal understanding.

Predictive eye movements during irrational actions have been assessed in one previous study of typically developing 6- and 12- month old infants (Gredebäck & Melinder, 2010). In this study, infants saw movies of rational and irrational feeding actions. During a rational action, one adult picks up a piece of banana with a spoon and brings it to a second adults' mouth. In an irrational action, the first adult picks up the banana and places it on the back of the recipients hand, who then eats the banana from her hand. Latency to fixate the end point of the action (head or hand) was calculated for each condition. Results showed that rational actions were anticipated faster than irrational actions. However there are a number of methodological problems with the way in which the stimuli was constructed for this type of analysis. Firstly, latency of fixation measures are extremely sensitive to the action kinematics and timing used (Rotman et al., 2006), two features that were not matched between conditions in this study. Secondly, predictive eye movements are driven by the action goal (Eshuis et al., 2009) and the speed of prediction is determined by goal salience (Henrichs, Elsner, Elsner, & Gredebäck, 2012). In their study, Gredeback and Melinder (2009) use the recipients' head and hand as the two action goals but these are not matched for saliency or predictability. These goal differences could result in the reduced anticipatory looking to the hand that is reported. In order to effectively measure anticipatory looking, actions need to be carefully matched for kinematics, timing, goal saliency and goal predictability. Additionally, previous studies that use latency of goal fixation as a measure take only the speed of action prediction as the measure of interest and do not account for differences in scan path prior to the predictive fixation. It is interesting to investigate where participants gather their information from, prior to making a predictive saccade as this may reveal systematic differences in the way in which goals are predicted between individuals.

A final, critical issue in this area is statistical independence in data analysis. There is increasing recognition that double-dipping in the analysis of rich datasets can inflate false-positives and is not good practice (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009). This is particularly an issue when data-analysis methods are not standardised and there are many possible approaches which could lead to different results. To avoid these problems, I record data from a sample of typical undergraduate students and examine a variety of measures in this dataset. Measures examined here included: looking time to goals, to the actor's face, to the hand performing the action, and to the environmental contsraints upon the action;

which goal was first fixated; the location of the fixation prior to making a saccade to the action goal; and the timing of predictive saccades to the action goal. I use this dataset to develop a full analysis protocol, selecting the measures which best reflect action understanding and action rationality in typical adults. This analysis protocol can then be applied to a sample of participants with ASC (see Chapter 4).

As mentioned in section 1.3, this study has one further aim. Within this paradigm it is possible to further test the claim that predictive eye movements are generated by the mirror system (see section 1.3 for a detailed argument of why this may be the case). If this is the case, we would expect to see predictive eye movements for all actions, regardless of their rationality. However, if predictive eye movements are modulated by action rationality, it is likely that the mirror system is not the only brain system involved in generating them. This is because the experiment in Chapter 2 demontrates that irrational actions engage additional brain systems for comprehension.

3.3 METHOD

3.3.1 PARTICIPANTS

Twenty typically developing, right-handed participants took part in this study. Data from two participants was excluded from analysis due to eye tracker failure (<70% of samples present in at least three blocks). Therefore, results reported here are based on a final sample of 18 participants (16 female, mean age 22.0 years).

3.3.2 STIMULI/APPARATUS

Eye movements were measured using a portable Tobii 1750 infrared recording system which sampled at a rate of 50Hz with 1^{o} precision and 0.5^{o} accuracy. A standard five point calibration procedure was successfully completed prior to each recording. The movies developed for the fMRI experiment in Chapter 2 were used. Thus a set of 18 movies depicting three levels of rationality (rational straight, rational curved and irrational curved) crossed with three levels of social form (face, no face and ball) for each of the two goal locations were used. All movies were exactly matched for action kinematics and timing on a frame by frame basis (see section 2.3.2 for details of how these stimuli were constructed). As with the fMRI study presented in Chapter 2, rational straight actions were included in the design to prevent the participant from always expecting a curved action but were not analysed because they are unmatched for action trajectory.

3.3.3 DESIGN

A within-participant two (action type) by three (social form) design was employed. Movies were presented in separate blocks of face, no face and ball trials. Each block contained 8 repetitions of each action in a random order. Thus in total, 48 movies were presented per block and the block lasted for approximately 6 minutes. To maintain alertness, participants were also asked to respond to three questions about the movies at random intervals within each block. These were simple questions about the visual properties of the movie. Answers to these questions were not analysed. All participants watched six blocks of movies (two of each type) in a pseudorandom order.

3.3.4 PROCEDURE

The study was approved by the School of Psychology ethics committee. All testing took place in a quiet testing laboratory. Participants sat approximately 64cm from the Tobii monitor with a table and a number keypad in front of them. They completed the five-point calibration procedure at the start of each of the six experimental blocks. Following the last block of movies, participants were shown each of the six action types again (with the actor fully visible) and asked to rate the rationality for each of the movies using a battery of 6 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 a total rationality score was computed for each participant for each movie (maximum score of 30 indicated most rational).

3.3.5 DATA PROCESSING

All data processing was completed using in-house scripts written in Matlab. To ensure data quality, individual trials were excluded from the analysis if more than 20% of eye movement samples were missing during the critical action period (the time at which the ball started to move to the time the ball enters the goal location, see Table 3.1 for trial exclusion rates). Within included trials, eye movement samples were then classified as fixations or saccades using a velocity-based algorithm with a threshold of 60 degrees/sec (Salvucci & Goldberg, 2000). Data samples with a velocity above this threshold were marked as occurring during a saccade and excluded from further analysis. Three levels of analysis were then conducted in order to identify attention to actions (looking time analysis), where saccades into the goal came from (saccade analysis) and the time at which saccades from the hand to the goal location were initiated (latency analysis). These analysis techniques are detailed in sections below.

Table 3.1. Number of trials included at each level of analysis.

Analysis Level	Inclusion Criteria		
Total trials completed	Based on 18 adults completing 6 blocks of 48 trials	5184	
		Include	**Exclude**
Step 1: Looking time analysis	<20% samples missing	4773	411
Step 2: Saccade analysis	Saccade to goal present	4256	517
Step 3: Latency Analysis	Goal saccade from hand present	1555	2701

3.3.5.1 LOOKING TIME ANALYSIS

A looking time analysis was conducted to see if allocation of attention to features of the scene differed between action type and social form. Each movie scene was divided into 6 areas of interest (AOIs). AOIs were defined by a close fitting rectangle around each of the goal locations, the start point, barrier and face. A moving area of interest was created for the ball by drawing a sphere (radius 70 pixels) around the central co-ordinate of the ball at each frame of each movie. To account for spatial sampling errors, a margin of one visual degree was added to each of these AOIs (see Figure 3.1). Looking time was calculated for each AOI as the percentage of data samples falling within the AOI over the course of each movie for each participant. Percentage of data samples that were within the frame of the movie but not within an AOI was calculated as 'background'. Looking times to the target goal, non-target goal, ball, barrier and face were analysed. I did not analyse looking time to the start or the background because these areas have no impact on the action and I have no apriori expectations that looking times to these regions should be affected by action rationality or social form.

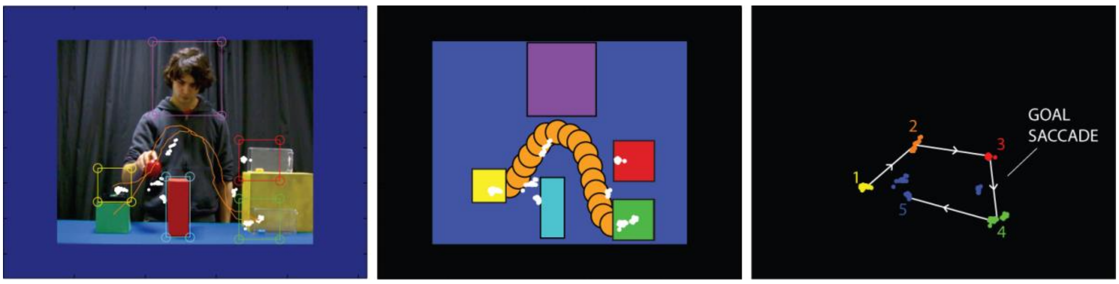

Figure 3.1 Panel representing each of the stages of analysis. <u>Left:</u> Raw sample data (white dots) overlaying a still frame of a rational curved movie. Areas of interest (AOIs) are drawn over the scene. <u>Middle:</u> A schematic diagram of the AOIs used in this study with sample data plotted in white dots. Looking time is calculated as the percentage of samples falling within each AOI. <u>Right:</u> Data samples are labelled according to the AOI they fall within (colours correspond to the middle panel). The first saccade into the goal is identified. The origin of this saccade is used in the saccade analysis and the timing of this saccade is used in the latency analysis.

3.3.5.2 SACCADE ANALYSIS

The saccade analysis was conducted in order to see where people were attending immediately prior to making a saccade to the action goal. This measure indicates where participants gathered information from in order to predict the action outcome. Trials were only included in this analysis if there was a saccade to the goal of the action present within the trial (see trial inclusion rates in Table 3.1). To calculate where goal saccades came from, eye movement samples for each trial were divided into gaze segments between saccades. The gaze position of these segments was labelled according to the focus of the majority of samples within the segment. An algorithm was written in Matlab to generate these labels based on five decision criterion (see Table 3.2 for a description and example of each). To validate the performance of this algorithm, a sample participant was hand coded and the results were compared. Over 48 trials, the sample participant made 393 saccades, giving 501 gaze segments. Percentage of gaze segments coded by each criterion point for this participant is reported in column 4, Table 3.2. Of these 501 gaze segments, the algorithm was able to code 499 in the same way as a human coder. Also see Figure 3.2 for an illustration of the algorithm performance on one trial.

The first saccade into the target goal was identified and the origin of this saccade was recorded (see Figure 3.1). For each movie type, the percentage of saccades from each AOI into the target goal was calculated for each participant. In this level of analysis I analyse saccades from the non-target goal, the ball/hand and the face. The non-target goal was selected as increased saccades into the target goal may reflect more prediction errors in which participants are anticipating the action to end at the alternate goal. In contrast, saccades directly from the hand may indicate easier action prediction. Saccades from the face were selected to explore whether participants use the information provided by the face to predict actions.

Table 3.2. Description and frequency of use of the decision criterion used to generate labels for the focus of each gaze segment.

Decision Criterion	Example Event Description	Outcome	% Segments Coded
If 80% of data samples in a segment are within one AOI, code as that AOI.	94% of data samples were within the hand AOI, 6% were elsewhere.	Label segment as hand. (see Figure 3.2E, segment 5)	66%
If data samples are split between an AOI and elsewhere, code as the AOI.	55% of data samples were within the barrier AOI, 45% were elsewhere.	Label segment as the barrier. (see Figure 3.2E, segment 2)	23%
If data samples are split between a goal and the hand, code as the goal but mark as smooth pursuit if the samples on the hand occurred earlier than the samples on the goal.	45% of data samples were within the hand AOI, followed by 55% of the samples on the goal.	Label segment as the hand but count it as a goal saccade with 0ms latency.	9%
If data samples are split between the start and the hand, code as the hand.	30% of samples are within the start AOI, 70% in the hand AOI.	Label segment as the hand.	<1%
If >50% of samples are missing, code as missing data.	65% of samples were missing, 20% were within the hand AOI, 15% were within the top goal AOI.	Label the segment as missing data.	<1%

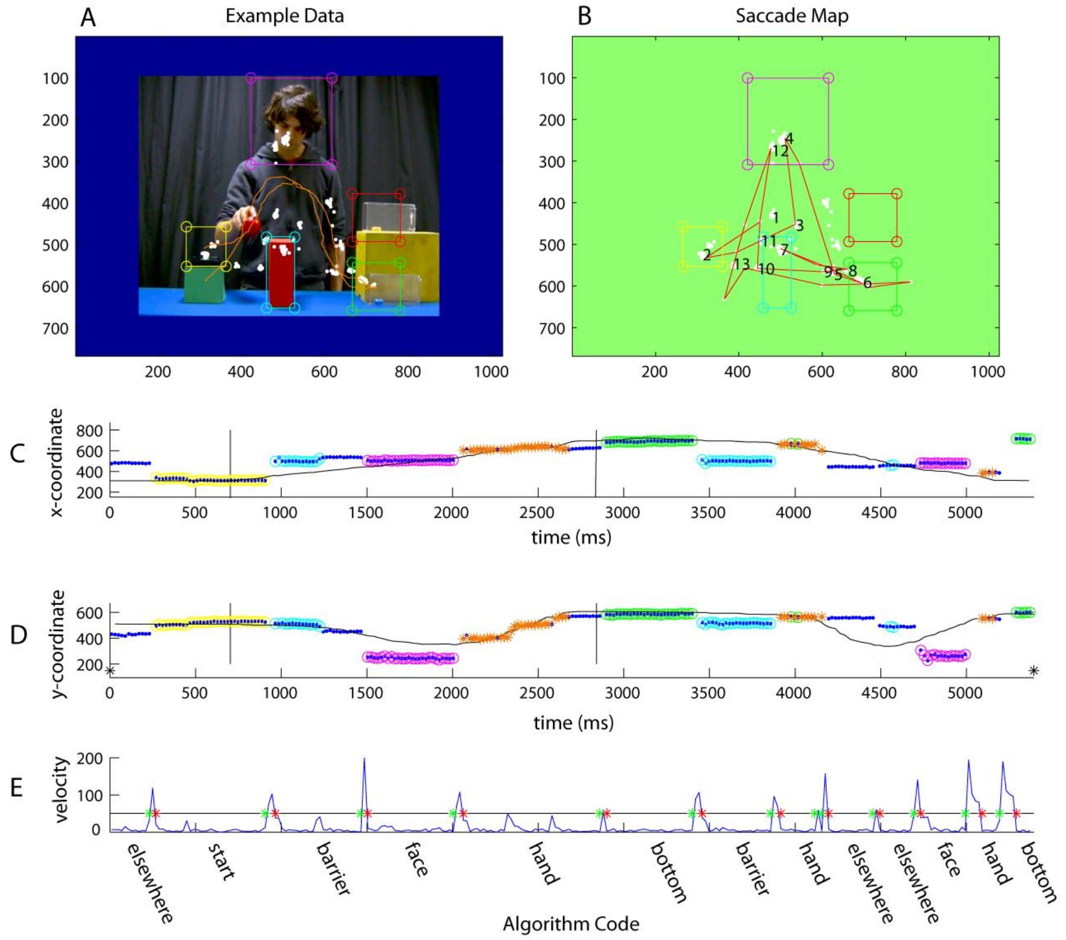

Figure 3.2. Sample data from one trial to demonstrate the performance of the gaze segment labelling algorithm. <u>Panel A</u> shows sample data from a rational curved trial from one participant (white dots) plotted over a still frame from the movie. Coloured lines indicate AOIs. <u>Panel B</u> shows aaccade map from the same trial. Data samples plotted in white dots. Saccade start and end points are denoted by numbers and joined with a red line. <u>Panels C and D</u> show the X- and Y- co-ordinates of data samples over the course of the trial (blue dots). Black lines indicate the location of the hand over the course of the trial. Coloured marks indicate which AOI the sample falls within. Vertical lines indicate the critical action period. <u>Panel E</u> plots the velocity of data samples over the course of the trial, measured in degrees/second (blue line). Green stars indicate the start of each saccade and red stars indicate the end of each saccade. Horizontal line indicates the 60 degrees/second threshold used to identify saccades. Labels along the x-axis indicate the label assigned to that gaze segment by the algorithm.

3.3.5.3 LATENCY ANALYSIS

Latency of goal prediction was analysed to assess whether action type or social form modulate how quickly participants predict the action goal when they are attending to the hand. Trials were only included in this measure when the participant made a predictive saccade to the action goal from the hand before the hand reached the goal (see Table 3.1 for trial inclusion rates). This measure was selected in order to identify whether rationality modulates the speed of action prediction when participants are attending to the action kinematics. Latency of prediction was calculated by subtracting the time that the ball reached the goal from the time that the saccade to the goal was initiated. Thus negative fixation latencies indicate faster anticipation of the action. Outliers were removed if they were ±3 standard deviations from the mean. These data were then analysed using a hierarchical linear mixed model which accounted for the different amounts of data contributed by each participant. A participant identifier was entered as a hierarchical variable to account for correlation within subjects.

3.4 RESULTS

3.4.1 RATIONALITY RATINGS

Mean ratings of rationality are presented in Figure 3.3. A two (action) by two (goal) within participant ANOVA revealed a main effect of rationality ($F(1,17)=16.16$, $p=0.01$) in which rational curved actions were rated as more rational than irrational curved actions. No effect of goal (F(1,17)=0.21, p=0.65) and no interaction between rationality and goal (F(1,17)=0.99, p=0.33) was found.

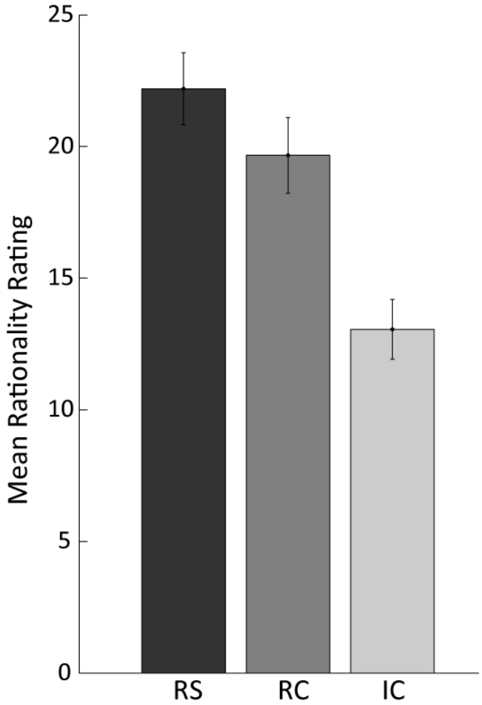

Figure 3.3. Mean ratings of rationality for each movie type. Higher ratings indicate that a movie was judged as more rational. Maximum possible score was 30. RS: rational straight, RC: rational curved, IC: Irrational curved. Error bars represent ±1 standard error of the mean.

3.4.2 LOOKING TIME ANALYSIS

Percentage looking time in each AOI was calculated for each movie type and is presented in Figure 3.4A and Table 3.3. Two (action type) by three (social form) by two (goal location) within participant ANOVAs were conducted for looking time to the target goal, non-target goal, barrier and ball. In trials when the face was visible, a two (action) by two (goal) within participant ANOVA was conducted on looking time to the face. All reported results are significant after Bonferroni correction for multiple comparisons.

Looking time to the target goal was modulated by the social form of the stimulus. Post-hoc t-tests show that there is a trend towards participants looking longer at the target goal during actions performed by the ball, compared to human actions. However, this effect is not statistically significant when correcting for multiple comparisons. There was no impact of action rationality or goal on looking time to the target goal (see Figure 3.4b and Table 3.3a)

Looking time to the non-target goal was also modulated by social form. Participants looked longer at the non-target goal during actions performed by the ball compared to human actions. This result is strongest when comparing actions where the face is visible to the ball and only a trending effect when comparing no face to ball actions. There was a trending effect of rationality on looking time to the non-target goal as participants looked longer at the non-target goal during irrational actions, compared to rational actions. However, this effect did not survive correction for multiple comparisons. The goal location had no impact on looking time to the non-target goal (see Figure 3.4c and Table 3.3b)

Participants looked longer at the ball/hand during human actions compared to those where the ball moved independently. A trending effect of rationality also revealed that participants looked longer at the ball/hand during irrational actions but this effect does not survive correction for multiple comparisons. Action goal had no impact on looking time to the ball/hand (see Figure 3.4d and Table 3.3c)

Participants looked at the barrier more during human actions compared to those where the ball moved independently. They also looked more at the barrier during rational actions. Furthermore, an interaction between rationality and social form shows that this bias to look more at the barrier during rational actions is only present when a human is performing the action. An effect of goal also indicated that participants looked more at the barrier during actions that ended at the bottom goal. See Figure 3.4e and Table 3.3d for results.

Looking time to the face was not modulated by action rationality or action goal (see Table 3.3e).

Table 3.3. Statistics for looking time analyses. Significant effects are marked in bold type. Alpha is corrected for multiple comparisons such that [a] indicates α=0.01 and [b] indicates that α=0.017.

Main Effects	direction	F/(t)	df	P
a) ANOVA 1: Looking Time to Target Goal				
Social Form		**5.09**	**2,34**	**0.01** [a]
	ball > face	(2.60)	17	0.02 [b]
	ball > no face	(2.33)	17	0.03 [b]
	no face > face	(1.01)	17	0.33 [b]
Rationality		0.85	1,17	0.37 [a]
Goal		0.87	1,17	0.37 [a]
b) ANOVA 2: Looking Time to Non-Target Goal				
Social Form		**5.89**	**2,34**	**0.006** [a]
	ball > face	**(3.23)**	**17**	**0.005** [b]
	ball > no face	(2.59)	17	0.02 [b]
	no face > face	(0.66)	17	0.52 [b]
Rationality	**irrational > rational**	**5.70**	**1,17**	**0.03** [a]
Goal		1.28	1,17	0.27 [a]
c) ANOVA 3: Looking Time to Ball				
Social Form		**59.67**	**2,34**	**<0.001** [a]
	face > ball	**(6.96)**	**17**	**<0.001** [b]
	no face > ball	**(7.80)**	**17**	**<0.001** [b]
	no face > face	(1.07)	17	0.30 [b]
Rationality		4.83	2,34	0.04 [a]
Goal		3.75	2,34	0.07 [a]
d) ANOVA 4: Looking Time to Barrier				
Social Form		**10.68**	**2,34**	**<0.001** [a]
	face > ball	**(4.51)**	**17**	**<0.001** [b]
	no face > ball	**(4.32)**	**17**	**<0.001** [b]
	no face > face	(0.06)	17	0.96 [b]
Rationality	**rational > irrational**	**86.75**	**1,17**	**<0.001** [a]
Goal	**top > bottom**	**15.80**	**1,17**	**0.001** [a]
Social Form x Action		**10.26**	**2,34**	**<0.001** [a]
	R – I face > R – I ball	**(4.19)**	**17**	**0.001** [b]
	R – I no face > R – I ball	**(4.95)**	**17**	**<0.001** [b]
	R – I no face > R – I face	(0.20)	17	0.84 [b]
d) ANOVA 5: Looking Time to Face				
Rationality		0.67	1,17	0.43 [a]
Goal		7.40	1,17	0.01 [a]

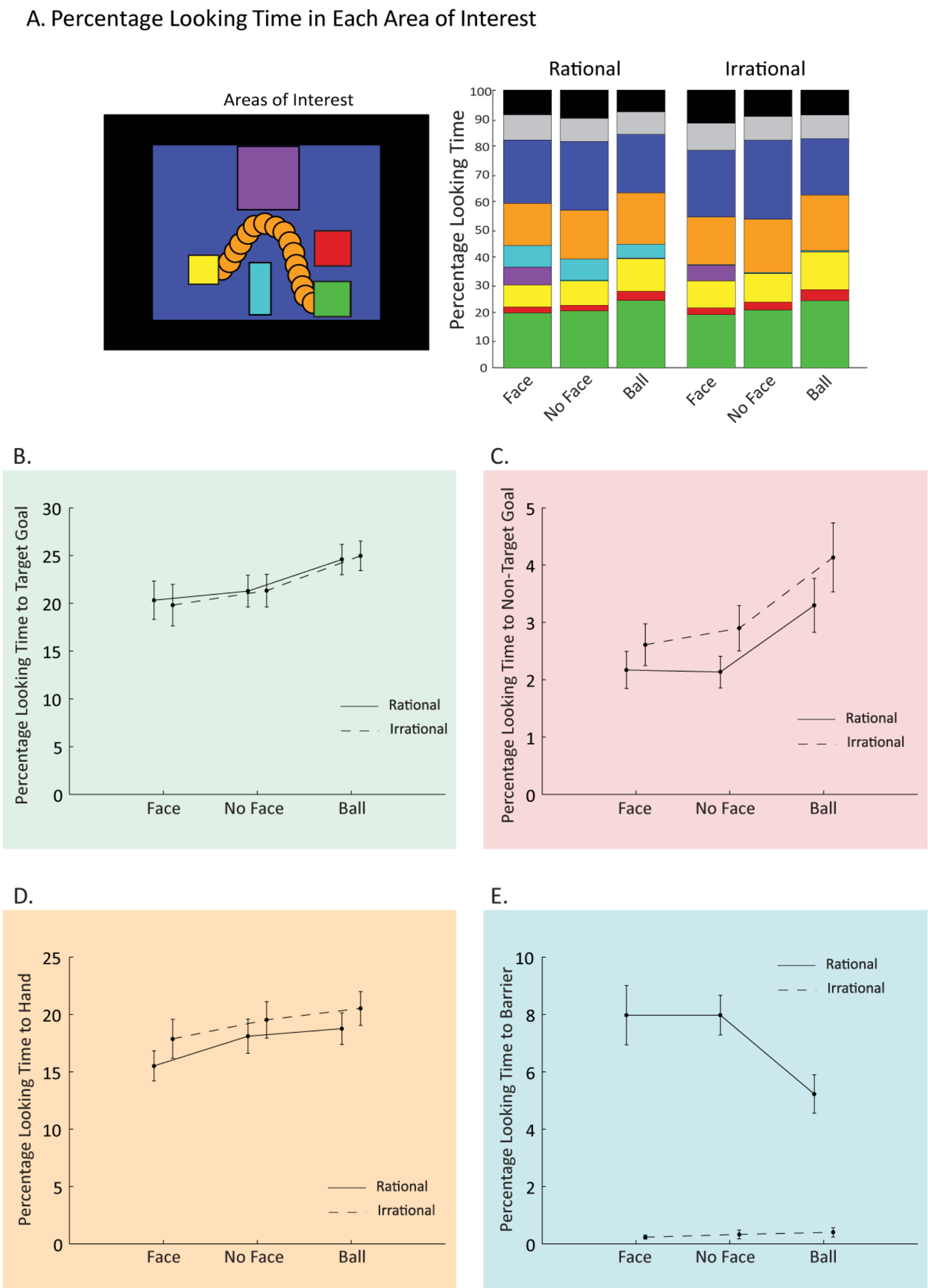

Figure 3.4. Percentage looking time for each area of interest. *Panel A shows the cumulative percentage of looking time to each area of interest in a stacked bar chart. Colours correspond to the areas of interest depicted on the left. Grey bars indicate the data points which were excluded because they occurred during a saccade. Black bars indicate missing data. Panels B-E show looking time for one area of interest plotted as a function of social form and action rationality. Background colours correspond to the areas of interest in panel A. Error bars represent ±1 standard error of the mean.*

3.4.3 SACCADE ANALYSIS

The origin of first saccades into the target goal was recorded and the percentage of these saccades from each AOI was calculated. As with the looking time analysis, this percentage of saccades was analysed using a three (social form) by two (rationality) by two (goal) within participant ANOVA for saccades from the non-target goal and the ball/hand. Percentage of saccades from the face to the goal was analysed using a two (rationality) by two (goal) ANOVA using only data from trials when the face was visible. The statistics are reported in Table 3.4.

Percentage of saccades from the non-target goal to the goal was not modulated by social form, action rationality or goal (see Table 3.4a). Similarly, the percentage of saccades from the ball to the goal did not differ for social form, action rationality or goal (see Table 3.4b). Finally, the percentage of saccades from the face to the goal was not affected by action rationality but there were more saccades from the face to the goal when the action ended in the bottom goal (see Table 3.4c).

Table 3.4. Statistics for the saccade analysis. Significant effects are marked in bold type. Alpha is corrected for multiple comparisons such that [a] indicates α=0.017.

	direction	F/(t)	df	p
a) ANOVA 1 : Saccades from Non-Target Goal to Goal				
Social Form		0.78	2,34	0.47 [a]
Rationality		0.02	1,17	0.89 [a]
Goal		0.21	1,17	0.65 [a]
b) ANOVA 2: Saccades from Ball to Goal				
Social Form		0.87	2,34	0.43 [a]
Rationality		1.42	1,17	0.25 [a]
Goal		2.58	1,17	0.13 [a]
c) ANOVA 3: Saccades from Face to Goal				
Rationality		2.01	1,17	0.17 [a]
Goal	**bottom > top**	**7.91**	**1,17**	**0.01** [a]

3.4.4 LATENCY ANALYSIS

The mean latency of saccades from the hand/ball to target goal was calculated for each movie type. Results are presented in Figure 3.5 and Table 3.5. Social form, action rationality and goal were entered into a full factorial linear mixed model. A main effect of social form indicated that participants were faster to anticipate actions that had less social information. Ball actions were predicted more quickly than human actions where the face was occluded and actions where the face was visible were predicted slowest of all.

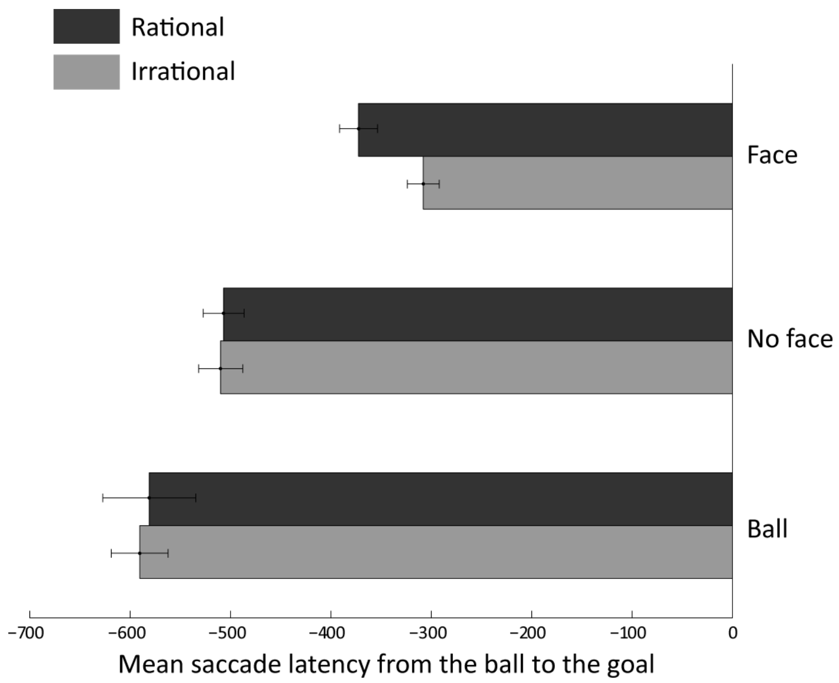

Figure 3.5. Mean latency of goal saccades from the ball as a function of action rationality and social form. Error bars represent ±1 standard error of the mean.

Table 3.5. Statistics for the latency analysis. Significant effects are marked in bold type. Alpha is corrected for multiple comparisons such that [a] indicates α=0.05 and [b] indicates that α=0.017.

	direction	F/(t)	df	p
Linear Mixed Model: Latency of Saccades from the Ball to the Goal				
Social Form		**41.81**	**2,1037**	**<0.001[a]**
	no face > ball	**(4.01)**	**756**	**<0.001[b]**
	face > no face	**(5.62)**	**655**	**<0.001[b]**
	face > ball	**(8.74)**	**681**	**<0.001[b]**
Rationality		0.55	1,1037	0.46[a]
Goal		0.04	1,1037	0.85[a]

3.5 DISCUSSION

The aim of the present study was to develop a robust measure of action comprehension for adults, using eye tracking. It also aimed to test the hypotheses generated by the fMRI experiment reported in Chapter 2 that during irrational actions participants will focus more on the action kinematics (i.e. look at the hand longer) and look more at the face. An analysis protocol was developed to thoroughly examine which features of eye movements reflect action rationality and are modulated by the social form of the agent.

With respect to my first aim, I briefly summarize the experimental results in relation to rationality detection and social form sensitivity and propose the cognitive processes that they may reflect.

3.5.1 RATIONALITY DETECTION

Rationality detection was mostly reflected in measures of looking time. Participants looked longer at the barrier during a rational compared to an irrational action. This is consistent with similar results reported in infants (Elsner et al., 2013) and suggests that participants are spending time evaluating the environmental constraints that impact upon an action. Gergely and Csibra (2003) argue that this process of rationalising the environmental constraints that impact an action is key for teleological reasoning about actions. Therefore, time spent looking at the barrier may be a marker of teleological reasoning. This interpretation is strengthened by the fact that there was an interaction between action rationality and the social form of the agent. It seems that participants spend longer evaluating the environmental constraints of rational actions performed by humans compared to balls.

There was a trending effect towards participants looking at the non-target goal more during irrational actions. Whilst this effect is not significant after correction for multiple comparisons, it hints that participants are either making more prediction errors or are dwelling on why the agent did not put the ball in the non-target goal as he originally planned. However, as this effect is only marginal, I do not make any big claims about the use of this measure.

Looking time to the ball/hand was also marginally affected by rationality with participants tending to look at the ball for longer during irrational actions. Again this effect is only a trend and not significant after correction for multiple comparisons but it does hint that participants pay more attention to the action kinematics during irrational actions. This could explain the increased activation in the IFG during irrational action observation that I reported in Chapter 2. Again, this finding must be taken cautiously because the effect is only trending towards significance.

Time spent looking at the face was not distinguishable for rational and irrational actions. This is inconsistent with previous studies which report increased looking at the face following an irrational action (Vivanti et al., 2011). It is possible that the time window between the completion of the action and the end of the movie was too short for participants to make a saccade to the face and reflect on why the action occurred in an inefficient manner. Alternatively, perhaps the face was not very salient as it did not provide any cues as to how the action would proceed. This is supported by the surprising finding that people look very little at the face of the actor when it is visible for all action types. This finding does not support the explanation for the increased activity in occipital cortex during irrational actions with the face visible as proposed in Chapter 2. However, these studies tested different groups of participants in very different experimental settings so it is difficult to draw firm conclusions about the eye movement behaviour of the group in the MRI scanner.

Latency of goal prediction was not sensitive to the rationality of actions. This is inconsistent with an earlier study of infants which showed longer fixation latencies for irrational actions (Gredebäck & Melinder, 2010). However, the present study used better controlled stimuli and corrected for a number of mismatches between the conditions in the previous study. If we include predictive fixations for the rational straight actions in the model, an action effect, driven by faster anticipation of rational straight actions is significant ($F(2,1537)=13.7$, $p<0.0001$). Therefore the latency analysis is very sensitive to action kinematics and basic motor properties of actions, not higher level rationalisation of actions. This finding provides further evidence in support of the hypothesis that predictive eye movements are generated by the mirror system (see section 7.2.1 for a more comprehensive discussion of this finding).

3.5.2 SENSITIVITY TO SOCIAL FORM

Participants spent more time looking at the goals of the actions and made faster predictive eye movements to the action goal when an action was performed by the ball moving independently, compared to human actions. These findings can be explained simply by the reduced visual detail on the screen during the ball actions. As there is less to look at, participants fixate the action goals faster and maintain their fixations for longer. Despite this, participants actually spent more time looking at the barrier during the human action conditions. This suggests that participants spend more effort evaluating the environmental constraint of an action if it is performed by a human actor. Participants also attend more closely to the ball/hand region during human actions compared to ball actions. This could be because the hand may provide important kinematic cues about the action whereas the ball does not. Despite this, participants are actually slower to predict actions when there is kinematic information available.

Remarkably, there was only one measure which yielded a significant interaction between action rationality and the social form of the agent. This was looking time to the barrier as previously discussed. The lack of any other interactions between these factors is consistent with the fMRI results presented in Chapter 2 and it suggests that action rationality is computed regardless of the social form of the agent.

3.5.3 CONCLUSIONS

The present study provides a thorough exploration of the use of eye tracking to investigate the cognitive processes that drive rationality comprehension. It also investigates the validity of the perceptual arguments put forward to explain the brain imaging data in Chapter 2. On the whole, some of the measures used in this paradigm were sensitive to action rationality and can be used as markers of rationality detection (increased looking time to non-target goal and ball) and evaluation of environmental constraint (looking time to barrier). Action prediction measures were not sensitive to action rationality, implying that these index basic goal comprehension rather than higher level reasoning involving the rationalisation of actions. The next chapter in this thesis will investigate the presence of these markers in participants with ASC.

CHAPTER 4. PREDICTIVE GAZE DURING OBSERVATION OF IRRATIONAL ACTIONS IN ADULTS WITH AUTISM SPECTRUM CONDITIONS

4.1 ABSTRACT

Understanding irrational actions may require the observer to make mental state inferences about why an action was performed. Individuals with autism spectrum conditions (ASC) have well documented difficulties with mentalizing; however the degree to which rationality understanding is impaired in autism is not yet clear. The present study uses eye-tracking to measure online understanding of action rationality in individuals with ASC. Twenty adults with ASC and 20 typically developing controls watched movies of rational and irrational actions while their eye movements were recorded. Measures of looking time, scan path and saccade latency were calculated. Results from looking time and scan path analyses demonstrate that participants with ASC have reduced visual attention to salient action features, regardless of action rationality. However, when participants with ASC do attend to these features, they are able to make anticipatory goal saccades as quickly as typically developing controls. Taken together these results indicate that individuals with autism have reduced attention to observed actions, but when attention is maintained, goal prediction is typical. I conclude that the basic mechanisms of action understanding are intact in individuals with ASC although there may be impairment in the top-down, social modulation of eye movements.

4.2 INTRODUCTION

We can accumulate a large amount of social information about a person by observing how they act. For example, seeing a person with a letter walk along the street, we might predict he will stop at the post box. If he makes a detour to avoid walking under a ladder, we might further infer that he is superstitious. Thus, we are able to predict behaviour and make mental state judgements about a person merely by observing their actions. Cognitive processes for predicting actions and understanding mental states have been differentially implicated in autism spectrum condition (ASC). In this chapter, I study eye gaze behaviour during observation of hand actions to determine if people with autism predict or understand actions differently.

As summarized in Chapter 1, section 1.4, individuals with ASC have well documented social difficulties (Frith, 2003) which may include specific impairments in mentalizing and action understanding. Evidence for a mentalizing impairment in individuals with ASC has consistently been shown in their failure to represent anothers' false belief (Baron-cohen, Leslie, & Frith, 1985; Frith, 2001) and through poor comprehension of stories that involve mental state reasoning (Jolliffe & Baron-Cohen, 1999). Participants with ASC are also less able to identify and label the mental states of animated shapes when they are interacting in an intentional way, compared to when they are physically interacting (Castelli, Frith, Happé, & Frith, 2002; Marsh & Hamilton, 2011). Some of these mentalizing difficulties have been attributed to a failure to orient to relevant social cues information in their environment (Klin, Jones, Schultz, Volkmar, & Cohen, 2002; Morris, Pelphrey, & McCarthy, 2002; Riby & Hancock, 2008) and that this reduction in social looking correlates with ASC symptom severity (Klin et al., 2002; Speer, Cook, McMahon, & Clark, 2007 (although see Fletcher-Watson, Leekam, Benson, Frank, & Findlay, 2009; Freeth, Chapman, Ropar, & Mitchell, 2010; Speer et al., 2007).

In contrast, evidence for an action understanding impairment in autism is mixed. Individuals with autism show diminished anticipation of future actions (Boria et al., 2009; Cattaneo et al., 2007; Fabbri-Destro et al., 2009), reduced comprehension of complex action sequences (Zalla, Labruyere, & Georgieff, 2006; Zalla, Labruyère, Clément, & Georgieff, 2010) and reduced imitation of goal-less actions (Wild, Poliakoff, Jerrison, & Gowen, 2012). However, individuals with ASC demonstrate superior postural knowledge compared to typically developing controls (Hamilton, Brindley, & Frith, 2009), and they are able to complete anothers' action goal after witnessing their failed attempt (Aldridge et al., 2000; Carpenter et al., 2001). A further study also shows intact goal-directed imitation in ASC (Hamilton, Brindley, et al., 2007). Recently, interest in implicit measures of action comprehension has increased. Tracking eye gaze provides an excellent way to record and probe the process of action comprehension in a natural, implicit and dynamic way. Studies of typical adults have shown that gaze during action observation is both predictive and socially oriented (see Chapter 1, section 1.3).

Eye movements during action observation have also been studied in participants with ASC. These studies show mixed results for both predictive gaze and social orienting. Typical predictive gaze during hand actions was shown by Flack-Ytter (2010). It was reported that five year olds with ASC, matched typically developing five year olds and a group of adults make predictive eye movements to action goals during action observation to the same degree, demonstrating that goal understanding for basic actions is intact in children with ASC (Falck-Ytter, 2010). However, when action prediction depends on the representation of another person's false belief, participants with autism fail to show predictive gaze (Senju et al., 2009). In a recent study of irrational action observation, Vivanti et al. (2011) demonstrated that both typically developing adolescents and adolescents with ASC orient to the face of an actor, following completion of an irrational action. This finding was suprising given the wealth of studes which show reduced social orienting in participants with ASC (Klin et al., 2002; Morris et al., 2002; Riby & Hancock, 2008; Speer et al., 2007). In the present study, I aim to go beyond previous research by thoroughly assessing how adults with ASC respond when seeing goal-directed actions performed by a human hand or a non-human ball. I am particularly interested in the distinction between understanding the basic goal of an action and understanding the beliefs of the actor.

The experiment presented in Chapter 2 demonstrates that studying irrational actions may provide an important bridge between basic comprehension of actions and mentalizing about why that action was performed. Given the mixed evidence for action understanding impairments in ASC and the clear mentalizing impairments, it is interesting to consider how irrational actions are processed in ASC. In a recent study, Marsh & Hamilton (2011) showed participants with ASC and matched typically developing adults movies of rational and irrational actions during fMRI scanning. Responses to rational actions were similar across the typical and ASC groups, indicating basic action comprehension is intact in ASC. In contrast, responses to irrational actions differed. The medial prefrontal cortex (mPFC), a region closely associated with mentalizing, differentiated rational from irrational actions in typical, but not ASC participants (this study is described in section 1.2.3 in more detail). This study was the first to demonstrate a clear difference in the processing of irrational actions in ASC but as yet, we do not understand the cognitive reasons for this neural difference. The aim of the present study is to use eye tracking to assess whether adults with ASC are able to detect action rationality and if so, whether they use this information to make inferences about why the action was performed in an irrational manner. Furthermore, social orienting during action observation has not been directly studied and the effect of having social information available (such as faces and eyes) on predictive gaze will be explored.

4.2.1 SUMMARY

Overall, this study has two aims. First, I aim to replicate the effects reported in Chapter 3 that show that eye gaze is modulated by action rationality, and test whether this modulation differs between typical and autistic participants. If participants with ASC have good basic action understanding but are not able to detect action rationality, we would expect their viewing patterns for rational and irrational actions to be similar. We would also expect their viewing patterns for these actions to be similar to those used by typically developing individuals during rational action observation. If instead, participants with ASC can detect action rationality but do not use this information to make inferences about the actions, it is expected that eye movement patterns which reflect rationality detection in typically developing individuals will also be present in individuals with ASC. However, measures which indicate that the participant is reflecting upon the reasons for an irrational action (e.g. looking at the face longer) will be absent in individuals with ASC. Second, I aim to test if eye gaze is influenced by the social form of an action (hand or ball) and whether this differs between typical and autistic participants. Gaze effects which are tied to action rationality may be stronger when viewing a full person compared to a moving ball. Such influences may also be stronger in typical participants than in participants with autism. Together, these analyses will give important insights into the cognitive processes underlying action comprehenion in typical and autistic adults.

4.3 MATERIAL AND METHODS

4.3.1 PARTICIPANTS

Twenty adults with ASC and 20 typically developing adults matched to the ASC group for age and IQ took part in this study. Participants were recruited through local colleges, universities and through ASC support groups. Care was taken during recruitment to match groups on age and full scale IQ, measured by the Weschler Adult Intelligence Scale (WAIS). Groups were not significantly different in age ($t(38)=1.9$, $p=0.06$) or IQ ($t(38)=1.25$, $p=0.22$) but as the groups are not similar enough to be considered matched (Carolyn & Bonita, 2004) , all analyses were also run on a subset of 17 participants from each group that were better matched for age ($t(32)=0.85$, $p=0.40$) and IQ ($t(32)=0.65$, $p=0.95$). The pattern of results was very similar when using this matched subset of participants so I report the statistics from the full group analysis here. The few differences between these analyses that did arise were the result of significant effects dropping to just below the alpha threshold when using the smaller sample. I note where this is the case in the text below.

Participants with autism had a diagnosis of high functioning autism (n=7), autism spectrum condition (n=2) or Aspergers syndrome (n=11). Diagnosis was confirmed using the ADOS Module 4 (Lord et al., 2000). One participant failed to meet criteria for autism spectrum on both the social and communication subscales of the ADOS but he had a clear diagnostic history and scored well above the threshold for autism on the Autism Quotient. Therefore, his data has been included in the full analysis. Typically developing participants reported no diagnoses of developmental disorders. All participants also completed the Autism Quotient (AQ, Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001) and typically developing participants scored significantly lower than the ASC participants on this measure of autistic traits ($t(37)=3.95$, $p<0.001$). See Table 4.1 for participant characteristics.

Table 4.1. Participant characteristics for the typically developing group and the ASC group. p indicates the p-value of the paired samples t-test comparing the TD and ASC groups on each attribute.

	TD	ASC	p
n	20	20	
Age	18.9 ± 4.0 (16-29)	22 ± 6.1 (16-32)	0.06
FSIQ	101.8 ± 17.5 (76-139)	94.7 ± 18.3 (69-132)	0.22
VIQ	103.1 ± 17.5 (80-142)	96.4 ± 19.8 (71-143)	0.26
PIQ	99.3 ± 15.6 (75-127)	92.8 ± 17.2 (68-136)	0.21
AQ	17.4 ± 4.5 (10-27)	24.9 ± 7.3 (14-40)	0.0003
ADOS	-	10.6 ± 4.1 (4-17)	-

Abbreviations: n- sample size; FSIQ – full scale intelligence quotient; VIQ – verbal intelligence quotient; PIQ – performance intelligence quotient; AQ – autism quotient; ADOS – autism diagnostic observation scale total score.

4.3.2 STIMULI/APPARATUS

The experimental setup, stimuli and study design was identical to that used in the experiment in Chapter 3.

4.3.3 PROCEDURE

All participants completed the eye tracking task and rationality ratings as described in Chapter 3. The only differences in procedure between this and the previous experiment was that testing took place in a quiet room in the participants' home or college in the present study. During each eye tracking block, the experimenter sat next to the participant and encouraged them to keep watching if their attention wandered. In addition to the eye-tracking task, all participants completed the Weschler Adult Intelligence Scale (WAIS) and the autism quotient (AQ) and participants with ASC completed the ADOS Module 4 with a trained examiner.

4.3.4 DATA PROCESSING

The data processing and analysis approach used in this study was predefined by selecting the measures which reflected action understanding from the experiment in Chapter 3 or those measures that we had specific apriori predictions about, based on the studies reviewed in Section 3.2.1. The measures selected for analysis are listed in Table 4.2.

Table 4.2. Inclusion criteria and the number of trials included at each stage of analysis for the typically developing and ASC groups.

Analysis Level	**Inclusion Criteria**	**ASC**		**TD**	
Total trials completed:		5760		5760	
		Include	**Exclude**	**Include**	**Exclude**
Step 1: Looking time analysis Target goal Non-target goal Ball Barrier Face	<20% samples missing	4282	1478	5100	660
Step 2: Saccade analysis Non-target goal Hand Face	Saccade to goal present	3477	805	4582	518
Step 3: Latency Analysis	Predictive goal saccade from hand present	1067	2410	2044	2538

4.4 RESULTS

4.4.1 BEHAVIOURAL RATINGS

Mean ratings of rationality are presented in Figure 4.1. A two (action) by two (goal) by two (group) mixed ANOVA revealed a main effect of rationality ($F(1,34)=5.02$, $p=0.03$) in which rational curved actions were rated as more rational than irrational curved actions. No effect of group ($F(1,34)=3.08$, $p=0.09$) or goal ($F(1,34)=1.50$, $p=0.23$) and no interactions between these variables were found.

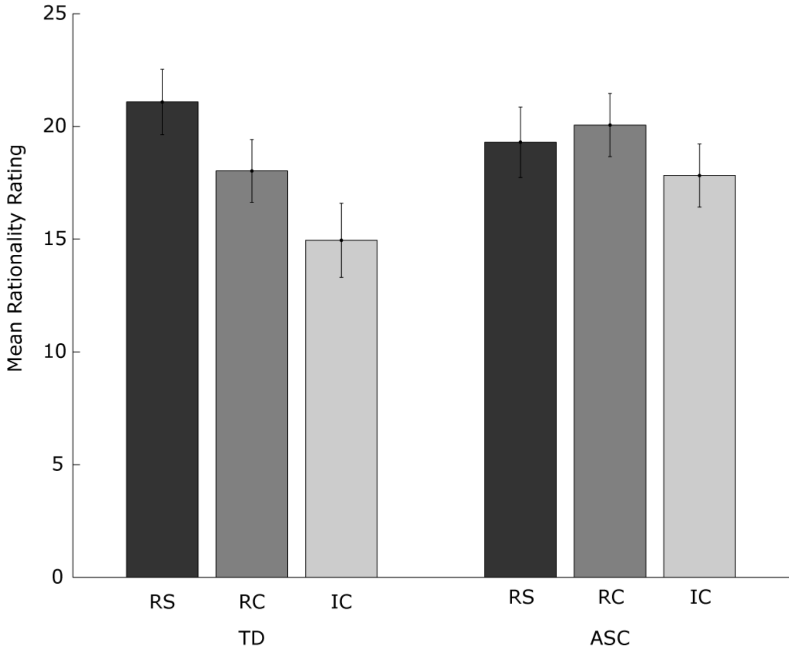

Figure 4.1. Behavioural ratings of rationality as a function of group and action type. Actions were rational straight (RS, dark grey bars), rational curved (RC, mid-grey bars) and irrational curved (IC, light grey bars). Rationality score was calculated as the total rating from a battery of six statements (maximum = 30). Error bars represent the standard error of the mean.

4.4.2 LOOKING TIME ANALYSIS

Percentage looking time in each AOI was calculated for each movie type and is presented in Figure 4.2 and Table 4.3. Two (action type) by three (social form) by two (goal location) by two (group) mixed ANOVAs were conducted for looking time to the target goal, non-target goal, barrier and ball. In trials when the face was visible, a two (action type) by two (goal) by two (group) mixed ANOVA was conducted on looking time to the face. All reported results are significant after Bonferroni correction for multiple comparisons.

In the analysis of looking time to the target goal, a significant main effect of social form of the stimulus was found. Bonferroni corrected t-tests revealed that looking time on the target goal was longer during actions in which the ball moved independently, compared to when an agent was present. This effect was reduced when comparing the smaller, matched groups of participants ($p=0.02$). A main effect of group was also found indicating that typical participants looked longer at the target goal than the autistic participants. No effect of rationality or goal and no interactions were found. See Table 4.3a and Figure 4.2b.

In the analysis of looking time to the non-target goal, a main effect of social form was also found. This means that participants looked longer at the non-target goal during actions in which the ball moved independently, compared to actions performed by a human agent. Again this effect was reduced when comparing the smaller, matched groups ($p=0.02$). The non-target goal was also looked at longer during irrational actions compared to rational actions. There was no main effect of group or goal on looking time to the non-target goal. A significant interaction between the social form of the stimulus and the goal was found. This interaction is driven by participants looking longer at the bottom goal compared to the top goal, but only during actions in which the ball moved independently. This goal bias is not seen when the ball was moved by a human agent. No other interactions were significant. Results are presented in Table 4.3b and Figure 4.2c.

In the analysis of looking time to the ball, a main effect of group revealed that typical participants looked longer at the ball compared to ASC participants. No effects of social form, action type or goal were observed and no interactions were significant. Results are presented in Table 4.3c and Figure 4.2a.

In the analysis of looking time to the barrier, a main effect of social form indicated that participants looked longer at the barrier during human actions compared to those completed by the ball. A rationality effect shows that participants also look longer at the barrier during rational compared to irrational actions. An interaction between rationality and social form was also found. This interaction shows that the bias for looking at the barrier more during rational actions is greater during actions performed by a human compared to those performed by the ball. Results are presented in Table 4.3d and Figure 4.2d.

Participants looked at the face for the same amount of time, irrespective of action type, group membership and goal. There were no significant interactions between these variables (see Table 4.3e).

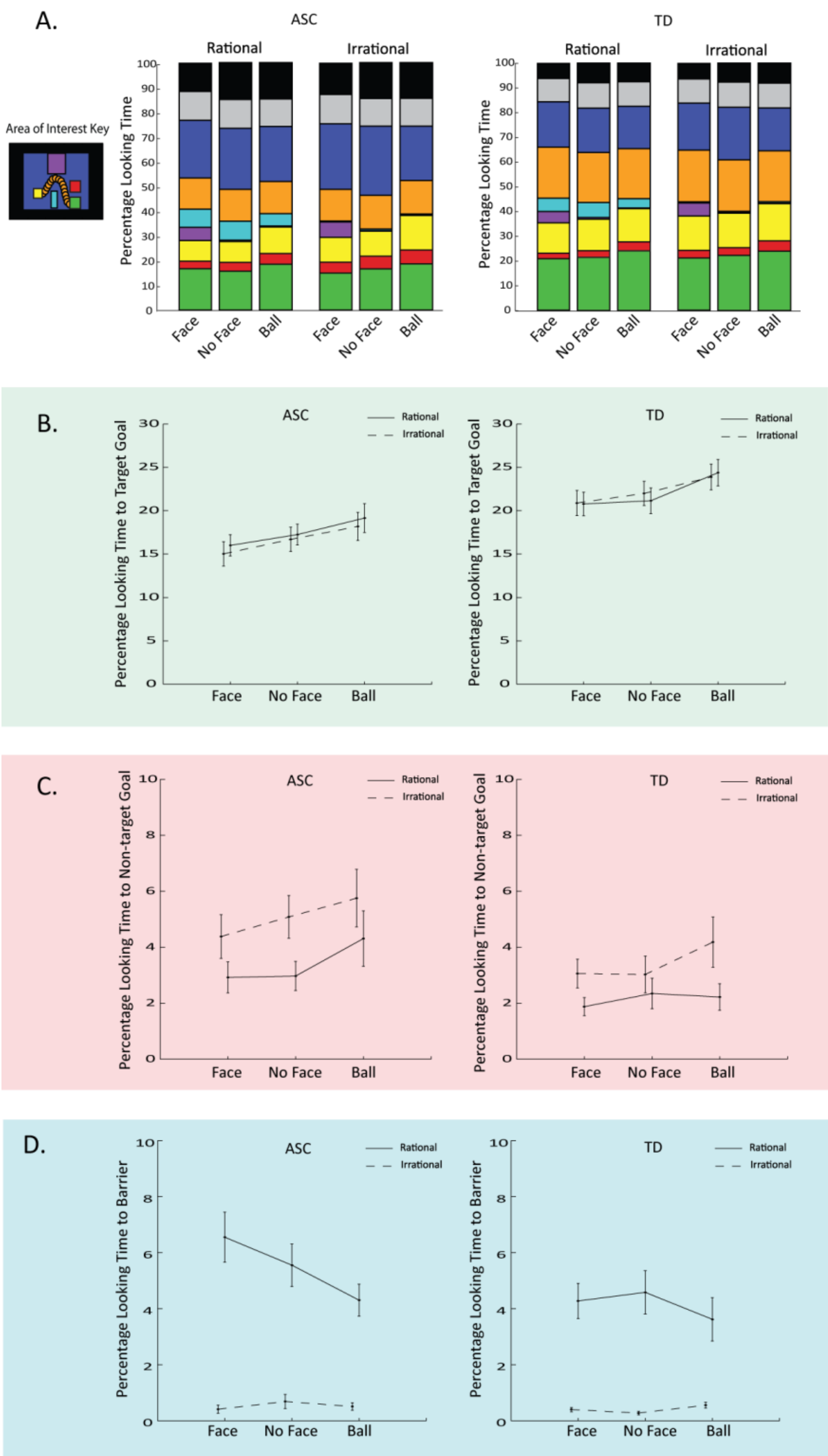

Figure 4.2. Percentage looking time for each AOI in ASC and typically developing participants. Panel A displays looking times as a function of rationality (rational- right cluster and irrational – left cluster) and social form. Colours correspond to the AOI key. Grey segments indicate the percentage of samples during a saccade (excluded from analysis) and black segments indicate missing data. Panels B-D show percentage looking time to each AOI as a function of group (ASC – left, TD – right), action type (rational – solid lines, irrational – dashed lines) and social form. Background colours correspond with the AOI key.

Table 4.3. Statistics for the looking time analysis for each area of interest. Values are the F statistic (or t-statistic when post hoc t-tests are used), degrees of freedom and p-values. Effects reported in bold type are significant after Bonferroni correction for multiple tests. [a] indicates the tests where α was 0.01 and [b] indicates tests where α was 0.0167.

Main Effects	direction	F/(t)	df	p
a) ANOVA 1: Percentage Looking Time to Target Goal				
Social Form		**8.26**	**2,76**	**0.001[a]**
	ball > face	**(3.37)**	**39**	**0.002[b]**
	ball > no face	**(3.13)**	**39**	**0.003[b]**
	no face > face	(0.97)	39	0.34[b]
Rationality		0.03	1,38	0.87[a]
Goal		0.86	1,38	0.36[a]
Group	**TD > ASC**	**9.30**	**1,38**	**0.004[a]**
b) ANOVA 2: Percentage Looking Time to Non-Target Goal				
Social Form		**9.11**	**2,76**	**<0.001[a]**
	ball > face	**(3.50)**	**39**	**0.001[b]**
	ball > no face	**(2.67)**	**39**	**0.01[b]**
	no face > face	(2.21)	39	0.03[b]
Rationality	**irrational > rational**	**17.71**	**1,38**	**<0.001[a]**
Goal		3.16	1,38	0.08[a]
Group		2.16	1,38	0.15[a]
Social Form x Goal		**8.34**	**2,76**	**0.001[a]**
	ball bottom > ball top	**(3.48)**	**39**	**0.001[b]**
	no face bottom > no face top	(0.77)	39	0.45[b]
	face bottom > face top	(0.28)	39	0.78[b]
c) ANOVA 3: Percentage Looking Time to Ball				
Social Form		0.02	2,76	0.98[a]
Rationality		2.82	1,38	0.10[a]
Goal		2.20	1,38	0.15[a]
Group	**TD > ASC**	**10.10**	**1,38**	**0.003[a]**
d) ANOVA 4: Percentage Looking Time to Barrier				
Social Form		**16.32**	**2,76**	**<0.001[a]**
	face > ball	**(3.78)**	**39**	**<0.001[b]**
	no face > ball	**(5.63)**	**39**	**<0.001[b]**
	no face > face	(1.62)	39	0.11[b]
Rationality	**rational > irrational**	**129.13**	**1,38**	**<0.001[a]**

Goal		3.87	1,38	0.06[a]
Group		1.67	1,38	0.21[a]
Social Form x Rationality		**19.04**	**2,76**	**<0.001**[a]
	R – I face > R – I ball	**4.83**	**39**	**<0.001**[b]
	R – I no face > R – I ball	**6.41**	**39**	**<0.001**[b]
	R – I no face > R – I face	1.11	39	0.28[b]
e) ANOVA 5: Percentage Looking Time to Face				
Rationality		1.53	1,38	0.22[a]
Goal		4.24	1,38	0.05[a]
Group		0.24	1,38	0.62[a]

4.4.3 SACCADE ANALYSIS

The origin of saccades to the goal was analysed and results are presented in Figure 4.3a and Table 4.4. As with the looking time analysis, two (action type) by three (social form) by two (goal location) by two (group) mixed ANOVAs were conducted on percentage of saccades from the non-target goal and from the ball to the target goal. In trials when the face was visible, a two (action) by two (goal) by two (group) mixed ANOVA was conducted on percentage of saccades from the face. Again, only significant results that survived Bonferroni correction are reported.

In the analysis of saccades from the non-target goal, there was a main effect of action. This effect showed that more saccades to the goal came from the non-target goal when the action was irrational. An effect of goal revealed that there were more saccades from the non-target goal if the action ended in the bottom goal. No effects of social form or group were found. A significant social form by goal interaction showed that participants made less saccades from the non-target goal to the goal when the action culminated at the top goal, but only during actions in which the ball moved independently. No other interactions were significant. See Figure 4.3b and Table 4.4a.

The analysis of saccades from the ball found a main effect of group and revealed that typical participants made more saccades from the ball to the goal, compared to ASC participants. There were no effects of social form, action type or goal on the number of saccades from the ball to the goal. An interaction between social form and goal revealed that participants made more saccades from the ball to the goal when the action ended at the top goal, but only when the ball moved independently. In addition, an interaction between action type and goal showed that participants made more saccades from the ball to the goal when the action ended at the bottom goal, but only when the action was rational. This effect is driven by data from the ASC participants. No other interactions were significant. See Figure 4.3c and Table 4.4b.

The analysis of the number of saccades from the face found no effect of action type, group membership or goal and no interactions between these variables. See Table 4.4c.

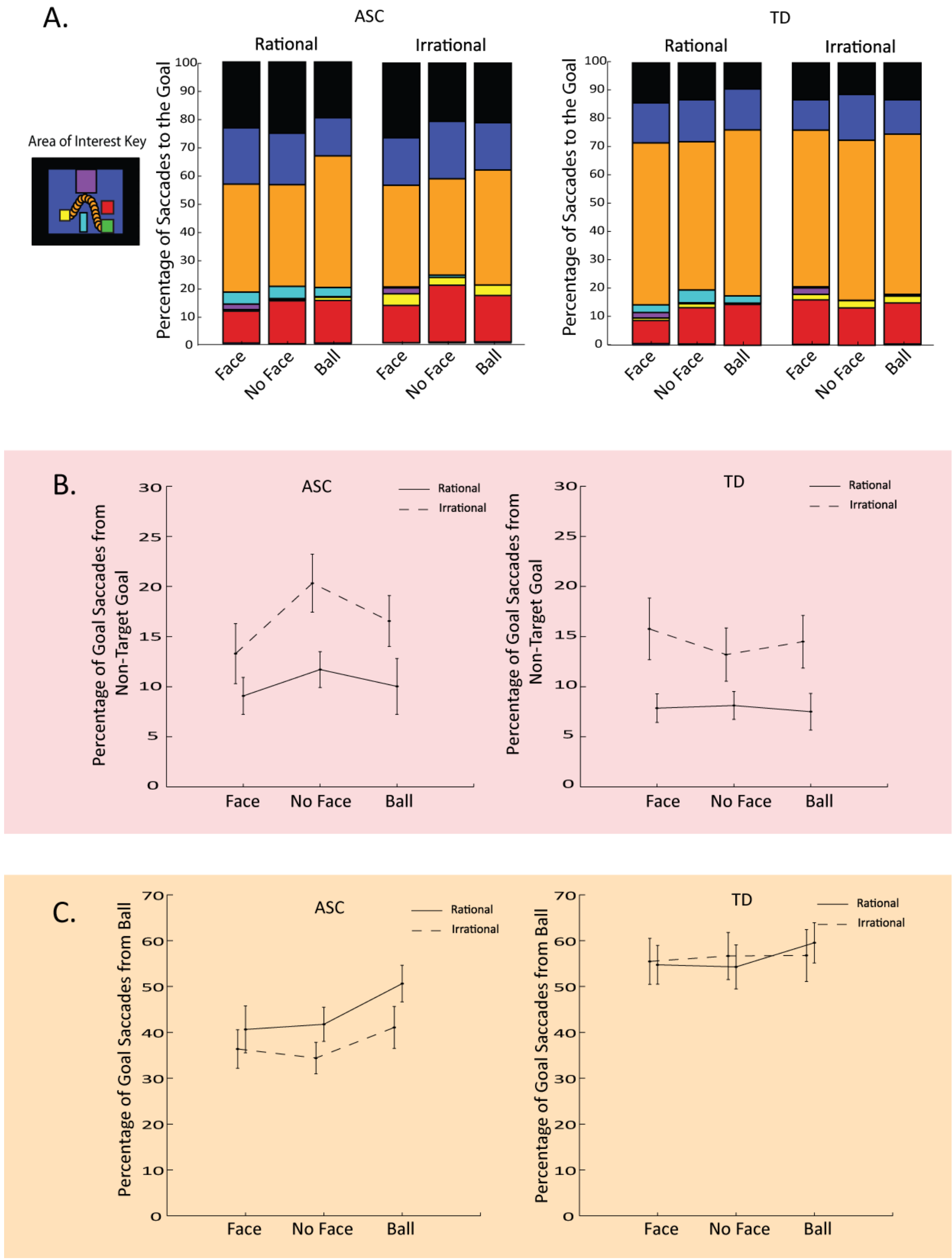

Figure 4.3 Percentage of goal saccades originating in each AOI in ASC and typically developing participants. Panel A displays these as a function of action type (rational- right cluster and irrational – left cluster) and social form. Colours correspond to the AOI key. Black segments indicate the percentage of trials in which no goal saccade was made. Panels B-C: Percentage of goal saccades that originated in each AOI as a function of group (ASC – left, TD – right), action type (rational – solid lines, irrational – dashed lines) and social form. Background colours correspond to the AOI key. Error bars represent ± 1 standard error of the mean.

Table 4.4. Statistics for the saccade analysis for each area of interest. Values are the F statistic (or t-statistic when post hoc t-tests are used), degrees of freedom and p-values. Effects reported in bold type are significant after Bonferroni correction for multiple tests. [a] indicates the tests where α was 0.0167, [b] indicates tests where α was 0.025 and [c] indicates tests where α was 0.0125.

Main Effects	direction	F/(t)	df	p
a) ANOVA 1 : Proportion of Saccades from Non-Target Goal to Goal				
Social Form		2.69	2,76	0.08[a]
Rationality	**irrational > rational**	**6.60**	**1,38**	**0.01[a]**
Goal	**bottom > top**	**9.77**	**1,38**	**0.003[a]**
Group		0.56	1,38	0.45[a]
Social Form x Goal		**10.70**	**2,76**	**<0.001[a]**
	ball bottom > ball top	**(6.07)**	**39**	**<0.001[a]**
	no face bottom > no face top	(1.48)	39	0.15[a]
	face bottom > face top	(0.25)	39	0.81[a]
b) ANOVA 2: Proportion of Saccades from Ball to Goal				
Social Form		3.75	2,76	0.03[a]
Rationality		1.19	1,38	0.28[a]
Goal		5.60	1,38	0.02[a]
Group	**TD > ASC**	**6.31**	**1,38**	**0.01[a]**
Social Form x Goal		**9.15**	**2,76**	**<0.001[a]**
	ball top > ball bottom	**(4.09)**	**39**	**<0.001[a]**
	no face top > no face bottom	(2.30)	39	0.03[a]
	face top > face bottom	(0.84)	39	0.41[a]
Rationality x Goal		**7.27**	**1,38**	**0.01[a]**
	RC top > RC bottom	**(3.02)**	**39**	**0.004[b]**
	IC top > IC bottom	(0.45)	39	0.66[b]
Rationality x Goal x Group		**8.49**	**1,38**	**0.006[a]**
	ASC RC top > ASC RC bottom	**(3.05)**	**19**	**0.007[c]**
	ASC IC top > ASC IC bottom	(1.32)	19	0.20[c]
	TD RC top > TD RC bottom	(1.15)	19	0.26[c]
	TD IC top > TD IC bottom	(0.77)	19	0.45[c]
c) ANOVA 3: IV = Proportion of Saccades from Face to Goal				
Rationality		0.13	1,38	0.72[a]
Goal		0.14	1,38	0.71[a]
Group		0.009	1,38	0.93[a]

4.4.4 LATENCY ANALYSIS

Mean saccade latency was calculated for each movie type and is presented in Figure 4.4. Social form, action type, group and goal were entered into a full factorial mixed linear model. A main effect of social form indicated that participants were faster to anticipate actions in the ball condition, compared to the no face condition. A main effect of goal location showed that the top goal was anticipated faster than the bottom goal. Participants were also quicker to anticipate actions that ended at the top goal when the action was completed by the ball moving independently. This pattern of results was more prominent in participants with ASC. However, this three way interaction disappears when comparing the subgroup that were better matched for age and IQ (p=0.08). No main effect of group membership or action rationality was found (see Table 4.5 for results).

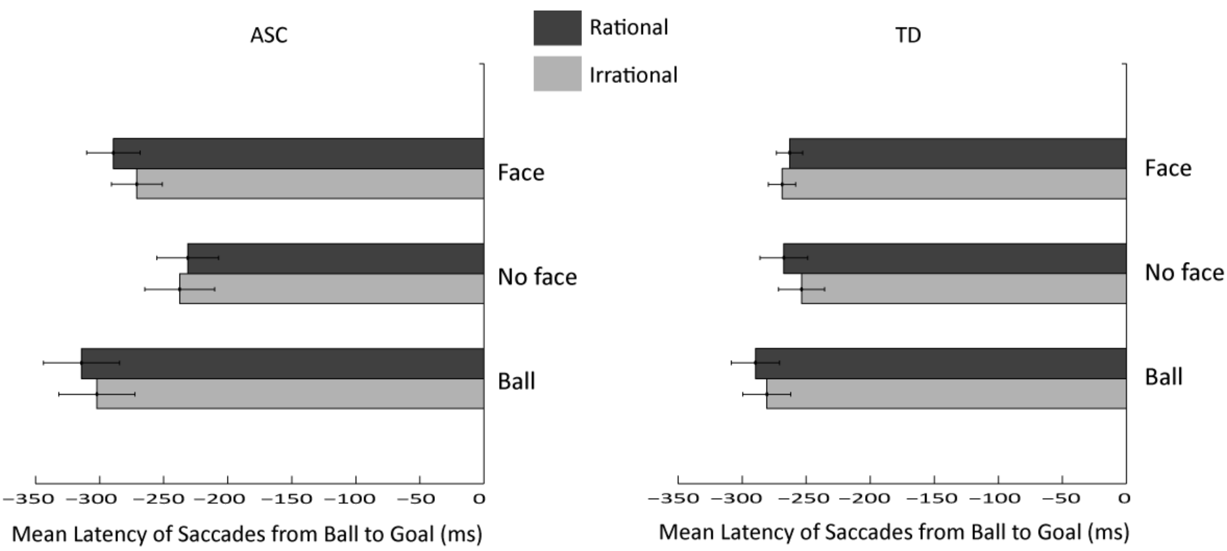

Figure 4.4. Mean latency of goal fixation as a function of group (ASC – left, TD – right), action type (rational – dark grey bars, irrational – light grey bars) and social form.

Table 4.5. Statistics for the latency of goal saccade analysis. Values are the F statistic (or t-statistic when post hoc t-tests are used), degrees of freedom and p-values. [a] indicates the tests where α was 0.05, [b] indicates tests where α was 0.0167 and [c] indicates tests where α was 0.0083.

Main Effects	**direction**	**F/(t)**	**df**	**p**
a) Linear Mixed Model: Latency of Saccades from the Ball to the Goal				
Social Form		**11.32**	**2,1818**	**<0.001[a]**
	no face > ball	**(4.35)**	**1244**	**<0.001[b]**
	face > no face	(2.25)	1163	0.02[b]
	face > ball	(2.11)	1271	0.04[b]
Rationality		0.26	1,1818	0.61[a]
Goal	**top > bottom**	**14.46**	**1,1818**	**<0.001[a]**
Group		0.33	1,1818	0.57[a]
Social Form x Goal		**12.42**	**2,1818**	**<0.001[a]**
	ball top > ball bottom	**(5.78)**	**675**	**<0.001[b]**
	face top > face bottom	(0.30)	594	0.76[b]
	no face top > no face bottom	(0.31)	567	0.76[b]
Social Form x Goal x Group		**3.13**	**2,1818**	**0.04[a]**
	ASC ball top > ASC ball bottom	**(4.40)**	**214**	**<0.001[c]**
	ASC face top > ASC face bottom	(0.77)	188	0.44[c]
	ASC no face top > ASC no face bottom	(1.21)	166	0.23[c]
	TD ball top > TD ball bottom	**(3.89)**	**459**	**<0.001[c]**
	TD face top > TD face bottom	(1.15)	404	0.25[c]
	TD no face top > TD no face bottom	(0.42)	399	0.68[c]

4.4.5 TASK ENGAGEMENT

As the number of trials included in each analysis is hierarchical, and dependent upon the presence of eye movement features that reflect attention to the actions, it is possible to use the number of trials included in each analysis as a measure of task engagement. From Table 4.2, it is clear that from the first level of data exclusion, there are more excluded trials in the ASC group compared to the typically developing group. This is despite the experimenter watching the live gaze recording and reminding participants to continue to pay attention if they looked away from the screen. Figure 4.5 shows this reduction in task engagement as a function of trial number through the block for both the typically developing and ASC groups. While task engagement reduced over the course of the block for both groups, the decline in task engagement for the ASC group was much greater. Beyond this initial exclusion stage based on data quality, the patterns of exclusion remain similar. The ASC group fail to look at the goal of the action in more trials than the typically developing group (exclusion level two) and only make saccades from the hand to the goal in 18% of trials, compared to 35% of trials for the typically developing group (exclusion level three). In summary, each of these levels of exclusion reflect reduced task engagement in participants with ASC.

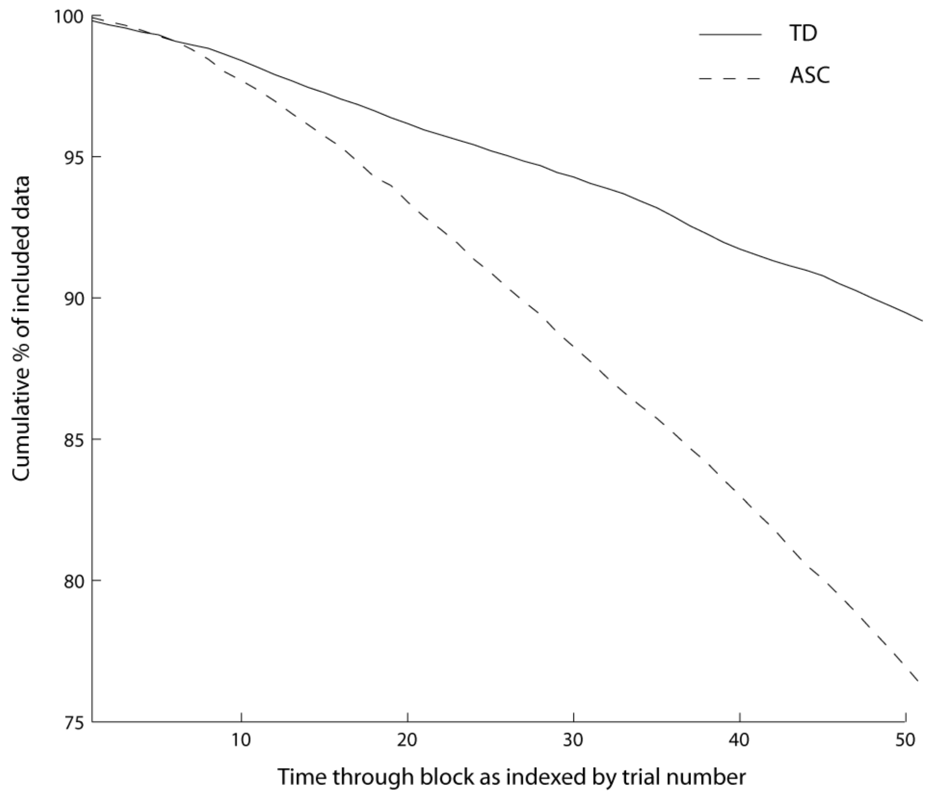

Figure 4.5. Cumulative percentage of included data from the ASC (dashed line) and TD (solid line) groups as a function of time course through the block. Time on the x-axis is indexed by trial number.

4.5 DISCUSSION

The current study aimed to examine action comprehension in adults with ASC using eye gaze. This was done by evaluating a number of different measures in a pilot dataset (presented in Chapter 2) before applying these measures to the experimental data here. The measures used were looking time, the origin of saccades to the action goal and latency of first goal fixation. First I discuss the results in relation to my two key questions of how eye movements are modulated by action rationality and by social form and whether these markers are present in participants with ASC.

4.5.1 Eye movements reflecting rationality comprehension

A number of eye tracking measures reflected the rationality of the observed action in both typical and ASC participants. Firstly, participants looked longer at the non-target goal and they made more saccades from the non-target to the target goal during irrational actions. Both of these findings suggest that participants are making goal prediction errors whilst watching irrational actions. As the action is curved for no reason, participants anticipate the action goal incorrectly and look at the non-target goal. Additionally, increased time spent looking at the non-target goal may reflect participants’ reasoning about why the ball was not placed in the non-target goal. Perhaps they were searching for an environmental constraint which altered the actors’ intention mid-action. This is consistent with the idea that participants try to rationalise an irrational action by seeking an explanation for their behaviour (Vivanti et al., 2011). However, unlike Vivanti et al., (2011) the present study reports no increase in looking at the face of the actor following an irrational action in either the ASC or the typical group. This lack of finding could be because this task has less social context than the previous study or because the face of the actor was not informative in determining the goal of the action.

Looking time to the barrier also differed between rational and irrational actions in both typical and ASC groups. Participants looked longer at the barrier during rational actions, suggesting that they are evaluating the environmental constraint that impacts upon the action. This is consistent with the pattern of results reported by (Elsner et al., 2013) in infants but it also goes beyond previous findings as I demonstrate that the bias for looking at the barrier more during rational actions is increased for human actions compared to those completed by the moving ball. This implies that a greater level of evaluation of the action constraint occurs during human actions and therefore may reflect mentalizing about why the actor performed the action in this way.

Surprisingly, the speed of action prediction was not modulated by action rationality in typically developing or ASC participants. This is inconsistent with previous evidence that irrational actions are anticipated more slowly than rational actions (Gredebäck & Melinder, 2010). However, this difference may be due to the precise control over the stimuli in the present study and the resolution of the criticisms of this measure that are reviewed in the introduction (goal saliency, matched kinematics). As predictive eye movements are not modulated by action rationality and are instead tied to the kinematics of the performed action, this provides evidence for the account which suggests predictive eye movements are linked to motor system activity (Ambrosini et al., 2012; Cannon & Woodward, 2006; Flanagan & Johansson, 2003; Gredebäck & Kochukhova, 2010). Furthermore, as participants with ASC made predictive saccades to the goal as quickly as typically developing participants, it seems that their basic goal understanding is intact. This is consistent with other studies implicating good goal comprehension in ASC (Dinstein et al., 2010; Falck-Ytter, 2010b; Hamilton et al., 2009; Marsh & Hamilton, 2011).

4.5.2 THE IMPACT OF SOCIAL FORM ON EYE MOVEMENTS

Social form had very little impact on gaze behaviour. All participants looked longer at both action goals during actions performed by a ball compared to those performed by a human agent. Additionally, participants were faster to predict the action goal when it was completed by a ball compared to the human actions. Both of these findings can be explained by the reduced amount of information on the screen during these ball actions. As the human is absent and there is less to look at, participants look at the goal more quickly and maintain their fixations for longer. Despite there being more to look at in the human actions, participants spent longer looking at the barrier in these movies compared to the actions performed by the ball. As mentioned previously, this may be due to the participant making more effort to evaluate the environmental constraints during human actions.

Contrary to my predictions, participants spent very little time looking at the face of the actor during movies where the face was visible. This contrasts with previous studies that report dramatic social orienting to the face and, in particular the eyes, of the agent on screen (Birmingham, Bischof, & Kingstone, 2008b; Klin et al., 2002). However, these studies report increased social orienting when the stimulus depicts a social interaction involving more than one agent (Birmingham, Bischof, & Kingstone, 2008a). The stimuli used in the present study did not depict multiple interacting agents and this may account for the lack of social orienting to the face in both typical and ASC participants. As the action was the key feature of each movie, orienting to the hand, rather than the face, is more informative.

Indeed, typically developing participants look at the hand more than the ASC participants, indicating that participants with ASC show less orienting to salient action features. However, as this effect was seen in both human and ball actions, it is difficult to argue that this orienting to the action is social orienting. It seems that the reduction in looking at the hand in ASC is a product of reduced attention to biological motion (Blake, Turner, Smoski, Pozdol, & Stone, 2003; Klin, Lin, Gorrindo, Ramsay, & Jones, 2009).

4.5.3 TASK ENGAGEMENT

The results that have been discussed so far reflect a very similar pattern of results between typical and ASC participants. The realm in which we see group differences emerge in this task is when we consider measures that reflect attention to the action. For example, ASC participants look at the action goal for less time than the typically developing participants. Additionally, they look less at the hand or ball performing the action and as such, they also make fewer saccades from the hand to the action goal. A reduction in social attention in ASC has previously been reported for faces (Riby & Hancock, 2008) and eyes (Speer et al., 2007) but this is the first to show reduced attention to actions. I also report a reduction in task engagement in the ASC group over the course of the experiment. This is evidenced by the number of trials excluded from the analysis due to missing data. It is unlikely that the increase in missing data in the ASC group is due to eye-tracker failure as strict calibration procedures were passed prior to the start of each block and live gaze visualisation was used to check that tracking continued throughout the experiment. Instead, participants with ASC were more likely to look outside of the frame of the movie, or away from the screen during the task. In these cases, the experimenter reminded the participant to keep watching the movies.

Both findings of reduced attention to actions and reduced task engagement are consistent with the social motivation hypothesis of ASC which predicts reduced social orienting and engagement (Chevallier, Kohls, Troiani, Brodkin, & Schultz, 2012). This theory also proposes that individuals with ASC have the underlying competence to process social stimuli yet spontaneously fail to do so. In this task we demonstrate that participants with ASC are able to detect action rationality and to predict rational and irrational actions to the same degree as typically developing individuals. However, this is only the case if we only use the trials in which participants with ASC were attending to the actions. The reduction in number of trials in which participants with ASC attended to the actions is indicative of reduced spontaneous action prediction and comprehension.

4.5.4 CONCLUSIONS

The present study provides a thorough examination of the eye tracking measures which reflect action rationality and the social form of the agent. I report very few differences in action observation between ASC and typically developing adults which provides support for the idea that rationality detection is intact in ASC. Only one eye tracking measure indicated that participants might be making inferences about why the irrational actions were performed in an unusual manner (looking time to the barrier) and this was the case for both ASC and typically developing adults.

There were differences in the amount of missing data between participant groups and this may reflect reduced social motivation in ASC. However when participants with ASC were attending to the actions, they show good action comprehension and prediction. Future work should focus on developing experimental tasks which include a measure of task engagement to ensure that reduced social motivation is not driving any group differences reported.

CHAPTER 5. THE SOCIAL MODULATION OF IMITATION FIDELITY IN SCHOOL-AGE CHILDREN

5.1 ABSTRACT

Children copy the actions of others with high fidelity, even when they are not causally relevant. This copying of visibly unnecessary actions is termed overimitation. Many competing theories propose mechanisms for overimitation behaviour. In the present study I examine these theories by studying the social factors that lead children to overimitate actions. Ninety-four children aged 5- to 8-years each completed five trials of an overimitation task. Each trial provided the opportunity to overimitate an action on familiar objects with minimal causal reasoning demands. Social cues (live or video demonstration) and eye contact from the demonstrator were manipulated. After the imitation phase, children's ratings of action rationality were collected. Substantial overimitation was seen which increased with age. In older children, overimitation was higher when watching a live demonstrator and when eye contact was absent. Actions rated as irrational were more likely to be imitated than those rated as rational. Children overimitated actions on familiar objects even when they rated those actions as irrational, suggesting that failure of causal reasoning cannot be driving overimitation. These data support social explanations of overimitation and show that the influence of social factors increases with age over the 5- to 8-year-old age range.

5.2 INTRODUCTION

In Chapter 4 I conclude that differences between typical and autistic participants on measures of rationality comprehension may be due to differences in social responsiveness to a given situation. This may be because individuals with ASC lack social motivation to affiliate with others (Chevallier et al., 2012). If this is the case then it should be possible to observe larger group differences in a rationality comprehension task which requires a social response. In order to develop such a task, I turn to the literature on overimitation which I have briefly reviewed in Section 1.5.3.

Observation and imitation of other people's actions is an important way for children to learn about the world, reducing the need for costly trial-and-error (Gardiner, Bjorklund, Greif, & Gray, (2012) and see (Frith & Frith, 2012) for a review). However, learning by observation is complicated by the fact that some objects are not transparent in their mechanism (Csibra & Gergely, 2009) and on some occasions the demonstrator may behave inefficiently due to habit, error or lack of experience with the object. The child must filter out actions that are causally necessary from those that do not contribute to the completion of the action (Brugger, Lariviere, Mumme, & Bushnell, 2007). Failure to exclude unnecessary actions from a sequence is termed overimitation (Lyons, Young, & Keil, 2007), whereas efficient pursuit of a goal alone is termed goal emulation (Whiten & Ham, 1992). In this chapter, I investigate which cues influence children's imitation fidelity and how these cues change with development.

Horner & Whiten (2005) demonstrated that chimpanzees are remarkably good at goal emulation if information about action causality is available. However, in the same task, a group of 3- to 4-year-old children failed to emulate the goal of the action, instead choosing to faithfully imitate both the necessary and unnecessary actions demonstrated. Many subsequent studies have demonstrated that from around 14 months of age, children overimitate actions, despite visible evidence that they are not causally relevant (Flynn, 2008; Lyons, Damrosch, Lin, Macris, & Keil, 2011; Lyons et al., 2007; McGuigan, Whiten, Flynn, & Horner, 2007; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009).

There are multiple theories which attempt to explain overimitation in children. Broadly speaking, these theories fall into causal reasoning explanations and social explanations, although nuances within these categories are debated. Firstly, causal reasoning explanations follow the argument that if a demonstrated action upon an object is perceived as intentional, the child will believe that the action is important. This judgement of importance may be due to the demonstration distorting the child's causal understanding of the object such that they believe the action is necessary to achieve the goal (automatic causal encoding hypothesis, Lyons et al. (2007)) or it may be judged as important but that the purpose of the action is unknown (unspecified purpose hypothesis, Horner & Whiten (2005); Whiten et al. (2009)). In this case, it is a 'safe bet' to copy everything and to refine later (Whiten et al., 2009). Alternatively, social hypotheses propose that overimitation performs a social function. Either the child has a desire to be like the demonstrator and finds it intrinsically rewarding to share their experiences (shared experience hypothesis, Nielsen & Blank, (2011); Nielsen, (2006)) or they want to communicate 'likeness' with the demonstrator in an attempt to affiliate (affiliation hypothesis, Over & Carpenter, (2009). Finally, a recent theory proposes that children learn prescriptive norms about the 'right way' do things when actions are demonstrated. Therefore overimitation occurs because children are conforming to these perceived norms (normative behaviour hypothesis, Kenward, Karlsson, & Persson, (2011); Kenward, (2012)).

There is very little consensus over which of these processes may be driving overimitation and indeed, perhaps some work in combination, or at different ages. One previous review paper argues that all of these hypotheses can explain some part of overimitation behaviour by emphasising the role of the child's goal in an imitative situation (Over & Carpenter, 2012). This theory can also explain the co-occurrence of selective imitation and overimitation in children. Over and Carpenter propose that a child can adopt a social goal, a learning goal or a learn-to-be-social goal in an imitative situation and this goal determines whether they faithfully or selectively imitate. With a social goal, their priority is to imitate the model faithfully as this serves an affiliative function, similar to mimicry. Evidence for this account comes from studies showing more overimitation when a child interacted with a sociable demonstrator compared to a demonstrator who was socially aloof (Nielsen, 2006), and when the demonstration was presented live rather than in a video (McGuigan et al., 2007; Nielsen, Simcock, & Jenkins, 2008). Additionally, children primed by observing ostracism were more likely to overimitate than children who witnessed a comparable scenario without ostracism (Over &

Carpenter, 2009). In contrast, under a learning goal children are more likely to be selective in their imitation. This is evidenced by a study which demonstrates that children given a social copying task prior to an overimitation task were more likely to overimitate than those children given a collaborative learning task first (Yu & Kushnir, 2009). Here, the child's goal is changed by the aims of the initial task. Finally, Over and Carpenter (2012) propose that with a learning-to-be-social goal, the child aims to learn the social rules of a given situation. This view parallels the normative behaviour hypothesis and explains why children justify their overimitation in terms of normative language (Kenward et al., 2011) and protest when someone else omits the unnecessary action (Kenward, 2012). While the theory proposed by Over and Carpenter (2012) has good explanatory power and pulls together a diverse range of theories, it is not yet clear how children adopt a specific goal and what cues they use to switch between them.

One potential reason for the diversity in explanations of overimitation behaviour may be because the field is muddied by the diverse range of overimitation tasks and the precise definition of overimitation. Originally, overimitation was classed as the imitation of *visibly* irrelevant actions (Horner & Whiten, 2005). However, the objects used in demonstrations vary considerably with respect to how mechanically complex they are (complex: Lyons et al., 2011 vs simple: Marsh, Pearson, Ropar, & Hamilton, (2013) (see also Chapter 6)) and whether they are transparent (Lyons et al., 2011; McGuigan et al., 2007; McGuigan, 2013) or opaque (Nielsen & Blank, 2011; Nielsen & Tomaselli, 2010). Many studies make the assumption that because an object is physically transparent, the actions performed upon it are cognitively transparent to children, however a recent study demonstrates that children make errors in ascribing action relevance for even very simple objects (Kenward et al., 2011). Therefore, children's replication of actions on these more complex objects may be due to object learning, rather than social drives (Marsh et al., 2013). This can explain why causal reasoning explanations have been provided for studies involving overimitation on mechanically complex objects (Lyons et al., 2011). Recent studies have also extended the definition of overimitation to include faithful imitation of tool selection (Over & Carpenter, 2009) and tool use (when it is simpler to use your hand, Nielsen et al., 2008) or imitation of the number of irrelevant actions performed (Nielsen, Slaughter, & Dissanayake, 2012). These can be considered faithful reproductions of action but may be functionally different to classic overimitation in which a causally irrelevant action is completed. To ensure that children understand the mechanics of how each object works, and therefore ensure that the irrelevant action is visibly so, the present study utilises very simple, transparent objects that have no mechanical components and do not involve the use of tools to operate. Furthermore, irrelevant actions on the objects are hand actions that do not result in physical outcomes (noises or changes to the appearance of the object). This should prevent object-learning based imitation being coded as overimitation.

I argue that children will adopt a social goal if the learning component of the task is reduced but they will be likely to overimitate for social reasons. To test this, I compare rates of overimitation for live and video demonstrations using simple, non-mechanical objects. Previously, a comparison between live and video demonstrations has been used to demonstrate that overimitation is socially driven as children copy more when seeing a live demonstration compared to a video demonstration (McGuigan et al., 2007). Further, this increase in overimitation persists when the demonstration is given via a live video feed compared to a pre-recorded video, suggesting that it is the opportunity for social interaction that drives this increase (Nielsen et al., 2008). I predict that children will overimitate despite the objects being cognitively transparent and that overimitation will increase for the live demonstration condition.

I also test the claim that social overimitation and mimicry are functionally related (Over & Carpenter, 2011). Evidence for this account shows that both overimitation and mimicry are modulated by the same social conditions. For example, overimitation and mimicry both increase when interacting with people with high social status compared to low social status (Cheng & Chartrand, 2003; McGuigan, Makinson, & Whiten, 2011; McGuigan, 2013), and participants primed with anti-social cues such as ostracism were more likely to overimitate or mimic than participants who witnessed a comparable scenario without ostracism (Lakin, Chartrand, & Arkin, 2008; Over & Carpenter, 2009; Wang & Hamilton, 2013). To further test this claim we examine whether direct eye contact can also enhance overimitation behaviour as it does for mimicry (Wang, Newport, & Hamilton, 2011). Previously, Brugger et al (2007) showed that 14-to 16-month-olds overimitate following social engagement (eye contact and a relevant comment) more than a non-engagement condition (look to wall and an irrelevant comment). However, the study by Brugger et al. does not distinguish the between the verbal and eye contact cues. Further, these cues were presented at the start of each action sequence and so we cannot say whether the cue is increasing general attention to the demonstration or whether it is specifically prompting the infant to complete the unnecessary action. The present study investigates the role of eye contact in an overimitation paradigm further.

Another puzzling feature to emerge from studies of overimitation is that this behaviour actually increases throughout early childhood (ages 2- to 5-year-olds (McGuigan et al., 2007; McGuigan & Whiten, 2009), and remains in adulthood (Flynn & Smith, 2012; McGuigan & Whiten, 2009). One previous study has looked at overimitation in children across a wider age range (2-to 13-year-olds) in Kalahari Bushmen children (Nielsen & Tomaselli, 2010). Again, an increase in overimitation is reported in this sample yet the authors do not discuss the implications of this finding. Increased overimitation may be due to better social skills. The present study will systematically test how imitation fidelity changes over middle childhood and assess whether these changes are related to changing sensitivity to social cues.

A further way in which to test whether overimitation is socially motivated is to ask participants to explicitly rate the actions as necessary or unnecessary. In a previous study, 5-year-old children were asked to report whether they will perform the unnecessary action and to justify their decision prior to acting (Kenward et al., 2011). While only 10% of participants justified the unnecessary action as causally relevant, the remaining 90% were unable to justify why they would complete the unnecessary action. However, a caveat of this study is that children were only included in the analysis if they completed the unnecessary actions. It is interesting to study the differences in ratings between children who choose to faithfully imitate and those who do not as this may provide insight into their decision-making process.

Overall, the present study will test four predictions. Firstly, if overimitation is socially modulated then overimitation will occur more in situations that elicit more social engagement. Thus, unnecessary actions that are demonstrated live will be overimitated more frequently than those demonstrated in a video. The second hypothesis examines the role of eye contact in overimitation. If overimitation and mimicry are operating on the same social mechanisms (Over & Carpenter, 2012), then eye contact prior to an unnecessary action should increase overimitation of that action, as it does for mimicry (Wang, Newport, et al., 2011). Third, this study will investigate the developmental change in overimitation. Previous studies have reported overimitation in children aged between 14-months and 13-years or in adults but no study has tried to link developmental changes in overimitation behaviour to the development of other social and cognitive processes. Finally, no previous study has linked overimitation behaviour to explicit ratings of the rationality of the demonstrated actions. If children overimitate for causal reasons, they should report all actions as sensible whereas if they are socially overimitating, they should report the unnecessary action as silly.

5.3 Method

5.3.1 Participants

Ninety-four children aged 5- to 8-years took part in this experiment. The final sample consisted of 26 five-year olds (16 female), 25 six-year-olds (8 female), 22 seven-year-olds (12 female) and 21 eight-year-olds (11 female). Children were recruited through the 'summer scientists week' scheme at the University of Nottingham. Groups of children from the local area were invited to come and take part in a fun session of games and experiments during their summer holidays. All parents gave written, informed consent and the study was approved by the University of Nottingham Ethics committee.

5.3.2 Design

A mixed model design was used. Children were randomly assigned to one of two between-participant experimental conditions (live demonstration or video demonstration) that were matched for age and gender. Eye contact was manipulated within participants. Eye contact was counterbalanced for action (either preceding a rational or irrational action) and for trial (which apparatus was used) across participants.

5.3.3 STIMULI

The action sequences used in the practice and experimental trials are detailed in Table 5.1. Movies were created for each trial of the video demonstration condition. These commenced with a demonstrator (D) sitting at a table with the trial apparatus in front of her. Over the course of the movie, D performed the sequence of actions required to complete the goal (see Table 5.1). Within each trial D once paused and looked at the camera for approximately 1 second before looking down and continuing the action. The eye contact either directly preceded a rational action or directly preceded an irrational action. Thus, two versions of each demonstration were filmed. For example, when building the block tower, version one shows D place block one in the centre of the table, pause and look directly at the camera, then continue by picking up block two, rotating it 360 degrees before placing it on block one (in this case, eye contact occurred directly prior to the irrational action) and finally placing block three on top of block two. Version two shows exactly the same action sequence but the pause and eye contact occurred before picking up block one (directly prior to a rational action).

Table 5.1. Descriptions of each action within each trial. (R) indicates a rational action. (I) indicates an irrational action.

Goal	Action 1	Action 2	Action 3
Warm-Up trials			
Make a pattern with beads on the rack	Place bead 1 onto a peg	Place bead 2 on top of bead 1	Place bead 3 on top of bead 2
Put doll into a container	Remove lid from container	Put doll into the container	Put lid back on container
Experimental trials			
Retrieve toy duck 	Unclip fastenings of box (R)	Tap the top of the box twice with index finger (IR)	Remove the lid of the box and retrieve duck (R)
Retrieve toy elephant 	Remove elastic band (R)	Slide box along the table and back again (IR)	Remove the lid of the box and retrieve elephant (R)
Retrieve toy lion 	Pull box towards you (R)	Stroke the top of the box twice with index finger (IR)	Remove the end of the box and retrieve lion (R)
Build tower of blocks 	Place block 1 in centre of table (R)	Turn block 2 360◦ in your hands (IR)	Place block 2 on top of block 1 and place block 3 on top of block 2 (R)
Make a paper fan 	Gather up concertina paper (R)	Tap paper on the table twice (IR)	Fold the paper in half to produce a fan (R)

5.3.4 PROCEDURE

For testing, each child sat at a child-size table next to the experimenter (E). Parents were present if the child preferred it, and sat behind the child so that they were not distracting. A video camera recorded the child's actions to allow independent coding of imitation behaviour.

All children started the experiment by completing two practice trials. Practice trials were included to ensure that the participants were able to meet the basic motor demands of the task. They also familiarised participants with the routine of the study – first they watched an adult playing with some toys, then they will be given the opportunity to play themselves. During piloting this was found to reduce the child's attempts to reach out for the objects before the demonstration. In practice trial 1, E said *'I am going to make a pattern with some beads on this peg. When I am done, I would like you to make the same pattern on a different peg so watch me carefully'*. E then placed three beads, one at a time, onto a peg. She then offered the three remaining beads to the child and said *'Now it is your turn, can you make a pattern on this peg'* (pointing to a different peg). Praise was given on completion, regardless of whether the same or a different pattern was made. For practice trial 2, E said *'Next up, we are going to play with my doll called Ted. He wants to hide in the pot. Watch me carefully and then you will get a turn to hide Ted.'* E then takes the lid off the pot, places Ted in and puts the lid back on. When finished, E then takes Ted out of the pot, hands him to the child and says *'Now it is* *your turn, can you hide Ted in the pot?'* Upon completion, E praised the child. All the children were able to complete both of the practice trials without difficulty.

After the practice trials, the experimental trials began. E said *'Now we are going to play with some more toys but this time you can see Kate playing first. Let's see what toys Kate has.'* For children assigned to the video demonstration condition, E produced a laptop and placed it in front of the child. E then ran a matlab script which presented the trials in a random order. Each trial started with E saying *'Look Kate has a toy [duck]'* whilst showing the child a picture of the last frame of the movie that depicted the end goal of the action. E then continued by saying *'Kate is going to show you how she got the [duck] out of the box', watch her carefully and then you will get a turn.'* E then played the movie demonstration. Once the movie was over, E put the laptop to one side (still displaying the end goal on the screen) and gave the child the apparatus whilst saying '*Can you get the [duck] out', do it as quickly as you can'.* Square brackets indicate where the name of the toy was substituted on each trial. Note here that the instructions emphasise the action goal and speed, but not the means by which the action is achieved. This instruction ensures that children clearly understand their goal in the situation and should reduce any copying that is driven by demand characteristics. These instructions have been used previously and rates of overimitation are comparable to studies with other instructions (Marsh et al., 2013). The child attempted the task, was praised and then started a new trial.

Once all five trials were completed, the children were then shown 10 short clips from the action sequences again. Five of these were rational actions and 5 were irrational, presented in a random order. After the clip, they were given a 5-point scale with a smartly dressed man above the 1 and a clown above the 5. They were asked how sensible (E points to the smartly dressed man) or how silly (E points to the clown) was that action? E noted down the child's verbal or point response and moved on to the next clip.

The procedure for children assigned to the live demonstration condition was the same as for the video demonstration except there was no laptop. E had laminated photographs of the goal of the action to put in front of the child. Trial order was randomised by shuffling the photos between each participant. E's script was identical to the video condition. When it was time for the demonstration, a demonstrator (D) brought the apparatus to the table and sat directly opposite the child. When cued by E, D performed the action sequence. Then D reset the stimulus objects to their original configuration behind a screen, then removed the screen and moved out of sight. E then handed the object to the child, with the same instructions as the video condition. Throughout the live demonstrations, a second video camera was positioned to capture D's actions in order to check that the live demonstration was accurate. After all five trials, D came back and performed the same 10 sections of the action sequences that were used in the video ratings. After each, the child was presented with the sensible/silly action rating scale and was asked by E to rate the action.

In addition to the overimitation task, each child completed the British Picture Vocabulary Scale II (BPVS-II), a standard measure of verbal abilities (Dunn, Whetton, & Pintillie, 1999) with a separate researcher and parents completed the Social Aptitudes Scale (SAS, Liddle, Batty, & Goodman, (2009)), a general measure of social abilities. These measures were completed to check that participants in the live and video groups did not differ on verbal ability or social skills and were entered as predictors in a regression model to predict overimitation.

5.3.5 CODING AND DATA ANALYSIS

All coding was based on the video recordings. The coder was blind to the eye contact condition whilst coding the movies. However, the coder was able to tell whether the child had received live or video demonstrations based on the experimental setup. For each trial, the coder was asked to judge whether the goal of the action was achieved and whether the irrational action was performed by the child. The irrational action was judged to be performed if the child made a definite and purposeful movement on the object, as described in Table 5.1. For each trial, the child was awarded a score of 1 for each irrational action completed and 0 otherwise. Therefore, each child had a total score out of 5 for overimitation. Data from 35 children (37%) were double coded by an independent coder. Overall agreement between coders was 93%. Cohen's Kappa = 0.92.

All children were able to achieve the goal of each action so this was not analysed. There were no significant gender differences or gender by overimitation interactions within this dataset so gender shall not be considered further. Table 5.2 shows participant statistics for each randomly-allocated group. As there was a group difference for BPVS and SAS scores (see Table 5.2), all analyses include these scores as covariates to partial out the variance attributed them.

Table 5.2. Participant group characteristics. Numbers displayed are group means (and standard deviations) for participants in each condition.

	Live	**Video**	**Difference (p)**
n	42	52	
Age	6y9m (1y1m)	6y8m(1y1m)	0.67
BPVS	109.9 (10.6)	115.6 (10.2)	0.01
SAS	26.2 (5.1)	23.3 (5.6)	0.01
Overimitation	2.9 (1.9)	1.2 (1.5)	0.001

For data analysis, I ran three ANCOVAs to test each of our three main research questions (every model included age as a factor), followed by a logistic regression incorporating all variables. First, I compared the effect of live and video demonstration. The total overimitation score out of five for each child was entered into a univariate ANCOVA, with demonstration type entered as a between-participant factor and age in years and months, SAS and BPVS entered as covariates.

Second, the effects of eye contact on overimitation were analysed on a trial by trial basis, due to an unequal number of trials with and without eye contact per child (either two or three). Thus, demonstration type, direct eye contact preceding an irrational action and apparatus type were entered into a univariate ANCOVA as between trial factors and age, BPVS and SAS were added as covariates. Interaction terms for demonstration type and eye contact with age and demonstration type with eye contact were also entered into the model.

Third, rationality ratings were analysed by calculating a rationality difference score for each trial, by subtracting the child's rating of the rational action from their rating of the irrational action. Thus each trial for each child had a rationality rating ranging from -4 (irrational actions rated as more rational than rational actions) to 4 (irrational actions rated as more irrational than rational actions). A score of 0 reflected no perceived difference in rationality between the rational and irrational action. I tested if overimitation on a trial is related to the later rationality rating given on that trial. Rationality difference scores were also analysed on a trial-by-trial basis and entered as the dependant variable into a univariate ANCOVA. Overimitation behaviour, eye-contact and demonstration type were entered as a between trial factors and age, BPVS and SAS were entered as covariates.

Finally, I performed a binary logistic regression to establish which factors are good predictors of overimitation behaviour. Age, BVPS, SAS, demonstration type, eye contact and rationality ratings were entered as single variables and demonstrator eye contact by age, demonstrator eye contact by condition and rationality ratings by age were entered as interaction terms. All variables were entered into a backwards likelihood ratio model.

5.4 RESULTS

Sixty-two percent of children completed at least one unnecessary action in at least one trial in this sample. Rates of overimitation, split by demonstration condition and apparatus type are presented in Table 5.3. Participants in the live demonstration condition consistently overimitated more compared to those in the video demonstration condition. Overimitation behaviour also differed by apparatus type as participants overimitated least on the fan trial compared to all other apparatus types. Apparatus type was therefore modelled as a nuisance variable in all analyses and will not be considered further.

Table 5.3 Percentage of trials in which overimitation occurred, as a function of demonstration and apparatus type. Figures are the mean (and standard deviation) of rationality difference ratings for each apparatus type.

Trial Type	**Live: % overimitation**	**Video: % overimitation**	**Rationality Difference Ratings**
Blocks	70	23	1.43 (1.97)
Duck	70	31	2.20 (1.75)
Elephant	65	19	1.94 (1.75)
Fan	23	15	1.71 (1.86)
Lion	72	31	2.14 (1.70)

5.4.1 VIDEO VS LIVE DEMONSTRATION

Percentage overimitation for each age group as a function of demonstration type is presented in Figure 5.1. Overimitation score was entered as the dependant variable in a univariate ANCOVA with demonstration type entered as a between participant factor and age, BPVS and SAS entered as covariates. A significant main effect of demonstration type revealed that children were more likely to over-imitate a model who demonstrated the action live, compared to a video demonstration ($F(1,77)=15.035$, $p<0.0001$). There was also main effect of age ($F(1,77)=4.50$, $p<0.05$), showing that older children were more likely to over-imitate than younger children. No main effect of BPVS ($F(1,77)=0.09$, $p=0.76$) or SAS ($F(1,77)=0.14$, $p=0.71$) was found. Furthermore, when analysing a subset of the data in which groups were matched for BPVS and SAS (n=39 in each condition), the same pattern of results was observed.

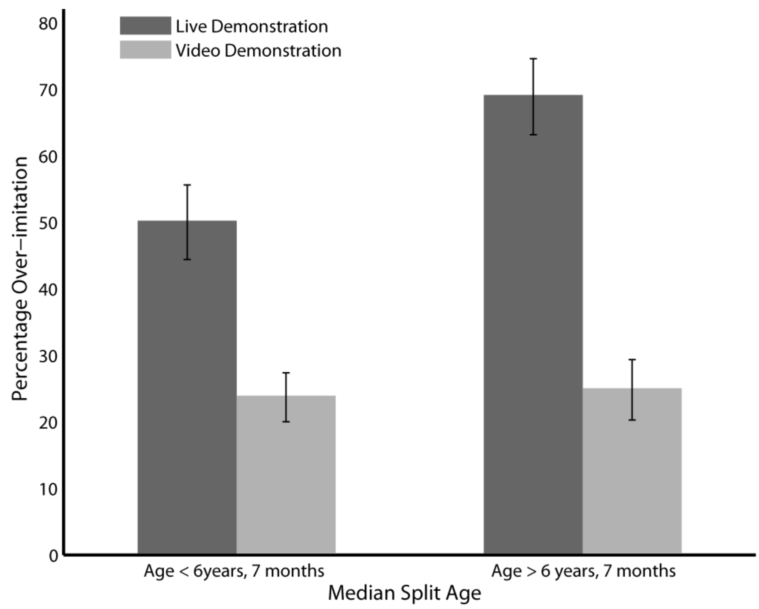

Figure 5.1. Overimitation score for younger and older children (based on a median split) as a function of demonstration type. The use of a median split for age is for visualisation purposes only; all analyses were run using age as a linear covariate.

5.4.2 EYE CONTACT PRECEDING IRRATIONAL ACTIONS

Percentage overimitation for each age group as a function of preceding eye contact is presented in Figure 5.2. Overimitation was entered as the dependant variable in a univariate ANCOVA with eye contact and demonstration type entered as between trial factors and age, BPVS and SAS entered as covariates. As with the previous analysis, a main effect of demonstration type ($F(1,367)=46.73$, $p<0.0001$) and a main effect of age ($F(1,367)=7.05$, $p=0.008$) was present. No main effect of eye contact preceding an irrational action is reported ($F(1,367)=0.01$, $p=0.97$) although a significant age by eye contact interaction was found ($F(1,367)=5.99$, $p=0.01$). A post hoc t-test shows that this interaction is driven by an increase in overimitation in the older children when eye contact is absent (t(225)=2.04, p=0.04). In addition, an interaction between age and demonstration type (F(1,367)=4.82, p=0.03) was found. This suggests that as children get older, they are more likely to over-imitate the live (t(214)=2.48, p=0.01) but not the video condition (t(263)=-0.26, p=0.79).

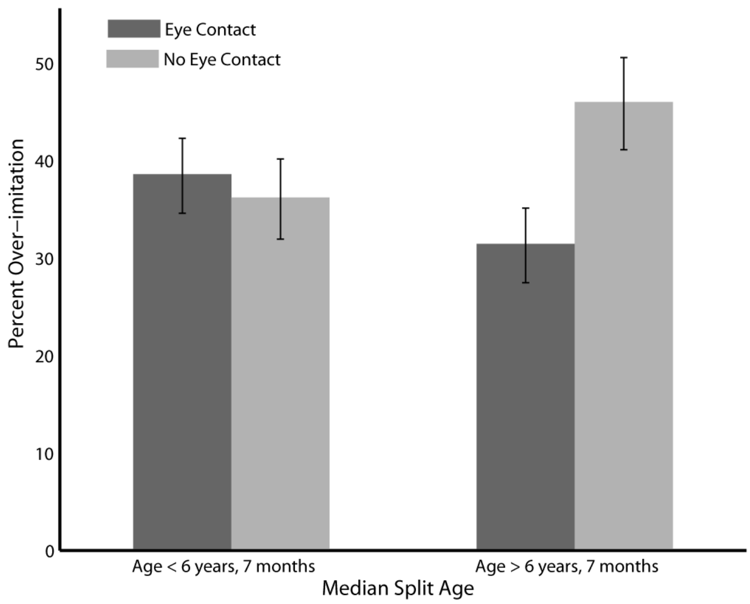

Figure 5.2. Overimitation score for younger and older children (based on a median split) as a function of preceding eye contact. The use of a median split is for visualisation purposes only; all analyses were run using age as a linear covariate.

5.4.3 RATIONALITY RATINGS

Rationality difference ratings as a function of overimitation behaviour are presented in Figure 5.3. Difference ratings for each trial were entered as the dependant variable into a univariate ANCOVA with overimitation behaviour, eye contact and demonstration type entered as between-trial factors and age, BPVS and SAS entered as covariates. Children who overimitated an action subsequently rated that action as more irrational than the actions that they did not overimitate ($F(1,364)=3.89$, $p=0.05$). In addition, older children reported larger rationality differences between rational and irrational actions, compared to younger children ($F(1,364)=16.92$, $p<0.001$). Effects of eye contact ($F(1,364)=0.31$, $p=0.58$), demonstration type ($F(1,364)=3.74$, $p=0.06$), BPVS ($F(1,364)=3.28$, $p=0.07$) and SAS ($F(1,364)=1.33$, $p=0.25$) were not significant.

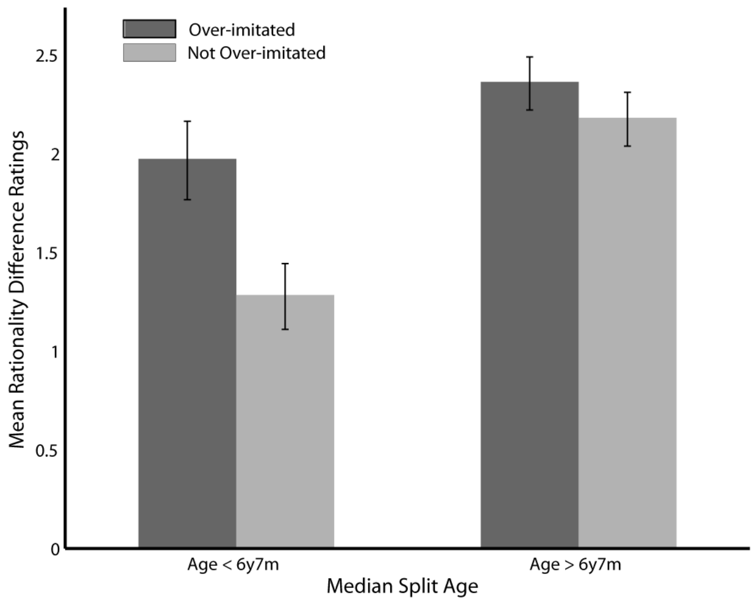

Figure 5.3. Mean difference in rationality ratings between rational and irrational actions that were either overimitated or not overimitated. Results are visualised using a median split for age but all analyses were run using age as a linear covariate.

5.4.4 PREDICTORS OF OVERIMITATION BEHAVIOUR

I used a logistic regression model to determine which of all the factors measured in this study best predicts overimitation behaviour. Results are shown in Table 5.4. The final model accounted for 26% of the variance in overimitation behaviour (NagelKerke $R^2 = 0.259$) using four of ten variables. Firstly, overimitation was most likely when participants saw a live demonstration, compared to a video demonstration. Second, overimitation occurred less when participants were given the fan trial compared to all other trials. Rationality ratings predicted overimitation as the higher the rationality difference rating, the more likely the participant was to overimitate. Lastly, an age by eye contact interaction was also a significant predictor of overimitation, showing that in the older children, eye contact reduced propensity to over-imitate. Child age, the age by rationality rating interaction, BPVS, SAS, demonstrator eye contact and the demonstration type by rationality rating interaction did not predict overimitation behaviour. Overall, this model was able to correctly predict overimitation behaviour on 73% of trials using these four variables.

Table 5.4. Variables entered into the binary logistic regression. Values are the beta weights, the Wald statistic and the p-value for each significantly contributing variable. Variables listed in italics indicate those variables entered but excluded during analysis.

Variable	**Beta**	**Wald**	**p**
Demonstration Type	-1.41	34.38	0.0001
Apparatus Type (fan)	-1.70	16.28	0.0001
Rationality Ratings	0.14	4.08	0.04
Age x EC	0.48	9.49	0.002
Age	*Excluded – step 1*	-	-
Age x Rationality Ratings	*Excluded – step 2*	-	-
BVPS	*Excluded – step 3*	-	-
SAS	*Excluded – step 4*	-	-
Eye Contact	*Excluded – step 5*	-	-
Demonstration x EC	*Excluded – step 6*	-	-

5.5 DISCUSSION

The present study aimed to identify the social modulators of overimitation whilst reducing the demands of causal inference. I found substantial levels of overimitation which increased with age, despite testing older children than previous studies and using simple objects with minimal causal reasoning demands. These data further show that social cues had a larger impact on older children, who overimitated more following live demonstrations but less following eye contact. Finally, actions that were rated as least rational were more likely to be copied than the actions rated as more rational. I now discuss what our results mean for social models of overimitation, causal reasoning models, and the development of overimitation in turn.

5.5.1 SOCIAL MODELS OF OVERIMITATION

Based on previous studies (Brugger et al., 2007; Nielsen, 2006), I predicted that overimitation would increase with increases in social engagement, that is, with live demonstration and with eye contact. Our predictions were confirmed for the video compared to live demonstration comparison. Across all ages in our sample, the live demonstrator was copied with higher fidelity than the videoed demonstrator. This is likely to be because the social presence is stronger in the live condition. This is consistent with previous findings that suggest increased social engagement elicits higher levels of overimitation (Brugger et al., 2007; Nielsen, 2006).

In contrast, the eye contact manipulation did not yield the predicted results. Previous studies show that socially cued action sequences were overimitated more than uncued action sequences (Brugger et al., 2007), and adults mimic faster following an eye contact cue (Wang et al., 2011). If overimitation and mimicry are dependent on the same underlying mechanism (Over & Carpenter (2012)), we would predict that direct eye contact prior to an unnecessary action should increase the propensity to imitate. The results from this manipulation were contingent upon the age of the participant. In the younger children there was no significant effect of eye contact on overimitation behaviour. In contrast, direct eye contact prior to an unnecessary action significantly reduced the propensity to overimitate in the older children.

This suggests we may need to re-think the role of eye contact in this situation and what it may signal. As an ostensive cue, eye contact could be interpreted as a cue to 'pay attention' and think about the action performed. In this case, the children may be made explicitly aware of the unnecessary action and choose not to copy it. The present results demonstrate that eye contact is a subtle cue that can be interpreted in different, context dependant ways. Further studies will be needed to understand the relationship between different eye contact cues in mimicry and those in overimitation.

5.5.2 CAUSAL REASONING MODELS OF OVERIMITATION

The present study used stimuli which are familiar to the child, with minimal causal reasoning demands. If causal misattributions are driving overimitation behaviour, we would expect to see very little overimitation in this task. Furthermore, we would expect overimitation behaviour to decrease with age and with rationality ratings. These predictions do not reflect the pattern of results that was observed. Sixty-two percent of children overimitated at least one trial in this sample, and rates of overimitation increased with age. Rationality ratings were collected to assess how children perceived each action. Somewhat surprisingly, the children who copied an unnecessary action subsequently rated it as more irrational than those who did not copy it. Again, this provides evidence against a causal learning explanation for overimitation behaviour as children who understand that an action is irrational (silly) are more likely to imitate that action. This finding adds to the existing literature as previously, ratings of actions have taken prior to the child completing the actions, and thus potentially influencing subsequent imitation (Kenward et al., 2011). In addition, Kenward et al. (2011) only included children who overimitated and as such, could not demonstrate the relationship between rationality ratings and behaviour that this study has identified. Previous studies that find evidence in support of the automatic causal encoding model have examined children under five years old (Lyons et al., 2011, 2007). It is possible that overimitation in this young group is driven by causal reasoning, while social factors dominate in older children as causal reasoning and social skills develop.

5.5.3 DEVELOPMENTAL CHANGES IN OVERIMITATION

This study explored overimitation over the 5-8 year old age range. Like previous studies, we find that overimitation increases with age (McGuigan et al., 2011) in a way that is inconsistent with a causal reasoning explanation. Perhaps more interestingly I report two interactions between age and the social manipulations in this study (namely demonstration type and eye contact). In both of these interactions, sensitivity to the social components of the task increases with age. Previous studies that support the automatic causal encoding hypothesis have tested younger children (2-5 year olds) and found persistence in overimitation despite social cues (Lyons et al., 2011, 2007). Again, this data suggests that causal reasoning dominates responding in this younger age group, while social cues are much more important in the older children studied here. This should be investigated more thoroughly in a wider age range of children.

Individual difference measures of verbal intelligence and social ability did not predict overimitation. The lack of predictive power of social ability was surprising, considering that the social features of the task have a large influence on overimitation behaviour. However, this sample did not include a full range of social abilities and the SAS is a limited social measure. Studies examining overimitation behaviour in a sample of children with autism have yielded different results. Two previous studies have shown that children with autism faithfully imitate inefficient tool selection and use (Nielsen & Hudry, 2010; Nielsen et al., 2012) but overimitation was absent in participants with autism for visibly unnecessary actions with minimal causal demands (Marsh et al., 2013 also see Chapter 6). These differences indicate that the apparatus types used have a huge bearing on social overimitation behaviour and further work should investigate precisely what object features are important for overimitation.

5.5.4 LIMITATIONS

I would like to acknowledge two limitations of the current study. Firstly, due to the difficulty in developing appropriate stimuli and restriction on experiment length, the number of eye contact vs no eye contact trials was unbalanced within subject. The analysis of this data on trial-by-trial basis minimises the problems associated with unequal trial numbers and I believe the results to be unaffected by this. Secondly, the use of familiar objects in traditional imitation tasks is criticised (Zentall, 2012) as participants can act on their prior knowledge of the object and therefore, it is difficult to distinguish imitative behaviour from normative behaviour. Contrary to this argument, results from our study show that despite object familiarity, children frequently complete unnecessary actions which are unlikely to have been produced without the demonstration of that action. I argue that in overimitation paradigms, the use of familiar objects actually strengthens our understanding of overimitation as causal reasoning explanations can be eliminated.

5.5.5 CONCLUSIONS

The present study demonstrates that overimitation increases with age and is modulated by social cues, even in a task with minimal demands for causal reasoning. This argues against a pure causal learning explanation of overimitation, and demonstrates that social factors play a critical role in the decision about what to imitate. Older children showed greater sensitivity to social cues, demonstrating that development of social interaction skills continues over the primary school years. Here, I demonstrate that overimitation is linked to both social sensitivity and understanding of action rationality. Therefore, this is an ideal task to test the social motivation hypothesis of ASC whilst also probing rationality comprehension. This is the topic of study in Chapter 6.

CHAPTER 6. CHILDREN WITH AUTISM DO NOT OVERIMITATE

6.1 ABSTRACT

Children copy unnecessary actions with high fidelity, this is termed overimitation. The degree to which children overimitate is socially modulated. Children with autism have documented social difficulties and may also have an imitation deficit. The present study investigates whether children with autism engage in overimitation. Previously, children with autism have been shown to faithfully imitate inefficient tool selection and use with novel objects. The aim of this study was to see if children with autism continue to engage in overimitation with familiar objects. 31 children with autism, 30 chronological age (CA) and 30 verbal mental age (VMA) matched controls had the opportunity to overimitate on five trials. Following imitation, children were asked to rate how 'sensible' or how 'silly' each action in the sequence was. Children with autism overimitated unnecessary actions significantly less than both the CA- and VMA- matched controls. Furthermore, children with autism were less able to differentiate sensible and silly actions when asked explicitly. These results show that children with autism accurately copy goal-directed actions but do not overimitate in circumstances where typical children do. This lack of overimitation means that children with autism miss out on a wealth of social learning opportunities that typical children exploit.

6.2 INTRODUCTION

Copying the behaviour of others is important for forming social bonds with other people and for learning about the world (Carpenter, 2006). After seeing an actor demonstrate actions on a novel object, typically developing children faithfully copy both necessary and visibly unnecessary actions (Horner & Whiten, 2005). This 'overimitation' is commonly described in terms of learning about the object, but may also reflect a social process such as the child's motivation to affiliate with the demonstrator (Over & Carpenter, 2012) or to conform to perceived norms (Kenward, 2012). This literature has been discussed in more detail in Section 5.2 of this thesis. The results from the experiment presented in Chapter 5 support the social view of overimitation, demonstrating that the presence or absence of the demonstrator has a large impact on children's decisions to faithfully imitate. In addition, children were more likely to imitate an unnecessary action when it was subsequently rated as silly. This shows that a lack of understanding or uncertainty is not driving faithful imitation behaviour.

Given that overimitation appears to be socially motivated, it is interesting to consider how children with ASC perform on this task. Previous studies have demonstrated that children with ASC imitate in a goal-directed way (Hamilton, Brindley, et al., 2007), and that they imitate meaningful actions more than meaningless actions (Rogers, Bennetto, McEvoy, & Pennington, 1996). We also know that individuals with ASC are less likely to imitate the style of an action whilst still imitating the action goal (Hobson & Lee, 1999) and this is especially pronounced when comparing goal-directed and goal-less actions (Wild et al., 2012). Considering this evidence and the finding that overimitation behaviour is socially-driven (see Chapter 5), we can make a strong prediction that children with ASC will not overimitate.

Contrary to this prediction, two previous studies have directly tested this hypothesis and concluded that children with autism do engage in overimitation behaviour (Nielsen & Hudry, 2010; Nielsen et al., 2012). This is a puzzling finding but close examination of the methods used in these studies reveals that they may confound object learning and social components of overimitation behaviour. The objects used in both of these studies were physically opaque and the demonstrated actions that led to the opening of the box involved the use of tools. Furthermore, the irrelevant actions performed on these objects also involved using a tool to interact with the object in some way. As described previously (section 5.2), this use of tools and novel, opaque objects cannot separate object learning and social imitation because the task inherently involves learning about the object. Even though researchers consider these objects to be causally transparent in their mechanism, young children's causal reasoning about novel objects is unclear (Kenward et al., 2011).

In the present study I re-examine the hypothesis that children with ASC will not overimitate by isolating and measuring the social component of overimitation. To do this, I will use simple, non-mechanical objects, which preclude object learning. As in Chapter 5, I will also assess how imitation fidelity changes with improvements in social skills.

6.3 METHOD

6.3.1 PARTICIPANTS

Participants were 31 children with autism (ASC), 30 typically developing children matched for chronological age (CA-match) and 30 typically developing children matched for verbal mental age (VMA-match). Table 6.1 describes the profile of each group. There was no difference in chronological age between the ASC and the CA-match participants ($t(59)=1.39$, $p=0.17$) and no difference in verbal mental age (assessed by the British Picture Vocabulary Scale - BPVS, Dunn, Dunn, Whetton, & Pintillie, 1999) between the ASC and VMA-match participants ($t(59)=0.15$, $p=0.88$).

All children in the autism group had a diagnosis of autism, autism spectrum condition or Asperger's syndrome from an independent clinician or paediatrician. This diagnosis was confirmed using parent reports of the social communication questionnaire lifetime edition (SCQ, Rutter, Bailey, & Lord, 2003) in 27 participants. Additionally, one participant scored just below the recommended cut-off for autism on this measure and three parents failed to complete it. These four participants were all recruited through specialist schools for autism or through an autism unit at a mainstream school so I am confident of their diagnoses. However, to ensure that these participants did not alter my results, all analyses were performed with and without these participants and the results remain unchanged (see section 6.4.1). Parents of all children completed the Social Aptitudes Scale (SAS, Liddle, Batty, & Goodman (2009)), a measure of their child's current social abilities. As expected, children with ASC scored significantly lower on this measure than children in the CA-match and VMA-match groups (CA: $t(53)=14.5$, $p<0.001$, VMA: $t(55)=12.8$, $p<0.001$). Two children with autism scored just outside of the recommended cut-off for autism on this measure, although they both met criteria for autism on the SCQ and had a clinical diagnosis. No children in either of the typically developing groups met the recommended criteria for autism on the SAS and parents of these children reported no developmental disorder.

Children with autism were recruited from schools in the Nottingham area. Typically developing children took part in the study as part of the Summer Scientists week event where children complete a number of cognitive tasks over half a day at the University of Nottingham. The parents of all children gave written informed consent before testing began.

Table 6.1. Participant characteristics for chronological age (CA) matched, verbal mental age (VMA) matched and autism spectrum condition (ASC) groups. Figures reported are group mean ± standard deviation and (range).

Group	**CA- match**	**VMA- match**	**ASC**
n	30	30	31
Age	8.66 ± 2.0 (4.9 - 12.7)	6.0 ± 1.3 (4.2 - 8.6)	9.4 ± 2.3 (5.2 - 13.6)
BPVS raw	94.5 ± 19.9 (57 - 137)	65.9 ± 20.6 (35 - 122)	66.7 ± 21.5 (33 - 119)
SAS	27.6 ± 4.7 (10 - 39)	24.1 ± 4.1 (17 - 32)	9.2 ± 4.6 (0 - 19)
Overimitation	2.6 ± 1.9 (0 - 5)	2.2 ± 2.1 (0 - 5)	1.1 ± 1.6 (0 - 5)
Rationality Discrimination	2.5 ± 0.8 (0 - 3.4)	2.2 ± 1.2 (-0.8 - 4)	1.3 ± 1.2 (-1.2 - 4)
Theory of Mind (%)	not collected	not collected	57.7 ± 28.7 (0 - 100)
SCQ scores	not collected	not collected	25.5 ± 4.9 (15-33)

Abbreviations: CA- chronological age; VMA- verbal mental age; ASC- autism spectrum conditions; BPVS- British Picture Vocabulary Scale; SAS-Social Aptitudes Scale; SCQ- Social Communication Questionnaire.

6.3.2 PROCEDURE

The procedure for this study was identical to that used in the live condition of the study presented in Chapter 5. All participants were tested in a quiet room of the University or their school. As with the previous study, participants completed the overimitation task followed by the rationality ratings task.

In addition to the tests of overimitation and rationality discrimination, participants completed the British Picture Vocabulary Scale (BPVS-II) for VMA-matching. In order to explore the relationship between overimitation and theory of mind ability, ASC participants also completed a standard theory of mind battery, including six false belief questions and six trials of a penny hiding task as used in (Hamilton, Brindley, et al., 2007).

6.3.3 DATA CODING AND ANALYSIS

The entire testing session was video recorded and coding was completed retrospectively. All participants correctly completed the warm-up trials. Correct goal achievement was recorded if the participant was able to open the box or build the object. Performance was 100% for the typically developing children on all tasks. One child with ASC failed to retrieve the duck or build the block tower due to increased sensory interest in the objects, and two children with ASC failed to make the fan, instead folding the paper in the wrong way. For these participants, their overimitation score was computed as a proportion of the number of trials that they did complete. Overall performance for the ASC group was 97%. Overimitation was scored from the videos. On each trial, a participant was given a score of 1 if he/she completed the unnecessary action and a score of 0 if he/she did not. Scores were summed to give a participant overimitation score range from 5 to 0. All coding was completed by two independent researchers and reliability between coding was good (Cohen's kappa = 0.95).

A rationality discrimination score was calculated for each trial by subtracting the participant's rating of the necessary action in the sequence from his/her rating of the unnecessary action. This score therefore ranges from -4 to 4 and indicates the degree to which the participant is able to discriminate rational and irrational actions, with higher scores indicating good discrimination and zero scores indicating chance performance. Each participant's mean rationality discrimination score was calculated for further analysis.

Analysis of overimitation and rationality discrimination was conducted using separate univariate ANCOVAs for comparisons between the each of the typically developing groups and the ASC group. Group membership (TD or ASC) was entered as a between-subjects variable in each model. When comparing the VMA-matched group to the ASC group, raw BPVS score was added as a covariate and when comparing the CA-matched group to the ASC group, age was entered as a covariate.

In this study, eye contact did not influence overimitation in either typically developing or ASC participants (CA-match: $t(141)=1.24$, $p=0.22$; VMA-match: $t(137)=0.21$, $p=0.84$; ASC: $t(148)=0.76$, $p=0.45$), so all further analyses reported in this chapter are collapsed across eye contact condition.

6.4 RESULTS

6.4.1 OVERIMITATION

Children with ASC showed less overimitation than the CA-matched ($F(1,58)=12.84$, $p<0.001$) or VMA-matched ($F(1,58) = 7.01$, $p=0.01$) typically developing children. Typically developing children copied 43% (VMA-matched) and 57% (CA-matched) of the unnecessary actions but children with autism copied only 22% (see Figure 6.1). There was no effect of age or BPVS on overimitation behaviour. To ensure that the four children without a confirmed diagnosis on the SCQ are not driving this difference, we performed the analyses again with these children excluded. The results remain unchanged (CA-match v. ASC subgroup: $F(1,53)=12.9$, $p=0.004$) and VMA-match v. ASC subgroup: ($F(1,53)=6.2$, $p<0.01$)). Furthermore, following the exclusion of these four participants the groups remain matched for chronological age (CA-match: $t(55)=0.66$, $p=0.51$) and verbal mental age (VMA-match: $t(55)=0.70$, $p=0.49$).

The number of children who failed to overimitate on any trial varied between groups. In the chronological age-matched group 7 children did not overimitate at all, this is compared to 12 children in the VMA-matched group and 17 in the ASC group.

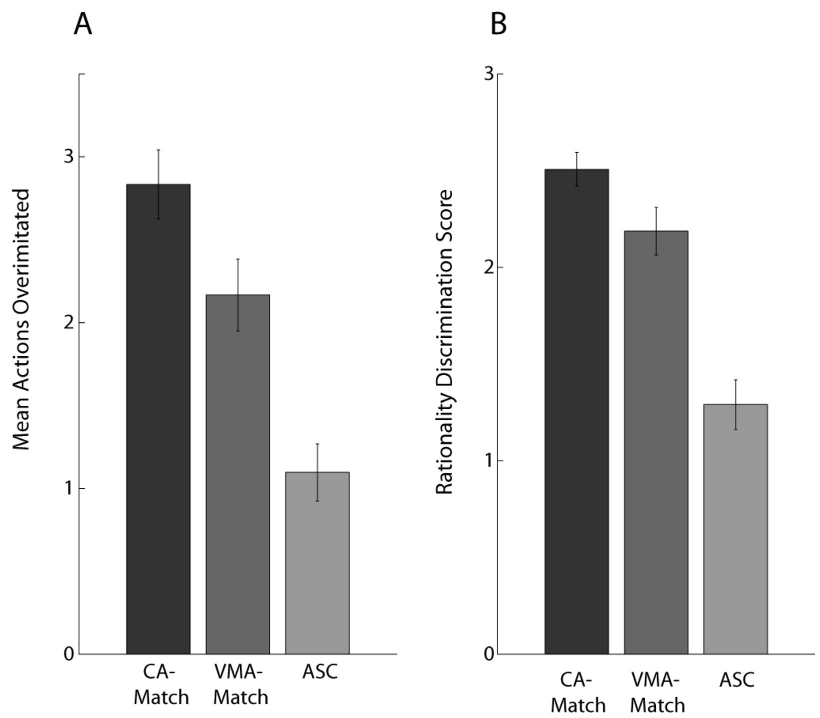

Figure 6.1. Panel A shows the mean number of irrational actions copied (maximum 5) for the chronologial age matched (dark grey), verbal mental age matched (mid grey) and autism spectrum condition (light grey) groups. Panel B shows the mean rationality discrimination score (ranging from -4 to +4) for each of these groups. Error bars represent ± 1 standard error.

6.4.2 RATIONALITY DISCRIMINATION SCORE

The rationality discrimination score was calculated by subtracting the ratings of the necessary actions from the ratings of the unnecessary actions. All three groups performed significantly above chance (zero) (CA-match: $t(29)=16.1$, $p<0.001$; VMA-match: $t(29)=10.2$, $p<0.001$; ASC: $t(30)=5.9$, $p<0.001$) on this measure (see Figure 6.1). However, children with ASC were significantly worse at judging the rationality of actions, when compared to CA-matched ($F(1,58)=19.62$, $p<0.001$) and VMA-matched ($F(1,58)=9.29$, $p=0.003$) groups. These results remain unchanged when the four ASC children without SCQ diagnosis are excluded from the sample (CA-match v. ASC subgroup: $F(1,53)=22.8$, $p<0.001$) and VMA-match v. ASC subgroup: ($F(1,53)=10.6$, $p=0.002$). Histograms of the ratings given by each group are presented in Figure 6.2. Both groups of typically developing children rated almost all the necessary actions as 1 and rated the unnecessary actions as 4 or 5. Children with ASC are performing this task in a similar way, with the majority of responses falling at the extremes of the scale. However, they are also making more errors than the typically developing children, scoring more necessary actions as 5 and unnecessary actions as 1. This can account for the reduced rationality discrimination scores found in the ASC group.

In order to control for the effects of rationality discrimination ability on overimitation, all analyses were repeated with rationality discrimination score included as a covariate. The group difference in rates of overimitation between the typically developing groups and the ASC group remains unchanged (CA-match: $F(1,57)=6.19$, $p=0.02$; VMA-match: $F(1,57)=4.74$, $p=0.03$). Furthermore, the effect of rationality discrimination score on overimitation was not significant (CA-match: $F(1,57)=1.42$, $p=0.24$; VMA-match: $F(1,57)=0.46$, $p=0.50$).

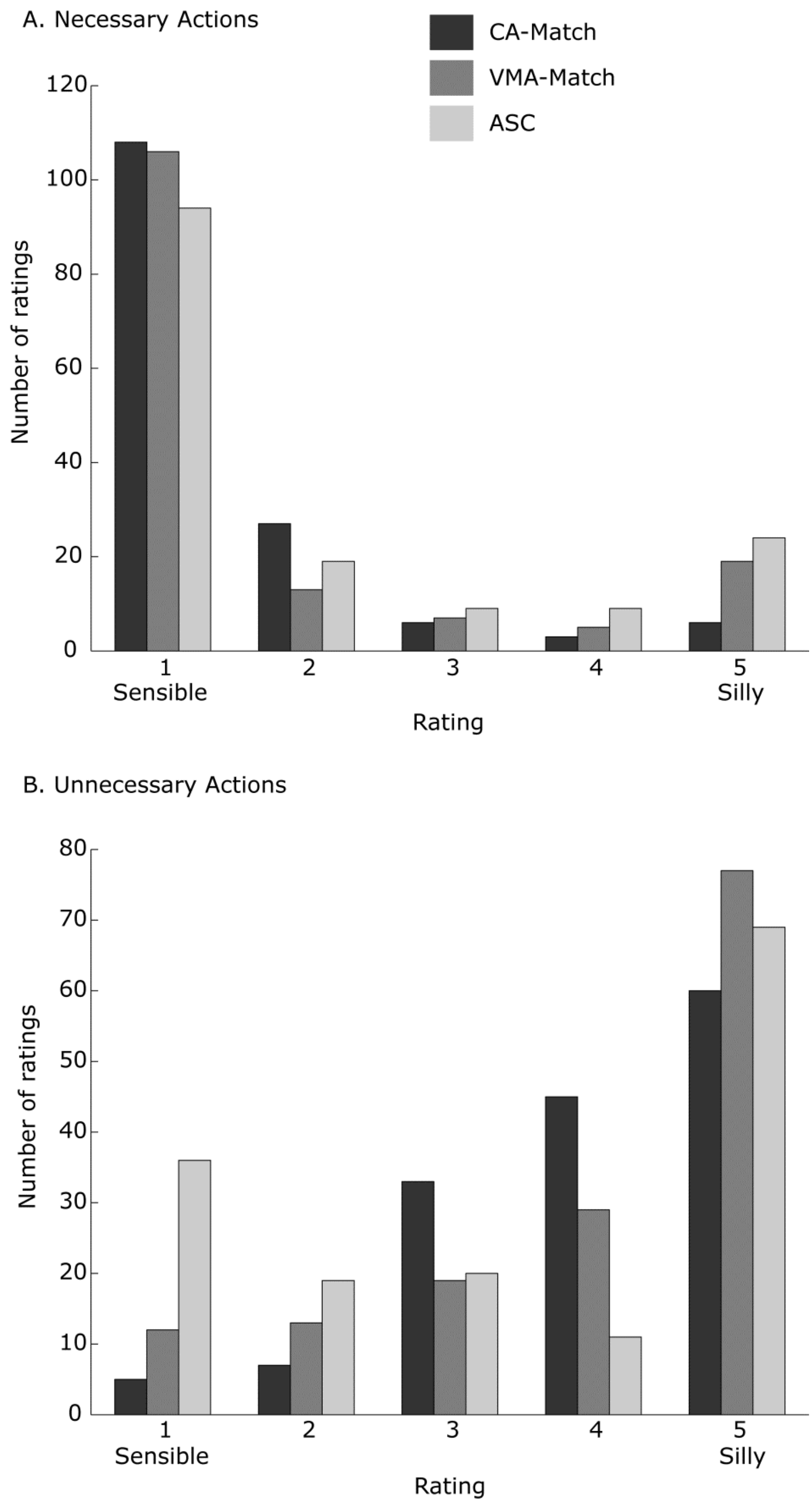

Figure 6.2. Histograms of rationality ratings for necessary (panel A) and unnecessary (panel B) actions as given by CA-matched TD participants (dark grey bars), VMA-matched participants (mid-grey bars) and ASC participants (light grey bars).

6.4.3 PREDICTORS OF IMITATION

I also investigated what factors predict a child's overimitation score. Children with autism completed a battery of theory of mind tasks and their parents completed the lifetime version of the SCQ. These measures were not available for the typically developing children due to time constraints. A composite theory of mind score was generated for each child, averaging performance on the false belief tasks and the penny hiding tasks. I used linear regression to test if overimitation performance in children with autism was predicted by their age, BVPS score, ToM score, SAS score or SCQ score. In total this model accounted for a significant proportion of the variance in overimitation scores (R^2=0.44, p=0.02). However, no single variable was a significant predictor (age: t=0.41, p=0.68; BPVS: t=1.93, p=0.07; theory of mind: t=0.67, p=0.51; SAS: t=0.02, p=0.99; SCQ: t=1.30, p=0.21). Note that our sample size of 31 is small for this type of analysis, and further study of the relationship between overimitation and other measures of social cognition would be valuable.

6.5 DISCUSSION

The aim of the present study was to test whether children with ASC overimitate when the object-learning component of a task is reduced. The results reported here have some important implications. First, typically developing children show substantial overimitation of unnecessary actions on familiar objects, despite understanding that these actions are 'silly'. These results lend support for the position that overimitation in typical children is a social phenomenon rather than being driven by the child's causal learning about the objects. This social overimitation may index a child's motivation (Chevallier et al., 2012) to affiliate (Over & Carpenter, 2012) or to conform to perceived norms (Kenward et al., 2011).

Second, children with autism show significantly less overimitation of the demonstrator's actions. This is not driven by weak motor skill because all the unnecessary actions were familiar simple actions (e.g. tapping a box) and all children were able to complete the more complex goal-directed actions in the sequence. It is also not driven by superior causal reasoning, because the children with ASC also performed worse on the rationality discrimination task. The data go beyond previous studies which showed reduced imitation of action style (Hobson & Lee, 1999) and reduced spontaneous imitation (Ingersoll, 2008) where differences in behaviour could be driven by the children with autism failing to adopt the same goal as the demonstrator. In this task, children are instructed that the goal is to make/retrieve the toy, and all are able to do so. The failure of children with autism to spontaneously copy unnecessary actions can best be explained in terms of reduced social motivation in these children, with less desire or ability to affiliate with or conform to the perceived norm.

The results from the present study contrast with those recently reported by Nielsen et al. (2012) which show high rates of overimitation in children with ASC. This is despite both studies aiming to test the same hypothesis in children with autism with similar ability profiles. There are several possible reasons for this difference. First, the types of objects used in the two studies are very different. The present study used simple, familiar objects that were transparent in both their causal mechanism and their physical appearance. Furthermore, we directly test whether the children understood the causal nature of the actions demonstrated. In contrast, Nielsen et al. (2012) used objects that were causally opaque in their mechanism and provide no check for participants' understanding. It is possible therefore, that the overimitation reported by Nielsen et al. (2012) reflects object learning as well as social imitation and it is the object learning that drives imitation in ASC children. A second difference between the studies is that the unnecessary actions in the present study were simple hand actions, whereas the unnecessary actions in the Nielsen et al. (2012) study involved the use of a tool. There is little previous research directly investigating the use of tools in overimitation compared to the use of unnecessary hand actions. The simple hand actions used in our study remove the need for object learning and causal reasoning about actions, and provide a cleaner measure of social imitation. However, further testing of the circumstances that drive children with autism to imitate would be valuable.

The results from this study do not lead us to conclude that children with ASC have difficulty understanding the causal relations between actions and objects. As, children with ASC were performing significantly above chance on the rationality discrimination measure, I conclude that they do understand the rating scale and are able to make judgements about the rationality of actions, yet they do not discriminate rational and irrational actions as clearly as typically developing children. Additionally, there is no evidence that reduced overimitation in autism is driven by better detection of action rationality or by better casual reasoning. This suggests that overimitation is independent of a child's ability to discriminate which actions are rational or irrational in a sequence. This finding is compatible with a social explanation of overimitation behaviour rather than an object learning or casual reasoning explanation.

Previous studies have examined social attention in autism using eye-tracking tasks (Klin et al., 2002), and have examined social motivation using brain-imaging of high functioning adults with ASC (reviewed in Chevallier et al. (2012)), but simple methods for measuring social motivation in children did not exist. The ease of implementing this task, and the close links between overimitation and social mimicry in adults (Over & Carpenter, 2012), mean that this approach can provide a powerful and general tool for examining social motivation in child and adult participants.

6.5.1 CONCLUSIONS

Overall, this experiment leads to two important conclusions. First, studies of social interaction can examine the social component of imitation behaviour independent of the object-learning component, and this can best be done using familiar objects. Second, children with autism do not show overimitation of actions on familiar objects. This specific difference in a behaviour linked to social affiliation and norm conformity is compatible with claims of abnormal social motivation in autism.

CHAPTER 7. GENERAL DISCUSSION

7.1 SUMMARY OF EXPERIMENTAL RESULTS

The experiments reported in this thesis draw on a range of methods with the general aim of identifying the processes which we use to understand the actions of others. More specifically, I aimed to evaluate and use irrational actions as a tool to examine the interplay between the action observation and the mentalizing networks of the brain. Additionally I aimed to examine the integrity of these systems in individuals with autism spectrum condition. Here I briefly summarize the results from each of the experiments in relation to these aims before discussing the implications of these findings and some emerging questions.

The experiment presented in Chapter 2 clearly demonstrates that the action observation and mentalizing networks of the human brain spontaneously differentiate action rationality when viewing irrational actions. Furthermore, these networks respond in a similar way when the action is performed by a human agent or by an animated ball, implying that we adopt a similar process of rationality resolution for human and non-human agents. Finally, I also demonstrate that explicit ratings of action rationality correlate with the BOLD signal within these networks. Together these results indicate that irrational actions do engage the action observation and mentalizing networks of the human brain simultaneously. Previously it has been proposed that these networks function independently (Van

Overwalle, 2009). Here, I provide new evidence that refutes this claim. Irrational actions can be used as a tool to probe the interaction of these networks and to establish how they work together to achieve full action comprehension.

To take this finding further and investigate the cognitive processes that the neural activity within these networks reflect, an exploratory eye tracking study was conducted. In Chapter 3, I report a number of eye tracking markers which demonstrate that typically developing participants are automatically detecting action rationality. During observation of an irrational action participants spend more time tracking the action and looking at the expected end state of that action. In contrast during the observation of rational actions, participants spend longer evaluating the environmental constraints that impact the actions. Perhaps this extra level of evaluation reflects the rationalisation of the unusual movement path. Lending weight to this interpretation is that finding that participants also spent longer evaluating the environmental constraints during irrational human actions compared to those performed by the moving ball. Other than this interaction, the social form of the agent had surprisingly little impact upon eye movements. This supports my previous conclusion that rationality is processed for human and non-human agents alike.

The final finding to emerge from this study was that predictive eye movements were modulated by the action kinematics, but not the rationality of the actions. This has important implications for the debate regarding whether predictive eye movements are generated by the mirror neuron system (Flanagan &

Johansson, 2003; see also section 1.3 for a full review of this debate). We know from previous neuroimaging work that analysis of action kinematics activates the mirror neuron system, and in particular the IFG (Hamilton & Grafton, 2008; Pobric & Hamilton, 2006). In contrast, the evaluation of action rationality recruits additional brain networks such as the mentalizing network (Brass, Schmitt, Spengler, & Gergely, 2007; Marsh & Hamilton, 2011; see also Chapter 2). As predictive eye movements were modulated by action kinematics but insensitive to action rationality, it is likely that the mirror neuron system is playing a key role in generating them.

The experiment reported in Chapter 4 was designed to establish whether rationality understanding is intact in individuals with ASC and to probe the integrity of the action observation and the mentalizing networks. I did this by applying the analysis method developed in Chapter 3 to a new dataset from adults with ASC and typically developing adults. The rationality detection markers established in the typically developing eye movement data from Chapter 3 were also present in individuals with ASC. This indicates that participants with ASC do automatically detect when an action is irrational. In addition to this finding, participants with ASC were able to explicitly rate the rationality of the actions and did not differ from typically developing participants in this regard. The realm in which typical and ASC participants did differ was when I looked at measures of attention to the action such as the time spent looking at the ball and the goal locations or the number of saccades from the ball to the goal. There were no differences in the latency of action prediction between groups and I replicate the finding from Chapter 3 which demonstrated that latency of goal prediction is modulated by the movement kinematics of an action and insensitive to action rationality.

Given that the ASC group showed very similar cognitive processes for rationality resolution when analysing their eye movements, I hypothesised that the neural differences previously reported during irrational action observation may be due to differences in social processing. The finding of reduced social attention in the eye movement data in individuals with ASC also supports this claim. Therefore, an interactive task which is dependent upon social responses to irrational actions may reveal larger group differences. In Chapter 5 I reported a study that used overimitation as a method to assess rationality understanding developmentally. I demonstrated that overimitation of irrational actions is both socially modulated and related to rationality understanding in typical development. Somewhat surprisingly this relationship revealed that overimitation of irrational actions actually increased with a child's understanding of how silly an action was. This suggests that overimitation of irrational actions does not indicate a lack of understanding about how an object works; instead it is a socially driven response to behave similarly to those around them. This study also demonstrates that overimitation can be used as a method to assess rationality comprehension and social responsiveness in combination.

Chapter 6 reported the results from the same task in children with ASC. As predicted, children with ASC were less likely to overimitate than their typically developing counterparts. Instead, children with ASC completed the tasks using the most efficient goal-directed means available, indicating a lack of social drive to affiliate or conform. Thus, at an implicit level, children with ASC have good rationality comprehension, effectively parsing out irrational actions from a demonstration and only including those actions which allow access to a given goal. However, children with ASC are less able to explicitly rate the rationality of the actions when compared to typically developing children. Instead, they give less certain responses and make more errors in their judgements. Overall, the findings from this study show that basic action comprehension and goal-directed imitation is intact in ASC but the social response to copy others faithfully is absent.

7.2 EMERGING QUESTIONS

Drawing together the results from each of these studies we can see some converging findings that answer some more general questions about how we understand others' irrational actions and whether understanding irrational actions is difficult for people with autism. I now address these questions, discussing how the data from the reported studies advance current thinking, and highlighting the areas that warrant more research.

7.2.1 HOW DO WE TYPICALLY UNDERSTAND IRRATIONAL ACTIONS?

In the introduction to this thesis I present the idea that irrational actions may be a useful tool in the investigation of how we understand the actions that we observe. Importantly, I proposed that irrational actions may be the key to studying the bridge between our understanding of *what* action has been performed and an understanding of *why* that action was performed. Indeed, the data presented in Chapter 2 shows that observing irrational actions can spontaneously engage both the mirror and mentalizing networks of the human brain in typically developing adults. This confirms previous findings (Brass et al., 2007; Marsh & Hamilton, 2011) but also advances our knowledge by demonstrating that this engagement was irrespective of the social form of the agent performing the action. Previously, both the human mirror system and the mentalizing system have been thought of as specific networks which are finely tuned to human action (Buccino et al., 2004; Press, 2011; Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004). However, recent work has shown that it is possible to attribute goals (Ramsey & Hamilton, 2010) and mental states (Castelli et al., 2000) to moving shapes with no human form using the mirror and mentalizing systems respectively. I now add to this literature by demonstrating that rationality can also be processed for non-human forms in the same neural networks. This is consistent with the arguments of Csibra who claims that the computation of rationality is conducted for human and non-human forms alike (Csibra, Gergely, Bíró, Koós, & Brockbank, 1999).

However, a question that remains unanswered from neuroimaging data is what are the cognitive processes that underlie irrational action understanding and why do irrational actions engage both mirror and mentalizing networks? Previously, this question has only briefly been touched upon with Brass et al. (2007) proposing that irrational actions prompt the observer to make inferences about why an action was performed inefficiently, thus additionally recruiting the mentalizing network.

To date, there is scant evidence to evaluate this claim although it seems that in some cases, observing an irrational action is not sufficient to activate the mentalizing network (Jastorff et al., 2010). A more comprehensive model of rationality understanding is required to elucidate the cognitive and neural processes that support irrational action understanding. The eye tracking data that I presented in Chapter 3 may help to break down the process of understanding irrational actions into discrete cognitive components that may be localised to different regions within the mirror and mentalizing networks. In the following paragraphs, I attempt to link different eye movement patterns to the cognitive processes that may be involved in understanding action rationality and the brain systems that support them.

During both rational and irrational action observation, participants spent a large amount of their time tracking the actions by following the ball as it moved across the screen. In addition, this action tracking increased when observing irrational actions. Action tracking may signal that participants are engaging in kinematic analysis of the action features. This kinematic analysis is crucial for evaluating the efficiency or rationality of an action and may also help the observer to make or test predictive inferences about the action goal. An ideal candidate brain system for these processes is the IFG. Previous research shows that the IFG is more active when participants are instructed to attend to the means by which an action is achieved (de Lange et al., 2008). In addition, the IFG is sensitive to variations in action kinematics despite identical action goals (Hamilton & Grafton, 2006) and this sensitivity to kinematic action features is reduced following TMS to the IFG (Pobric & Hamilton, 2006). Furthermore, the importance of the IFG for making predictive inferences about the outcome of an action are also highlighted (Kilner et al., 2004). For these reasons it is possible to draw a link between the increased action tracking seen in the eye movements and the increased IFG activity reported in the MRI results during irrational action observation.

A second feature which dominates looking time during both rational and irrational actions is the goal locations. Participants spent a large proportion of their time looking at the two possible locations where the ball could be placed. This visual analysis of the goals may reflect a process of goal identification. Indeed, there was an increase in looking time to the non-target goal during irrational actions. The increase in looking time in this case may reflect more effortful goal identification for these more complex actions. From previous studies we know that simple goal encoding is supported by the left anterior intraparietal sulcus, a portion of the left IPL (Hamilton & Grafton, 2006; Ramsey & Hamilton, 2010). This region did not differentiate action rationality in the MRI results reported in Chapter 2. Therefore, it seems that this region encodes simple goals and does not care about the unusual means by which these goals were achieved. This is consistent with previous reports (Hamilton & Grafton, 2008). However, I did identify an increase in activity in the right IPL during irrational actions. This increase was also reported in a previous study (Marsh & Hamilton, 2011). I propose that the additional engagement of the right IPL during irrational actions allows the observer to attribute goals to more complex actions and to identify those actions which violate the principle of rationality.

The third interesting pattern within the eye movement data was found when analysing the looking time to the barrier. In Chapter 3 I showed that participants spent more time looking at the barrier during rational, compared to irrational actions and that this increase was greater during human actions compared to ball actions. It is likely that this inspection of the environmental constraints that impact an action reflects mentalizing about why that action has been performed unusually (Elsner et al., 2013). Indeed, if we compare the pattern of responding in the mPFC across conditions to the pattern of time spent looking at the barrier across conditions, there is a good correspondence. Therefore, activity within the mPFC is likely to reflect rationality evaluation or resolution which can lead to an understanding of why an action has been performed.

A final interesting finding to come out of the eye tracking data is that predictive eye movements are not modulated by action rationality. This is somewhat surprising as irrational actions should be less predictable. However, this finding is consistent with a growing body of research which suggests that predictive eye movements are generated by the mirror system (see section 1.3). The studies in this thesis do not attempt to identify which component of the mirror system is generating these predictive eye movements. Both the IPL for its goal identification and the IFG for its role in making predictive inferences about actions would be good candidates. It is even possible that the two work in combination. Further research could use TMS to tease this apart.

I now aim to draw these components together into a neurocognitive model which sets out how irrational actions are identified and understood. According to Csibra's model of rationality understanding (Gergely & Csibra, 2003), detection of an irrational action relies on a comparison of the action goal and the means by which the action is achieved. Therefore, I propose that the IFG and the left IPL perform simple kinematic analysis and goal identification respectively. Only the combination of information from these systems is required to understand what an agent is doing if they are behaving rationally (see Figure 7.1). However, if there is a mismatch between the action kinematics and the goal such that the action was not performed in the most efficient way, additional processing is required for understanding. The engagement of the right IPL in these cases may reflect this rationality detection through the more complex identification of the goal. Following detection of an irrational action, the mentalizing system is then engaged in order to make inferences about why the action was performed in an unusual manner, taking into account the environmental constraints (see Figure 7.2).

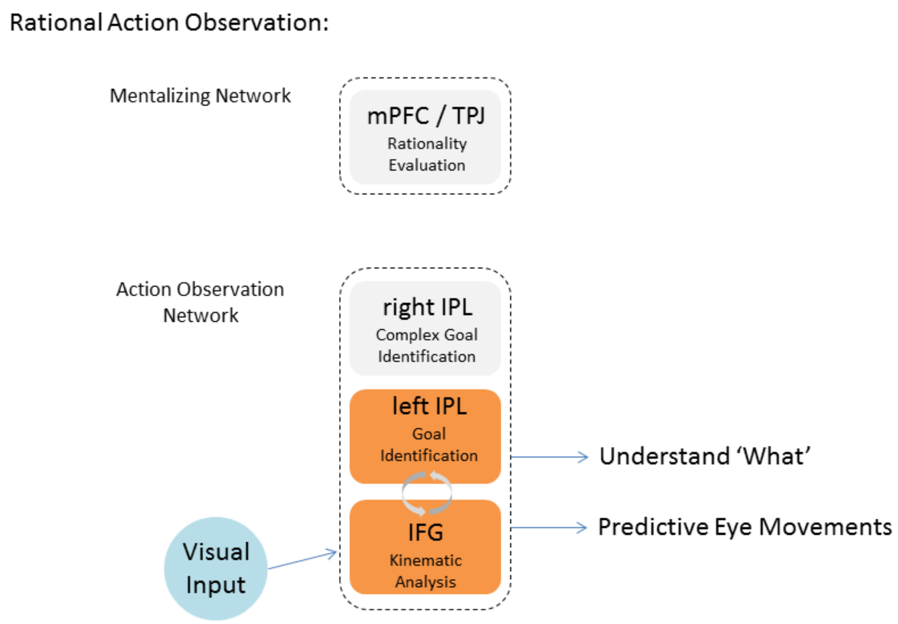

Figure 7.1 The neurocognitive processes involved in rational action observation

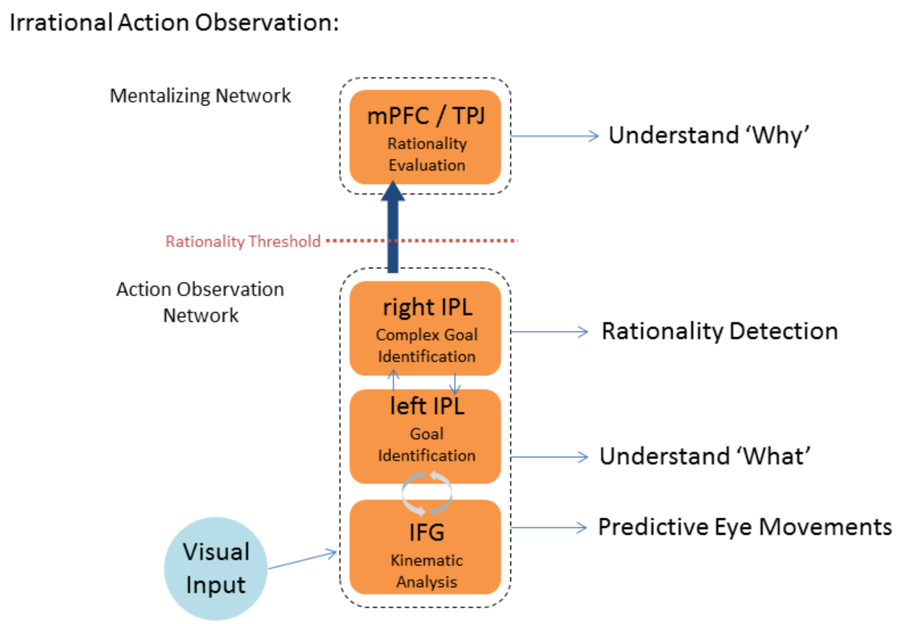

Figure 7.2 The neurocognitive processes involved in irrational action observation. During irrational actions the right IPL is additionally recruited when a mismatch between the action goal and the kinematics is detected. If the action is sufficiently irrational to surpass the rationality threshold, the mPFC is also recruited to evaluate why the action has been performed in this way.

However, one question that remains unanswered by the experiments in this thesis is how irrational does an action need to be before it is considered irrational and processed differently? From the comparison of analysis methods used on the fMRI data in Chapter 2, it is possible to see that the strength of activity in the action observation network correlates linearly with individual participants' ratings of rationality. However, the mentalizing network does not show this pattern of responding. Instead it seems that the mPFC only responds to categories of 'rational' and 'irrational'. It therefore seems plausible that within the action observation network there is some kind of rationality detection threshold which needs to be surpassed to additionally recruit the mentalizing network. Further work is needed to establish whether this is really the case and whether this threshold can be manipulated by social context or other action features.

7.2.2 WHAT IS THE TYPICAL SOCIAL RESPONSE TO IRRATIONAL ACTIONS?

We can learn a lot about a person by observing the way in which they behave. However, in most social situations we are also required to respond to others' behaviour in order to maintain a meaningful social interaction. The experiment reported in Chapter 5 of this thesis was designed to investigate imitative responses to irrational actions.

The primary finding from the study presented in Chapter 5 is that despite using simple, familiar objects and despite children demonstrating a good understanding of the rationality of the actions that they observed, children frequently persist in imitating irrational actions. This finding is inconsistent with causal reasoning explanations which suggest that children incorporate the irrational action into their understanding of how an object works. Instead, I propose that overimitation occurs for social reasons and could be a process of affiliation (Over & Carpenter, 2012) or conformity (Kenward et al., 2011; Kenward, 2012). One way in which this study advances current thinking about overimitation is the detailed investigation of the social cues which influence imitation. Clearly social presence has a huge influence on imitation behaviour as children of all ages copied irrational actions more when a demonstration was presented live compared to on a video. However, the exact nature of how this social presence boosts imitation behaviour is not fully understood. Originally I hypothesised that an increase in social engagement would lead to an increase in overimitation. This was true when comparing live and video demonstrations. However, when social engagement was increased with direct eye contact, overimitation actually decreased. Therefore, merely manipulating how socially engaging the demonstrator was does not impact overimitation in a simple way. Despite direct eye contact having the opposite effect to that which I expected, it is important and interesting to note that it still had a significant effect on behaviour. In order to explain how these social cues can have different effects on overimitation and to integrate these findings into my neurocognitive model of rationality understanding, I now draw on some ideas raised by an existing model which describes the social control of mimicry.

The theory of Social Top-down Response Modulation (STORM, Wang & Hamilton, (2012)) posits that social cues and context are integrated and evaluated within any given social interaction. Mimicry within the interaction is then subtly modulated by this evaluation in a strategic way that aids self-advancement. This is clearly demonstrated in a study in which participants who were instructed to affiliate with their interaction partner were more likely to mimic their partner than those who were given no instruction to affiliate (Lakin & Chartrand, 2003). Importantly for this model, social cues do not simply enhance mimicry but can also reduce mimicry under certain conditions in which mimicry could be detrimental to the social interaction. For example, participants displayed reduced mimicry of dominant behaviours that were performed by high-status individuals (Tiedens & Fragale, 2003). Thus the modulation of mimicry is bi-directional and subtly influenced by social information. Perhaps a similar mechanism of social evaluation takes place in an overimitation task and this can explain the enhancement and reduction of overimitation by different social cues that I reported in Chapter 5.

STORM theory also provides an account of how the control of mimicry is implemented in the brain (Wang & Hamilton, 2012). Mimicry is thought to rely on the mirror neuron system as a mechanism for observing an action and performing the same action. However, social signals, such as direct eye contact, person evaluation and context are simultaneously evaluated by the mentalizing network. This network then exerts top down control on the mirror system to guide and monitor mimicry. This top down control from the mPFC on the mirror system has been demonstrated in an fMRI study of mimicry, showing that direct eye contact during a mimicry task enhances the connectivity strength from the mPFC to the mirror system (Wang, Ramsey, & Hamilton, 2011). It is possible that a similar mechanism occurs during an overimitation task. Social context and rationality evaluation are processed in the mPFC and through its control over the mirror system, this region dictates whether faithful or selective imitation is most appropriate (see Figure 7.3). To date, the neural basis for overimitation has not been studied so this model remains speculative. However, recent developments in adult overimitation paradigms mean that this field of research is becoming more plausible for study.

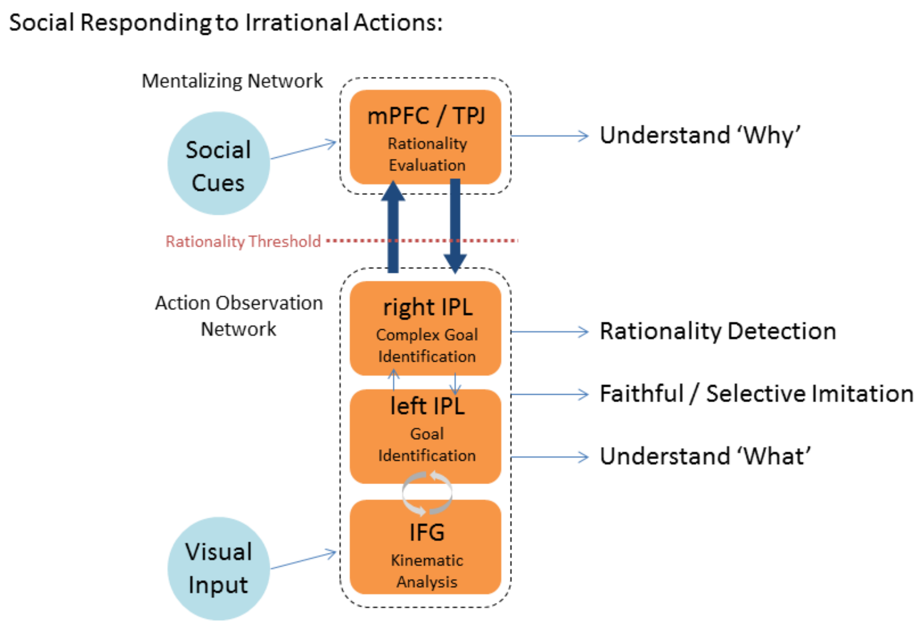

Figure 7.3 A neurocognitive model of the social response to irrational actions. Social cues and context are integrated with rationality evaluation in the mpfc. The mpfc then exerts top-down control over the action observation network to dictate whether faithful or selective imitation is employed.

There is one other interesting feature of the overimitation data which has not been discussed so far. This was the finding that not all of the irrational actions in the overimitation task reported in Chapter 5 were imitated to the same degree. In fact, the irrational action in the fan sequence was imitated significantly less than all others. This is interesting because it provides some evidence for the rationality threshold that I proposed in the previous section (7.2.1). Within the fan sequence, the actor gathered up a concertina of paper and tapped it on the table twice. This tapping action was unnecessary as it did not change the physical properties of the object however, the action is reasonably familiar or easier to rationalise because it is quite common to use this tapping action to realign separate pieces of paper. If this action was considered less irrational, perhaps not surpassing the rationality threshold required to induce the additional recruitment of the mentalizing network, this could explain why the action was treated differently. Further work needs to investigate how different types of irrational actions are understood and the role of familiarity of these actions can impact imitation behaviour in order to discover whether a rationality threshold truly exists.

7.2.3 DO INDIVIDUALS WITH AUTISM UNDERSTAND ACTION RATIONALITY?

One of the main aims of this thesis was to evaluate whether individuals with autism spectrum condition are able to detect when an action violates the principle of rationality and whether they comprehend irrational actions in the same ways as typically developing individuals. As reviewed in section 1.2.3, the study that sparked this line of investigation showed that when observing actions, activity within in the mPFC differentiated rational and irrational actions in typically developing participants. However, in matched autistic participants, activity within the mPFC was not modulated by the rationality of the actions (Marsh & Hamilton, 2011). I therefore determined to discover the reasons for this lack of differentiation. One possible reason could be that participants with ASC did not detect that an action was irrational and treated rational and irrational actions similarly. Alternatively, participants with ASC may not spontaneously make inferences about why an irrational action was performed, and therefore not engage the mPFC in a passive observation task. In the following sections I now evaluate each of these claims in light of the new evidence presented within this thesis.

One of the simplest ways to establish whether individuals with ASC are able to detect action rationality is to ask them to explicitly evaluate how rational an action was. In the adult eye-tracking study presented in Chapter 4, I did this by asking participants to rate each action based on six statements that reflected the rationality or efficiency of the actions. I found no group difference between typical and ASC adults on these explicit ratings for either rational or irrational actions. Furthermore, both groups rated irrational actions as less rational than the rational actions. This suggests that in adults with ASC, explicit rationality identification is intact. In support of this finding, the eye-tracking markers which reflected rationality detection in typically developing adults were also present in adults with ASC. I therefore conclude that the neural difference in the mPFC reported in Marsh & Hamilton (2011) cannot be due to a failure of adults with ASC to detect irrational actions.

A similar story is true for the children with ASC that took part in the overimitation experiment reported in Chapter 6. In this study explicit rationality understanding was assessed by calculating the differentiation of rational and irrational actions on a scale from ‘sensible’ to ‘silly’. Although children with ASC were poorer at discriminating the rational and irrational actions than the typically developing groups, their performance was still significantly above chance. Therefore, it seems that they are able to discriminate rationality in the right way (e.g. saying an irrational action is sillier than a rational action) but that they are less confident in their decisions or they had more difficulty using the rating scale. There is also evidence that children with ASC implicitly detect irrational actions because they effectively parse out the unnecessary actions that are demonstrated to them in each sequence and imitate in a goal-directed manner. Thus again I can conclude that even in children with ASC, the ability to detect an irrational action is spared.

If I now apply these findings to my neurocognitive model of rationality understanding (see Figure 7.4), it is likely that in ASC the action observation network is performing typically. This is evidenced by the eye-tracking markers which indicate that typical goal identification and kinematic analysis is occurring. Predictive eye movements to the action goals also corroborate this argument.

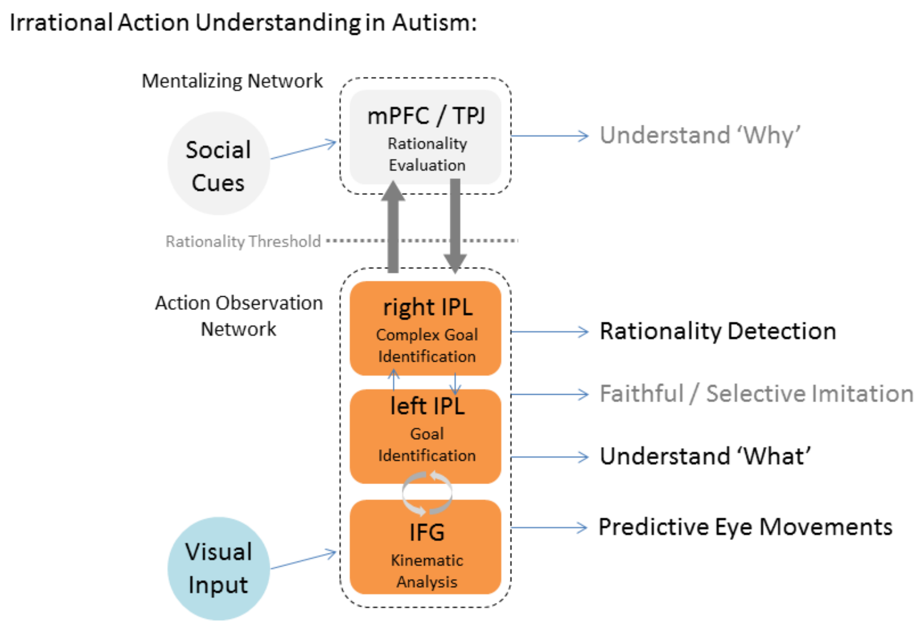

Figure 7.4 Rationality detection is intact in individuals with ASC (orange boxes). The deficits with irrational action understanding may originate in the mentalizing network (grey boxes). This could be due to a lack of rationality evaluation, a failure to integrate social cues with action knowledge or poorer top down control over the action observation network.

As I have managed to establish that individuals with ASC are able to detect action rationality, the next logical step is to evaluate whether they actually use this information to understand why an action has been performed differently. However, there is less clear evidence within this thesis to answer this question. From the eye-tracking data, we see that participants with ASC do spend time evaluating the environmental constraints upon an action by looking at the barrier. This may suggest that they are using the information about the rationality of the action to think about why it has been performed in that way. However, it is unclear whether this evaluation is done in a teleological fashion which precludes the need for mentalizing (Gergely & Csibra, 2003) or whether they are actually trying to guess the intentions of the agent based on their actions. Further work is needed to investigate whether participants with ASC can give rationalizations for others' odd behaviour when explicitly asked and whether they engage in these rationalizations spontaneously.

7.2.4 WHAT IS IMPAIRED IN AUTISM?

The studies in this thesis find very little evidence to suggest that individuals with autism are impaired when it comes to understanding action rationality. Specifically, there was no finding that could explain the lack of differential activation in the mPFC during the observation of irrational actions. Instead, the group differences that are common to both ASC experiments in this thesis seem to reflect a lack of social interest or social attention. For example, participants with ASC spent less time looking at the actions and this is reflected in measures of looking time to the hand, the goals and in the amount of missing data in the eye-tracking study. They also imitate less irrational actions in the overimitation study.

There are two possible explanations for these findings. Firstly, participants with ASC may have decreased motivation to be social (Chevallier et al., 2012) and so they are less interested in what the agent is doing because they have no desire to understand them. This can explain why they do not spend as much time looking at the actions or the goals. They may also be less motivated to please the experimenter and so they do not try so hard to maintain their attention during the tasks. This could explain both the increase in missing data and the reduction in imitation.

Alternatively, individuals with ASC may have be impaired in social top-down response modulation (Wang & Hamilton, 2012). If the mPFC plays a role in integrating social information such as social cues and social context and uses this information to guide social attention and behaviour, impairment in this top-down control could also explain these findings. For example, a lack of social attention guiding can explain why participants with ASC do not attend to the actions as closely as typically developing participants. This lack of social attention capture may also make the eye tracking task more boring for ASC participants, thus explaining the loss of data quality. Finally, failure of this control system may also prevent participants with ASC from engaging in overimitation behaviour.

Given the current evidence available it is difficult to promote either a social motivation explanation or a STORM explanation for the behaviour that we see in individuals with ASC. As yet, the social motivation hypothesis of ASC is poorly defined and therefore is difficult to test. However, it goes against a lot of anecdotal evidence that individuals with ASC do strive to engage in successful social interactions but fail during execution. However, STORM is easier to verify by testing the connectivity of the mPFC with the action observation network during an overimitation task. If indeed the mPFC is exerting control over the action observation network during overimitation in typically developing adults but not those with ASC then the STORM model has good explanatory power for these data.

7.3 FUTURE DIRECTIONS

There are a number of directions through which this field of research could progress. Most importantly I think it is necessary to test the models of rationality understanding that have been proposed in this thesis. Specifically, the concept of a rationality threshold that gates the additional recruitment of the mentalizing network needs more empirical support. One way in which to test this theory could be to use the overimitation phenomenon but apply it to a large number of different actions which may naturally vary with respect to their rationality. This natural variation could be dependent upon a number of dimensions such as action familiarity, predictability or the degree to which the action departs from its conventional course. If a rationality threshold does exist, we might expect that rational actions will be imitated faithfully, along with extremely irrational actions. However those actions that are not distinctly irrational would be imitated less. Therefore I predict that rates of imitation will form a u-shaped function with respect to the perceived rationality of an action. If this is the case, we could also apply this experimental paradigm to assess the shape of this function in individuals with ASC to determine whether their rationality threshold is altered in some way.

A second feature of the models presented here that needs further testing is the idea of the mentalizing system exerting top-down control on the action observation network during an overimitation task. Currently, neuroimaging data during overimitation has not been collected due to methodological issues with scanning children during interactive tasks. However, if a robust paradigm for overimitation in adults is developed then the possibility for testing this idea opens up. In particular it is important to look at the direction and strength of connectivity between the mentalizing and action observation networks in order to see whether similar control systems to those found in mimicry can be identified.

7.4 OVERALL CONCLUSIONS

In conclusion, understanding irrational actions engages both the action observation network and the mentalizing networks and so irrational actions can be used as a tool to probe the interaction of these systems. It seems that individuals with ASC are cognitively able to detect and understand irrational actions. Therefore, they do engage in teleological reasoning which is thought to be a precursor to mentalizing. Thus it is possible that individuals with ASC have the cognitive capacity to mentalize. However, it seems that difficulties with social modulation may interfere with this skill.

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