

Two systems for action comprehension in autism: mirroring and mentalizing

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Introduction

Imagine in a café, you order a cup of coffee and soon after, see the barista reaching toward the teabags. You quickly infer that she is about to make tea, but did she mis-hear your order, or is she serving someone else already? The ability to rapidly infer the goal of another person's action and make a guess about her underlying intention is critical in everyday social interaction.

Research on social cognition and the problem of understanding other minds has, over the last 30 years, been largely dominated by the idea of "Theory of mind," that is, the ability to consider the internal, mental states of other individuals. In Premack & Woodruff's (1978) original paper on Theory of Mind, they considered the problem of how to infer another actor's **intentions**, but research in the 30 years since then has been largely dominated by the question of how to infer an actor's **beliefs**. This is largely because false-belief tasks provide a clear-cut (and possibly the only) way to assess a participant's representational theory of mind

(Dennett, 1978). However, in the last few years, interest has grown in the brain and cognitive systems, which allow us to infer an actor's goal or intention by watching her actions.

The present chapter examines the problem of understanding goals and intentions in other minds, and the integrity of these systems in autism. In the first part, we summarize recent research on action understanding in the typical brain, distinguishing between brain networks associated with mirroring and those associated with mentalizing. In the second part, we examine current theories of action understanding in autism, in relation to recent behavioural and neuroimaging evidence. Finally, we evaluate the data in relation to the theories and consider some important future directions.

Part 1: Two networks in the typical brain

Neuroimaging studies over the last 15 years have identified two distinct brain networks which are reliably engaged when typical individuals engage in non-verbal social

interactions including observing actions (and possibly inferring goals), imitating actions, and considering other people's beliefs and desires. These two networks are associated with distinct cognitive functions and theoretical approaches. We briefly review the major and recent studies of each network.

The mirror neuron system

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, Ferrari, Gesierich, Rozzi, Chersi, & Rizzolatti, 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). Although 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, Zilles, Laird, & Eickhoff, 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). Secondly, Kilner, Neal, Weiskopf, Friston, & Frith, (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. Thus, these two studies provide the strongest evidence yet for populations of neurons in the human brain with the same mirror properties as those found in the macaque brain. Throughout this chapter, we 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 we 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, Giacomo, & Sinigaglia 2010). Similar mirror processes have been implicated in emotional contagion (Singer, Seymour, O'Doherty, Kaube, Dolan, & Frith, 2004; Wicker, Bruno, Keysers, Plailly, Royet, Gallese, et al., 2003). Some suggest that these processes may provide a fundamental step toward language (Rizzolatti, Giacomo, & Arbib 1998), empathy (Gallese 2003a) and even mentalizing (Gallese, Vittorio, & Goldman 1998) abilities. Thus, the mirror system has been hailed as a unifying basis for social cognition (Gallese, Vittorio, Keysers & Rizzolatti 2004). However, the evidence for some of these claims remains weak.

In the present section, we 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 inferior parietal lobule (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? When we see an action, for example, a child picking an apple, we can represent the action in multiple ways. It is possible to encode the shape of the child's hand (a kinematic feature), the object the child reaches toward (a goal feature) and the child's overall intention of picking the apple. 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 inferior frontal gyrus (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, Joyce, Flanagan, Frith, & Wolpert, 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; Hamilton & Grafton, 2006). BOLD responses in IFG are also sensitive to different hand apertures during grasping actions (Hamilton, & 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, Serventi, Simone, Rozzi, Ferrari, & Fogassi, 2011; Spinks, Kraskov, Brochier, Umiltà, & 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 & 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 with 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 vs. 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 a multi-voxel pattern analysis method that compared fine-grained activation of voxels across conditions. 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 with 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.

The mentalizing system

Mentalizing is the process of attributing mental states (beliefs, desires, and intentions) to another actor. 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. We focus here on the increasing number of studies that report engagement of this network during non-verbal or minimally verbal tasks in which participants attribute intentions or consider the longer term motivations underlying an action.

One of the earliest non-verbal 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, Schmitt, Spengler, & Gergely, (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 with 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 judged 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.

Further studies have refined our knowledge of when action understanding engages mentalizing brain systems. de Lange, Spronk, Willems, Toni, & Bekkering, (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.

Differential engagement of mentalizing and mirroring systems in the brain can also be driven by task demands. In an fMRI study by Spunt, Satpute, & Lieberman (2011), 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

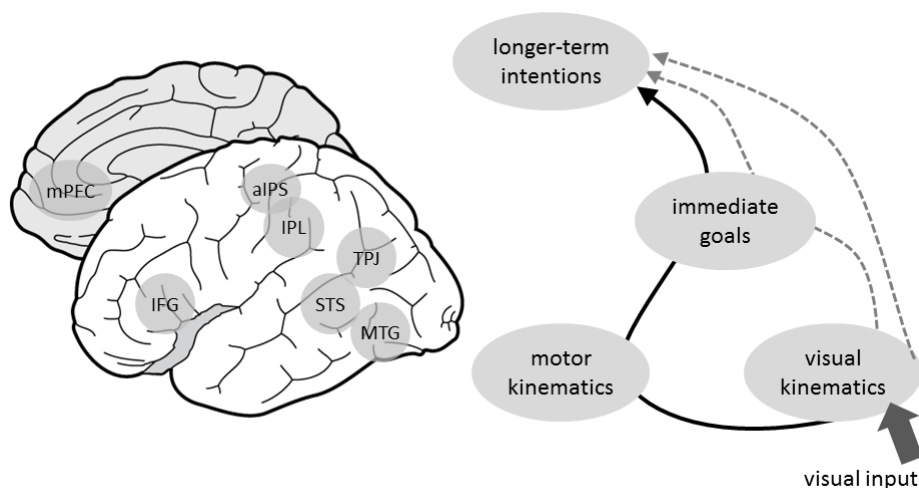


Figure 21.1 Brain and cognitive systems for action comprehension.

Left: Brain systems involved in mirroring (IFG: inferior frontal gyrus; IPL: inferior parietal lobule, aIPS: anterior intraparietal sulcus), mentalizing (mPFC: medial prefrontal cortex; TPJ: temporoparietal junction), and visual processing of human actions (MTG: middle temporal gyrus; STS: superior temporal sulcus). Right: A sketch of a cognitive model of action processing. Under a mirroring first model (black arrows) visual information processed (MTG/STS) is first matched onto the observers own motor system (IFG), before the goal of the action is extracted (aIPS/IPL) and then longer-term intentions can be defined (TPJ/mPFC). Under a visual inference model (dashed grey arrows), the visual processing (MTG/STS) is sufficient to allow immediate extraction of goals (aIPS/IPL) and longer term intentions (TPJ/mPFC) without the requirement for motor activation.

intentionality judgments, such as “they are recycling the can to save the environment.” Again, this study does not distinguish long-term intentions (“I want to recycle”) from beliefs that underlie the intention (“It is good to recycle”).

Summary

All of these studies suggest that the MNS is not the only brain system engaged in action comprehension, but that more complex tasks and situations may call on the mentalizing network. At least two ways in which mirroring and mentalizing systems might be related can be described (Hamilton, 2008). Under a “mirroring first” model (Figure 21. 1, black arrows), full engagement of frontal and parietal mirror regions is a necessary precondition for mentalizing about an observed action. In contrast, in a visual inference model (Csibra & Gergely, 2007), visual information alone is sufficient to determine the goal of an action and engage in mentalizing, and frontal mirror systems are not required. Understanding how the mirroring and mentalizing networks are related is an important area for future research. It is also a critical question in making sense of action understanding in autism. We consider the evidence for the integrity and relationship of mirroring and mentalizing processes in autism in the next section.

Part 2: Mirroring and mentalizing in 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 abnormal, 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 the next section, we examine each of these theories, then consider the evidence from each, looking at traditional behavioural tasks, implicit measures, such as eyetracking and EMG, and neuroimaging measures.

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, Leslie, & Frith, 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 these difficulties are symptoms of an inability to represent other people’s mental states (Frith, Morton, & Leslie, 1991), or to decouple mental states from reality (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 in which one actor has a false-belief about the location of an object. Participants are typically asked to say or point to the place where Maxi will look for his chocolate (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, Teglás, & 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. Recent data demonstrate that even high-functioning adults with Asperger's 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 abnormal 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 ongoing, and further developments in understanding the role of implicit theory of mind in autism are likely. For present purposes, we 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 abnormal processing in other social brain systems, for example the mirror system. We consider this question in the next section.

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). Children with autism may also have trouble with imitation tasks, as summarized in a meta-analysis (Williams, Whiten, & Singh, 2004). Some studies report abnormal brain responses in autistic children during imitation (Dapretto et al., 2006) and action observation (Nishitani, Avikainen, & Hari, 2004; Oberman, Hubbard, McCleery, Altschuler, Ramachandran, & Pineda, 2005). Based on these findings, it was suggested that dysfunction of the mirror system in children with autism might cause first a lack of imitation, and later difficulties in understanding other people's intentions or emotions in social situations (Iacoboni & Dapretto, 2006; Ramachandran & Oberman,

2006; Williams, Whiten, Suddendorf, & Perrett, 2001).

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 inferior parietal lobule (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 toward 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, Fabbri-Destro, Boria, Pieraccini, Monti, Cossu, 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 & 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).

Contrasting the mentalizing and broken mirror theories, some important differences emerge. The traditional mentalizing theory derives from a symbolic, abstract view of cognition (Leslie, 1987), while the broken mirror account is associated with an embodied approach which emphasizes the role of simulation in understanding others (Gallese, 2003b; Goldman, 2006). Similarly, the mentalizing theory places the primary deficit in “high level” reasoning about and representation of mental states, and assumes that abnormal social behaviour in simple situations are a consequence of this. Meanwhile, the broken mirror theory focuses on lower level problems with imitation and assumes that failure on theory of mind tasks arises because simpler simulation mechanisms are dysfunctional in autism. Neither theory attempts to account for all the characteristics of autism, including non-social problems such as repetitive behaviours or differences in perceptual processing that might be attributed to weak central coherence (Frith & Happé, 1994).

To test and discriminate between the mentalizing theory and the broken mirror theory, it is interesting to examine the realms where they overlap. In particular, goals and intentions are relevant to both theories. Mirror neurons in macaque monkeys respond only to goal-directed actions (Fogassi et al. , 2005; Gallese, et al. , 1996; Umiltà, Kohler, Gallese, Fogassi, Fadiga, Keysers, et al. , 2001), so goals are key to the original idea of mirror neuron function. The human mirror system seems to be more general, with some response even to actions without a goal, but goal-directed actions are a powerful stimulus which robustly activate this system (Gazzola, Rizzolatti, Wicker, & Keysers, 2007; Iacoboni, Molnar-Szakacs, Gallese, Buccino, Mazziotta, & Rizzolatti, 2005; Koski, Wohlschläger, Bekkering, Woods, Dubeau, Mazziotta, et al. , 2002). Damage to the human parietal mirror system, e. g. from stroke,

is known to cause difficulties with understanding and performing meaningful or goal-directed actions (Buxbaum, Kyle, & Menon, 2005). Therefore, a lack of goal understanding in autism is a key prediction of the broken mirror theory.

In this section, we evaluate the claims that either the whole mirror system or the ability to chain actions in a sequence is abnormal in autism. We focus mainly on recent studies that use implicit (eyetracking or EMG) measures of action comprehension and on neuroimaging studies. A large number of studies of imitation in autism have been reviewed in greater depth elsewhere (Hamilton, 2008; Southgate & Hamilton, 2008; Williams et al., 2001).

Behavioural studies of action understanding in autism

Multiple studies have reported poorer imitation performance in children with autism compared with typical children on general batteries of 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 there is a global imitation impairment in autism (Williams et al., 2004). However, more recent studies suggest autistic children successfully imitate when explicitly instructed to do so, whether imitating hand actions (Beadle-Brown, 2004) or facial expressions (McIntosh, Reichmann-Decker, Winkelman, & Wilbarger, 2006). They also show better performance in a highly structured imitation task than in a task requiring spontaneous imitation (Hepburn & Stone, 2006).

An interesting comparison in imitation studies is between imitation of a goal and imitation of kinematic features or action style, because these fall at different levels of the action hierarchy. Hobson and colleagues (Hobson & Hobson, 2008; Hobson & Lee, 1999) tested children with autism on a novel action imitation

task. For example, children were shown how to scrape two objects together to make a sound and were asked to copy. Children with autism were able to perform the same, goal directed action, but failed to mimic the style (loud or soft) with which the action was performed. 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 (Bekkering, Wohlschlaeger, & Gattis, 2000). In this task children were asked to copy an experimenter who touched one of two targets on the table in front of them. The experimenter sometimes made an ipsilateral movement of her hand to the nearest dot (e. g. left hand to left dot) and sometimes made a contralateral movement of her hand to the further dot (e. g. right hand to left dot). Both groups of children accurately imitated the action goal, i. e. they touched the appropriate dot on the table. More importantly, both typical and autistic children made systematic hand errors; when the demonstrator moved her hand across her body, the child correctly imitated the goal, but failed to use the appropriate hand (Hamilton, Brindley, & Frith, 2007). This is the pattern of behaviour taken by Bekkering and colleagues to be a signature of goal directed imitation. Children with autism are not imitating only the outcome of the action, but must be identifying the goal and selecting how to achieve that goal. Thus, the data provides evidence that both typical and autistic children have a goal hierarchy and can understand and imitate the goal of an adult's action. Furthermore, children with autism can and go beyond the immediately visible goal of an adult's action and imitate goals which they had not seen achieved. Two independent studies (Aldridge, Stone, Sweeney, & Bower, 2000; Carpenter, Pennington, & Rogers, 2001) found that children with autism completed the action of pulling apart the dumb-bell even when the adult

demonstrator had never successfully performed the action. In summary, it seems that autistic children are able to imitate 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.

Understanding of more complex goals or action sequences is being increasingly studied in autism, but results are contradictory. One study using a picture ordering task to compare understanding of mental state sequences to simpler goal-directed action sequences found that individuals with autism had no problems understanding and ordering the goal directed sequences (Baron-Cohen, Leslie, & Frith, 1986). However, a similar study found participants with autism did have trouble understanding object-directed action sequences (Zalla, Labruyere, & Georgieff, 2006), but surprisingly not interactive action sequences.

More recently, a study by Boria, Fabbri-Destro, Cattaneo, Sparaci, Sinigaglia, Santelli, 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.

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 (Flanagan & Johansson, 2003). In support of this claim, (Cannon & Woodward, 2008) demonstrated that predictive eye movements during action observation are disrupted by simultaneous performance of sequential finger movements, but not by the rehearsal of sequences of numbers. In a study of autistic 5-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

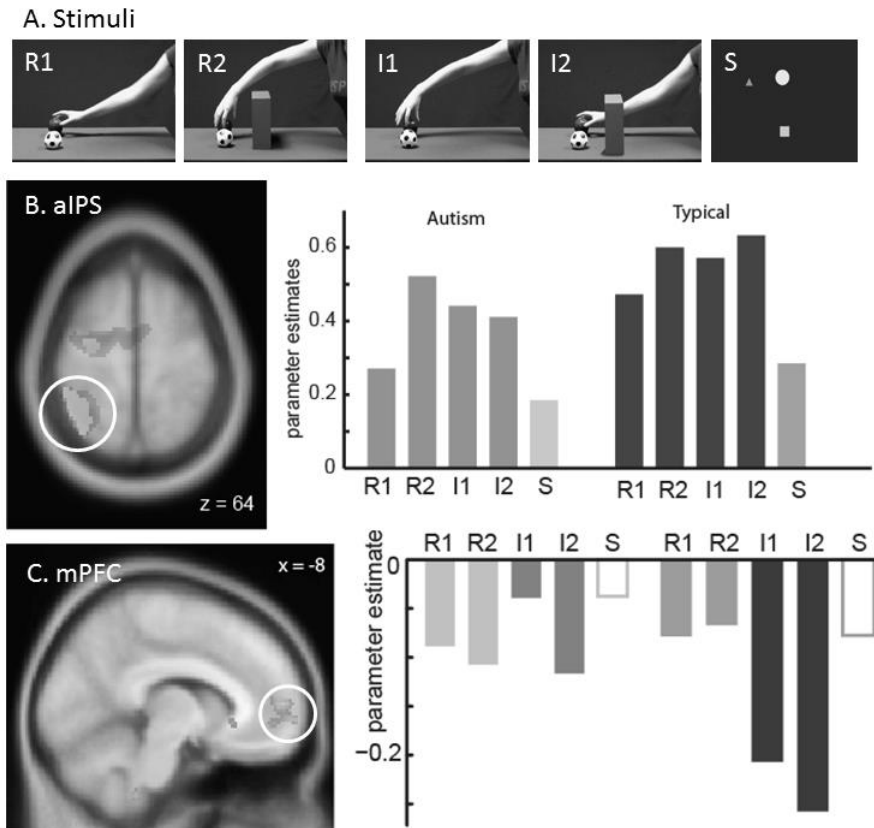


Figure 21. 2: Responses of mirroring and mentalizing brain systems in autism

(A) Still frames of the five movies types used in Marsh & Hamilton (2011). In each movie the hand started on the right, moved across to pick up an object and returned its original position. R1: rational action, R2: rational action with a barrier, I1: irrational action, I2: irrational action with a barrier, S: control movie showing three shapes, one of which moved linearly across the screen. (B) Activity in left aIPS was greater during the observation of hand actions compared with moving shapes in both autism and typical participants. (C) Activity in mPFC was sensitive to action rationality in the typical group, but not in the autism group.

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, Cattaneo, Boria, & Rizzolatti (2009) who used a similar

methodology to that of Johnson-Frey, McCarty, & Keen, (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.

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, Halligan, Kobayashi, Fregni, Tager-Flusberg, & Pascual-Leone (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 localization 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, Davies, Pfeifer, Scott, Sigman,

Bookheimer, 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.

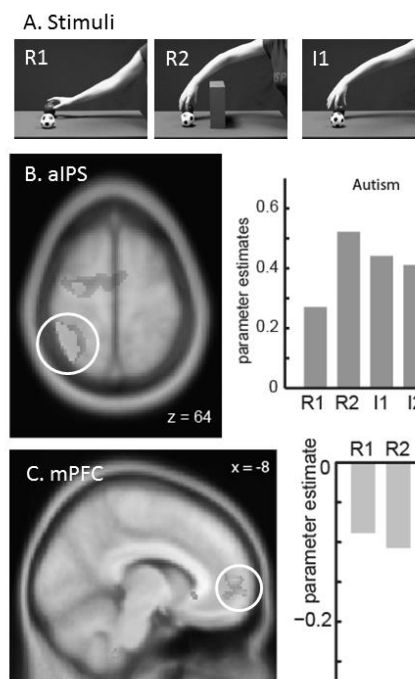
In a more comparable study of hand actions, Dinstein, Thomas, Humphreys, Minshew, Behrmann, & Heeger, (2010) asked participants to perform and observe sequences of simple hand postures during fMRI scanning. They report no group differences between autistic and typical participants during observation 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 (2011) 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 (Figure 21. 2, R1&R2) while in others the hand took an irrational route to reach the target object (Figure 21. 2, I1 & I2). 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 & Grafton (2006, 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.

Figure 2



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 with 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.

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. However, people with autism may have difficulty understanding sequences of actions, or chaining actions together and this area warrants further exploration.

Conclusions

From the studies reviewed in this chapter, no clear cut evidence emerges for a fundamental mirror system deficit in autism. Behavioural studies have shown that people with autism have a good understanding of action goals. Furthermore, two independent neuroimaging studies have reported that the parietal component of the mirror system is functioning typically in individuals with autism. Some evidence for the

action chaining account exists, but stringent neuroimaging studies need to test this further. 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.

An important future direction in this field is to establish the relationship between the mirror system and the mentalizing system. How does kinematic and goal information about actions translate into an understanding of intention? 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.

References

- Aldridge, M. A. , Stone, K. R. , Sweeney, M. H. , &Bower, T. G. R. (2000). Preverbal children with autism understand the intentions of others. *Developmental Science***3**:294–301.
- Amodio, D. , &Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *NatureReviews ofNeuroscience***7**(4): 268–77.
- Apperly, I. A. , &Butterfill, S. A. (2009). Do humans have two systems to track beliefs and belief-like states?*Psychological Review***116**(4):953–70.
- Avikainen, S, Kulomäki, T. , &Hari, R. (1999). Normal movement reading in Asperger subjects. *Neuroreport***10**(17):3467–70.
- Baron-Cohen, S. , Leslie, A. M. , &Frith, U. (1985). Does the autistic child have a ``theory of mind?'. *Cognition***21**:37–46.
- Baron-Cohen, S. , Leslie, A. , &Frith, U. (1986). Mechanical, behavioural and intentional understanding of picture stories in autistic children. *British Journal of Developmental Psychology***4**:113–25.
- Beadle-Brown, J. (2004). Elicited imitation in children and adults with autism : the effect of different types of actions. *Journal of Applied Research in Intellectual Disabilities*(1991), **17**:37–48.
- Bekkering, H. , Wohlschlaeger, A. , &Gattis, M. (2000). Imitation of Gestures in Children is Goal-directed. *Quarterly Journal of Experimental Psychology***53**(1):153–64.
- Bonini, L. , Serventi, F. U. , Simone, L. , Rozzi, S. , Ferrari, P. F. , &Fogassi, L. (2011). Grasping neurons of monkey parietal and premotor cortices encode action goals at distinct levels of abstraction during complex action sequences. *Journal of neuroscience : Official Journal of the Society for Neuroscience***31**(15):5876–86.
- Boria, S. , Fabbri-Destro, M. , Cattaneo, L. , Sparaci, L. , Sinigaglia, C. , Santelli, E. , Cossu, G. , &Rizzolatti, G. (2009). Intention understanding in autism. *PloS one***4**(5):e5596.
- Brass, M. , Schmitt, R. M. , Spengler, S. , &Gergely, G. (2007). Investigating action understanding: inferential processes vs. action simulation. *Current Biology***17**:2117–121.
- Buccino, G, Binkofski, F. , &Riggio, L. (2004). The mirror neuron system and action recognition. *Brain and Language***89**:370–6.
- Buxbaum, L. J. , Kyle, K. M. , &Menon, R. (2005). On beyond mirror neurons: internal representations subserving imitation and recognition of skilled object-related actions in humans. *Brain Research. Cognitive Brain Research***25**(1):226–39.

- Cannon, E. N. , &Woodward, A. L. (2008). Action anticipation and interference : A test of prospective gaze, Paper presented at the30th Annual Conference of the Cognitive Science Society.
- Carpenter, M. , Pennington, B. F. , &Rogers, S. J. (2001). Understanding of others' intentions in children with autism. *Journal of Autism and Developmental Disorders***31**(6):589–99. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/11814270>
- Caspers, S. , Zilles, K. , Laird, A. R. , &Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage***50**(3):1148–67.
- Castelli, F. , Frith, C. , Happé, F. , &Frith, U. (2002). Autism, Asperger syndrome and brain mechanisms for the attribution of mental states to animated shapes. *Brain : Journal of Neurology***125**(Pt 8):1839–49. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/12135974>
- Castelli, F, Happé, F. , Frith, U. , &Frith, C. (2000). Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. *NeuroImage***12**(3):314–25.
- Cattaneo, L. , Fabbri-Destro, M. , Boria, S. , Pieraccini, C. , Monti, A. , Cossu, G. , &Rizzolatti, G. (2007). Impairment of actions chains in autism and its possible role in intention understanding. *Proceedings of the National Academy of Sciences, USA***104**(45):17825–30.
- Csibra, G. , &Gergely, G. (2007). Obsessed with goals: Functions and mechanisms of teleological interpretation of actions in humans. *Acta Psychologica***124**(1):60–78.
- Dapretto, M. , Davies, M. S. , Pfeifer, J. H. , Scott, A. A. , Sigman, M. , Bookheimer, S. Y. , &Iacoboni, M. (2006). Understanding emotions in others: mirror neuron dysfunction in children with autism spectrum disorders. *Nature Neuroscience***9**(1):28–30.
- de Lange, F. P. , Spronk, M. , Willems, R. M. , Toni, I. , & Bekkering, H. (2008). Complementary systems for understanding action intentions. *Current biology: CB***18**(6):454–7.
- Decety, J. , Chaminade, T. , Grèzes, J. , & Meltzoff, A. N. (2002). A PET exploration of the neural mechanisms involved in reciprocal imitation. *NeuroImage***15**(1): 265–72.
- Dennett, D. (1978). Beliefs about beliefs. *Behavioral and Brain Sciences***4**, 568–70.
- di Pellegrino, G. , Fadiga, L. , Fogassi, L. , Gallese, V. , & Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Experimental Brain Research***91**: 176–80.
- Dinstein, I. , Thomas, C. , Humphreys, K. , Minshew, N. , Behrmann, M. , &Heeger, D. J. (2010). Normal movement selectivity in autism. *Neuron***66**(3):461–9.
- Fabbri-Destro, M. , Cattaneo, L. , Boria, S. , &Rizzolatti, G. (2009). Planning actions in autism. *Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation cérébrale***192**(3):521–5.
- Falck-Ytter, T. (2010). Young children with autism spectrum disorder use predictive eye movements in action observation. *Biology Letters***6**(3):375–8.
- Flanagan, R. J. , &Johansson, R. (2003). Action plans used in action observation. *Nature***424**:769–71.
- Fletcher, P. C. , Happe, F. , Frith, U. , Baker, S. C. , Dolan, R. J. , Frackowiak, R. S. J. , &Frith, C. D. (1995). Other minds in the brain: a functional imaging study of “theory of mind” in story comprehension. *Cognition***57**: 109–28.
- Fogassi, L. , Ferrari, P. F. , Gesierich, B. , Rozzi, S. , Chersi, F. , &Rizzolatti, G. (2005). Parietal lobe: from action organization to intention understanding. *Science***308**(5722):662–7.
- Frith, U. (2001). Mind blindness and the brain in autism. *Neuron***32**(6):969–79. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/11754830>
- Frith, U. (2012). Why we need cognitive explanations of autism, 38 Bartlett Lecture 2010. *Quarterly Journal of Experimental Psychology (Hove)***65**(11):2073–92.
- Frith, U, &Happé, F. (1994). Autism: beyond “theory of mind.” *Cognition***50**(1–3):115–32. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/12212920>

- Frith, U, Morton, J. , &Leslie, A. (1991). The cognitive basis of a biological disorder: autism. *Trends in Neurosciences***14**(10):433–8.
- Gallagher, H. L. , &Frith, C. D. (2003). Functional imaging of “theory of mind.” *Trends in Cognitive Sciences***7**(2):77–83. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/12584026>
- Gallese, V. (2003a). The roots of empathy: the shared manifold hypothesis and the neural basis of intersubjectivity. *Psychopathology***36**(4):171–80.
- Gallese, V. (2003b). The manifold nature of interpersonal relations: the quest for a common mechanism. *Philosophical Transactions of the Royal Society of London, B, Biological Sciences***358**(1431):517–28.
- Gallese, V, Fadiga, L. , Fogassi, L. , &Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain***119**:593–609.
- Gallese, V. , &Goldman, A. (1998). Mirror neurons and the mind-reading. *Trends in Cognitive Sciences***2**(12):493–501.
- Gallese, V. , Keysers, C. , &Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences***8**(9):396–403.
- Gazzola, V. , Rizzolatti, G. , Wicker, B. , &Keysers, C. (2007). The anthropomorphic brain: the mirror neuron system responds to human and robotic actions. *NeuroImage***35**(4):1674–84.
- Goldman, A. (2006). *Simulating Minds*. Oxford: Oxford University Press.
- Grill-Spector, K. , Henson, R. , &Martin, A. (2006). Repetition and the brain: neural models of stimulus-specific effects. *Trends in Cognitive Sciences***10**(1):14–23.
- Hamilton, A. F. de C, Brindley, R. M. , &Frith, U. (2007). Imitation and action understanding in autistic spectrum disorders: How valid is the hypothesis of a deficit in the mirror neuron system? *Neuropsychologia***45**(8):1859–68.
- Hamilton, A. F. de C. , &Grafton, S. T. (2006). Goal representation in human anterior intraparietal sulcus. *Journal of Neuroscience***26**:1133–7.
- Hamilton, A. F. de C. , &Grafton, S. T. (2008). Action outcomes are represented in human inferior frontoparietal cortex. *Cerebral Cortex***18**(5):1160–8.
- Hamilton, A. F. de C. , &Grafton, S. T. (2009). Repetition suppression for performed hand gestures revealed by fMRI. *Human Brain Mapping***30**(9):2898–906. doi:10.1002/hbm.20717
- Hamilton, A. F. de C. , Joyce, D. W. , Flanagan, J. R. , Frith, C. D. , &Wolpert, D. M. (2007). Kinematic cues in perceptual weight judgement and their origins in box lifting. *Psychological Research***71**(1):13–21.
- Hampton, A. N. , &Bosschaerts, P. (2008). Neural correlates of mentalizing-related computations during strategic interactions in humans. *Signals***105**(18):6741–6.
- Happé, F. G. (1994). An advanced test of theory of mind: understanding of story characters’ thoughts and feelings by able autistic, mentally handicapped, and normal children and adults. *Journal of Autism and Developmental Disorders***24**(2):129–54. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/8040158>
- Happé, F. G. (1995). The role of age and verbal ability in the theory of mind task performance of subjects with autism. *Child Development***66**(3):843–55. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/7789204>
- Heilman, K. M. , Rothi, L. J. , &Valenstein, E. (1982). Two forms of ideomotor apraxia. *Neurology***32**(4):342–6.
- Hepburn, S. L. , &Stone, W. L. (2006). Longitudinal research on motor imitation in autism. *Imitation and the Social Mind*. New York: Guildford Press.

- Hickok, G. (2009). Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *Journal of Cognitive Neuroscience***21**(7):1229–43.
- Hobson, R. P. , &Hobson, J. A. (2008). Dissociable aspects of imitation: a study in autism. *Journal of Experimental Child Psychology***101**(3):170–85.
- Hobson, R. P. , &Lee, A. (1999). Imitation and identification in autism. *Journal of Child Psychology and Psychiatry, and Allied Disciplines***40**(4):649–59. Available at:<http://www.ncbi.nlm.nih.gov/pubmed/10357170>
- Iacoboni, M. (1999). Cortical mechanisms of human imitation. *Science***286**(5449):2526–8.
- Iacoboni, M, &Dapretto, M. (2006). The mirror neuron system and the consequences of its dysfunction. *Nature Reviews of Neuroscience***7**(12):942–51.
- Iacoboni, M. , Molnar-Szakacs, I. , Gallese, V. , Buccino, G. , Mazziotta, J. C. , &Rizzolatti, G. (2005). Grasping the intentions of others with one’s own mirror neuron system. *PLoS Biology***3**(3):e79.
- Johnson-Frey, S. , McCarty, M. , &Keen, R. (2004). Reaching beyond spatial perception: Effects of intended future actions on visually guided prehension. *Visual Cognition***11**(2):371–99.
- Kilner, J. M. , Neal, A. , Weiskopf, N. , Friston, K. J. , &Frith, C. D. (2009). Evidence of mirror neurons in human inferior frontal gyrus. *Journal of Neuroscience***29**(32):10153–9.
- Koski, L. , Wohlschläger, A. , Bekkering, H. , Woods, R. P. , Dubeau, M-C. , Mazziotta, J. C. , &Iacoboni, M. (2002). Modulation of motor and premotor activity during imitation of target-directed actions. *Cerebral Cortex***12**(8):847–55. Available at:<http://www.ncbi.nlm.nih.gov/pubmed/12122033>
- Kovacs, A. M. , Teglas, E. , &Endress, A. D. (2010). The social sense: Susceptibility to others’ beliefs in human infants and adults. *Science***330**(6012):1830–4.
- Leslie, A. M. (1987). Pretense and representation : The origins of “theory of mind.” *Cognitive Development***9**(4):412–26.
- Marsh, L. , &Hamilton, A. (2011). Dissociation of mirroring and mentalizing systems in autism. *NeuroImage***56**(3):1511–19.
- McIntosh, D. N. , Reichmann-Decker, A. , Winkelman, P. , &Wilbarger, J. L. (2006). When the social mirror breaks: deficits in automatic, but not voluntary, mimicry of emotional facial expressions in autism. *Developmental Science***9**(3):295–302.
- Ming, X. , Brimacombe, M. , &Wagner, G. C. (2007). Prevalence of motor impairment in autism spectrum disorders. *Brain &Development***29**(9):565–70.
- Nishitani, N. , Avikainen, S. , &Hari, R. (2004). Abnormal imitation-related cortical activation sequences in Asperger’s syndrome. *Annals of Neurology***55**(4):558–62.
- Oberman, L. M. , Hubbard, E. M. , McCleery, J. P. , Altschuler, E. L. , Ramachandran, V. S. , &Pineda, J. A. (2005). EEG evidence for mirror neuron dysfunction in autism spectrum disorders. *Brain Research. Cognitive Brain Research***24**(2):190–8.
- Onishi, K. H. , &Baillargeon, R. (2005). Do 15-month-old infants understand false beliefs?*Science***308**(5719):255–8.
- Oosterhof, N. N. , Wiggett, A. J. , Diedrichsen, J. , Tipper, S. P. , &Downing, P. E. (2010). Surface-based information mapping reveals crossmodal vision-action representations in human parietal and occipitotemporal cortex. *Journal of Neurophysiology***104**(2):1077–89.
- Pascual-Leone, A. , Walsh, V. , &Rothwell, J. (2000). Transcranial magnetic stimulation in cognitive neuroscience—virtual lesion, chronometry, and functional connectivity. *Current Opinion in Neurobiology***10**(2):232–7. Available at:<http://www.ncbi.nlm.nih.gov/pubmed/10753803>
- Pobric, G. , &Hamilton, A. F. DeC. (2006). Action understanding requires the left inferior frontal cortex. *Current Biology***16**:424–9.
- Premack, D. , &Woodruff, G. (1978). Does the chimpanzee have a theory of mind?*Behavioral and Brain Sciences***4**:515–26.

- Ramachandran, B. V. S. , &Oberman, L. M. (2006). Broken mirrors: A theory of autism. *Scientific American***295**(5):62–9.
- Ramsey, R. , &Hamilton, A. F. DeC. (2010). How does your own knowledge influence the perception of another person’s action in the human brain?*Social Cognitive and Affective Neuroscience***7**(2):242–51.
- Rizzolatti, G. , &Arbib, M. A. (1998). Language within our grasp. *Trends in Neuroscience***21**(5):188–94.
- Rizzolatti, G. , &Fabbri-Destro, M. (2010). Mirror neurons: from discovery to autism. *Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation cérébrale*, **200**(3–4), 223–37.
- Rizzolatti, G. , &Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nature Reviews Neuroscience***11**(4):264–74.
- Rizzolatti, G. , Fabbri-Destro, M. , &Cattaneo, L. (2009). Mirror neurons and their clinical relevance. *Neurology***5**(1):24–34
- Saxe, R. , &Powell, L. J. (2006). It’s the thought that counts: specific brain regions for one component of theory of mind. *Psychological Science***17**(8): 692–9.
- Saxe, R. , &Kanwisher, N. (2003). People thinking about thinking people The role of the temporo-parietal junction in “theory of mind.” *NeuroImage***19**:1835–42.
- Senju, A. , Southgate, V. , White, S. , &Frith, U. (2009). Mindblind eyes: an absence of spontaneous theory of mind in Asperger syndrome. *Science***325**(5942):883–5.
- Singer, T. , Seymour, B. , O’Doherty, J. , Kaube, H. , Dolan, R. J. , &Frith, C. D. (2004). Empathy for pain involves the affective, but not sensory components of pain. *Science***303**:1157–62.
- Southgate, V. , &Hamilton, A. F. De C. (2008). Unbroken mirrors: Challenging a theory of autism. *Trends in Cognitive Sciences***12**(6):225–9.
- Spinks, R. L. , Kraskov, A. , Brochier, T. , Umiltà, M. A. , &Lemon, R. N. (2008). Selectivity for grasp in local field potential and single neuron activity recorded simultaneously from M1 and F5 in the awake macaque monkey. *Journal of Neuroscience : Official Journal of the Society for Neuroscience***28**(43):10961–71.
- Spunt, R. P. , Satpute, A. B. , &Lieberman, M. D. (2011). Identifying the what, why, and how of an observed action: an fMRI study of mentalizing and mechanizing during action observation. *Journal of Cognitive Neuroscience***23**(1):63–74.
- Théoret, H. , Halligan, E. , Kobayashi, M. , Fregni, F. , Tager-Flusberg, H. , &Pascual-Leone, a. (2005). Impaired motor facilitation during action observation in individuals with autism spectrum disorder. *Current Biology CB***15**(3):R84–5.
- Umiltà, M. a, Kohler, E. , Gallese, V. , Fogassi, L. , Fadiga, L. , Keysers, C. , &Rizzolatti, G. (2001). I know what you are doing. a neurophysiological study. *Neuron***31**(1):155–65. Available at:<http://www.ncbi.nlm.nih.gov/pubmed/11498058>
- Van Overwalle, F. (2009). Social cognition and the brain: a meta-analysis. *Human Brain Mapping***30**(3):829–58.
- Wicker, B. , Keysers, C. , Plailly, J. , Royet, J. P. , Gallese, V. , &Rizzolatti, G. (2003). Both of us disgusted in My insula: The common neural basis of seeing and feeling disgust. *Neuron***40**(3):655–64. Available at:<http://www.ncbi.nlm.nih.gov/pubmed/14642287>
- Williams, J. H. G. , Whiten, A. , &Singh, T. (2004). A systematic review of action imitation in autistic spectrum disorder. *Journal of Autism and Developmental Disorders***34**(3):285–99. Available at:<http://www.ncbi.nlm.nih.gov/pubmed/15264497>
- Williams, J. H. , Whiten, A. , Suddendorf, T. , &Perrett, D. I. (2001). Imitation, mirror neurons and autism. *Neuroscience Biobehavioral Review***25**(4):287–95.
- Wimmer, H. , &Perner, J. (1983). Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children’s understanding of deception. *Cognition***13**:103–28.

- Yoshida, W. , Seymour, B. , Friston, K. J. , & Dolan, R. J. (2010). Neural mechanisms of belief inference during cooperative games. *Journal of Neuroscience***30**(32):10744–51.
- Young, L. , Dodell-Feder, D. , & Saxe, R. (2010). What gets the attention of the temporo-parietal junction? An fMRI investigation of attention and theory of mind. *Neuropsychologia***48**(9):2658–64.
- Zalla, T. , Labruyere, N. , & Georgieff, N. (2006). Goal-directed action representation in autism. *Journal of Autism Development and Disorders***36**(4):527–40.