Neuropsychologia 45 (2007) 1859–1868

NEUROPSYCHOLOGIA

www.elsevier.com/locate/neuropsychologia

Imitation and action understanding in autistic spectrum disorders: How valid is the hypothesis of a deficit in the mirror neuron system?

Antonia F. de C. Hamilton [a,*], Rachel M. Brindley [b], Uta Frith [b]

[a] Department of Psychological and Brain Sciences, Dartmouth College, Hanover, NH, United States
[b] Institute of Cognitive Neuroscience, University College London, London, United Kingdom

Received 8 September 2006; received in revised form 22 November 2006; accepted 30 November 2006
Available online 17 January 2007

Abstract

The motor mirror neuron system supports imitation and goal understanding in typical adults. Recently, it has been proposed that a deficit in this mirror neuron system might contribute to poor imitation performance in children with autistic spectrum disorders (ASD) and might be a cause of poor social abilities in these children. We aimed to test this hypothesis by examining the performance of 25 children with ASD and 31 typical children of the same verbal mental age on four action representation tasks and a theory of mind battery. Both typical and autistic children had the same tendency to imitate an adult's goals, to imitate in a mirror fashion and to imitate grasps in a motor planning task. Children with ASD showed superior performance on a gesture recognition task. These imitation and gesture recognition tasks all rely on the mirror neuron system in typical adults, but performance was not impaired in children with ASD. In contrast, the ASD group were impaired on the theory of mind tasks. These results provide clear evidence against a general imitation impairment and a global mirror neuron system deficit in children with autism. We suggest this data can best be understood in terms of multiple brain systems for different types of imitation and action understanding, and that the ability to understand and imitate the goals of hand actions is intact in children with ASD.

Keywords: Autism; Imitation; Mirror neuron system; Goal; Action; Social cognition

1. Introduction

The ability to understand another person's action and, if needed, imitate that action, is a core component of human social behaviour which can be observed even in young children. Imitation skills have attracted particular attention in the search for the underlying causes of the social difficulties that characterize autism. In recent years, a number of investigators have reported abnormal performance by children with ASD on a variety of imitation tasks (Williams, Whiten, & Singh, 2004). Interest has grown further since the discovery of a mirror neuron system (MNS) underlying imitation performance in typical adults (Buccino et al., 2004; Iacoboni et al., 1999; Rizzolatti & Craighero, 2004), and it has been proposed that this MNS may play a critical role in autism (Williams, Whiten, Suddendorf, & Perrett, 2001).

Based on work in both humans and monkeys, the MNS has been defined as the regions in the inferior parietal and inferior frontal cortex which respond both when an individual performs an action and when he observes another person's action (Rizzolatti & Craighero, 2004). In this way, the MNS allows matching between the actions of the self and of others, and supports inference of the goals and intentions of other people (Hamilton & Grafton, 2006). Thus, at least two distinct behaviours, imitation and action understanding, are supported by the mirror neuron system. The ability to understand actions and goals using the mirror neuron system might in turn provide a basis for variety of social skills including theory of mind (Gallese & Goldman, 1998; Gallese, Keysers, & Rizzolatti, 2004). Children with autism are known to have poor social skills, problems with imitation (Williams et al., 2004) and problems with theory of mind (Baron-Cohen, Leslie, & Frith, 1985). It has been suggested that these children might have an abnormal mirror neuron system, and that this deficit is the cause of observed weaknesses in imitation performance, poor theory of mind skills and impaired social cognition in autism (Williams et al., 2001).

* Corresponding author. Tel.: +1 603 646 0175.
E-mail address: antonia.hamilton@dartmouth.edu (A.F.de.C. Hamilton).

0028-3932/$ – see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.neuropsychologia.2006.11.022

This is an ambitious hypothesis, which can be better understood as three linked proposals: (1) The MNS supports imitation and inferences of goals and intentions; (2) This MNS is deficient in children with ASD, leading to impaired performance on imitation tasks and impaired inferences of goals and intentions; (3) These low level imitation/goal inference impairments in ASD are a causal factor in poor theory of mind and social abilities in these children. There is evidence for part (1) from neuroimaging of typical adults (reviewed in Rizzolatti & Craighero, 2004), while part (3) remains speculative. The aim of the current paper is to examine part (2), the link between autism and the ability to infer and imitate goals using the mirror neuron system; we will refer to this as the autistic mirror neuron dysfunction (AMND) hypothesis.

We will begin by restricting our account to the ‘classical’ motor MNS which matches performed and observed hand actions (Rizzolatti & Craighero, 2004) and is localised in the inferior frontal gyrus and inferior parietal lobule in the human brain. There is evidence for mirroring as a more general principle which applies to tactile sensation (Keysers et al., 2004) and to emotions such as disgust (Wicker et al., 2003) and pain (Singer et al., 2004). Though these empathic mirroring systems might have a role in autism, we will not discuss them here. Instead, we focus solely on the motor MNS which was first discovered in macaque monkeys (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) and has now been extensively studied in humans, and will discuss our behavioural tasks with reference to neuroimaging studies of this system.

The motor MNS in the human brain supports both the imitation of human actions (Iacoboni et al., 1999) and inferences about the goals or intentions underlying observed actions (Fogassi et al., 2005; Hamilton & Grafton, 2006). Imitation of other’s movements is particularly important in the process of learning a new motor skill, where the MNS has a prominent role (Buccino et al., 2004). Furthermore, inferring action goals is a basic component of non-verbal social interaction. For example, on seeing your companion at dinner reach towards the salt cellar, you would infer that he wants some salt and might reach out and pass it to him. Recent work demonstrates that the goals of other people’s actions are represented in the human anterior intraparietal sulcus and inferior parietal cortex (Hamilton & Grafton, 2006), which is part of the MNS.

Thus, two simple social-motor behaviours – imitation and goal inference – seem to rely on the human MNS. The autistic mirror neuron dysfunction (AMND) hypothesis predicts that these behaviours should be abnormal in children with autism. We report here the results of four experiments testing imitation of goals, mirror imitation, grasp planning and gesture recognition in children with and without autism. The same group of children participated in all experiments and we assess the overall impact of our results on the AMND theory in the general discussion.

2. General methods

2.1. Participants

Twenty-five children with an independent clinical diagnosis of autism or autism spectrum disorder were recruited from schools in London and the south east of England specialising in the education of children with autism. This group had a mean chronological age of 8 years 1 month, and a mean verbal mental age (VMA) of 4 years 3 months (Table 1). VMA was established using the British Picture Vocabulary Scale (Dunn, Dunn, Whetton, & Burley, 1997). The autistic group were severely impaired in their ability to attribute mental states to others, as measured by a theory of mind battery described below. Hand preference for each child was assessed by three tests: writing their name on a piece of paper, picking up a hollow tube to look through it, and pretending to brush their teeth, and the hand used on the majority of tests was deemed to be the preferred hand.

We compared these children to 31 control children with no diagnosed special needs who were recruited from nurseries and primary schools in and around London. Control children were also assessed for VMA using the British Picture Vocabulary Scale and for handedness. Characteristics of the groups are summarised in Table 1. The control group were matched for VMA with the ASD group and completed all the same tasks as the ASD group. All the children, their parents and their schools gave consent to take part in this study, which was approved by the local ethics committee.

2.2. Theory of mind testing

Every child was tested on a battery of theory of mind tests from four sources. We used tests of diverse desires, diverse beliefs, knowledge access, contents false belief (smarties) and explicit false beliefs (Wellman & Liu, 2004), as well as the classic Sally-Ann task (Baron-Cohen et al., 1985), an interpretive diversity task (cow task, Luckett, Powell, Messer, Thornton, & Schulz, 2002) and a penny hiding task (Devries, 1970). These are all simple tasks requiring awareness of another individual’s mental state, which are appropriate for children with a VMA near 4 years. On all tests, the child was given a score of one for demonstrating evidence of theory of mind and zero otherwise,

Table 1
Characteristics of each group

Group	Number of children	Chronological age	Verbal mental age	Theory of mind
ASD	25 (19/22)	8; 1 ± 1; 12 (4; 5–12; 9)	4; 3 ± 1; 2 (2; 4–7; 5)	3.5 ± 3.0 (0–10)
Control	31 (21/25)	4; 1 ± 0; 7 (3; 1–5; 4)	4; 7 ± 1; 1 (2; 10–6; 0)	7.7 ± 3.2 (0–13)

The number of children is given as total (male/right handed). CA and VMA are given in years and months as mean ± standard deviation (range). Theory of mind scores are out of 13 points and are given as mean ± standard deviation (range). The ASD group and control group were matched on VMA, gender and handedness but differed in CA and theory of mind score.

leading to a maximum score of 13. Table 1 lists the results of background testing for each group. The ASD group and the control group did not differ significantly in verbal mental age, but did differ in their theory of mind score, as tested in an ANCOVA with VMA as a covariate ($p < .001$, $F = 23.9$, $df = 1, 49$). The children with ASD failed almost all the theory of mind tasks, confirming that they have a poor understanding of other people's knowledge and beliefs relative to their verbal abilities. The control children scored at the level expected for their VMA, passing approximately half the questions. VMA had a significant impact on theory of mind performance across groups ($p = .001$, $F = 11.5$, $df = 1, 49$), as expected.

2.3. General methods

Children were tested individually in a quiet room in their own school. Each child took part in two or three testing sessions and performed a range of tasks, including the ones reported here. Task order was randomised and praise was given to the child on all tasks after every trial regardless of correctness. Each task began with two training trials which were repeated until it was established that the child understood the instructions. Individual tasks are described in more detail below. A few of the children refused to participate in some tasks, so subject numbers are given for each task in the results.

All data were analysed using a repeated measures ANCOVA in SPSS, with verbal mental age as a covariate and a threshold of $p < .05$ for statistical significance. Some tests had only a small number of possible scores (e.g., 0–4) which might not be normally distributed and not conform to the assumptions of a parametric analysis. To deal with this, we used a resampling procedure (Howell, 2001) to generate pseudo-F distributions for each of these data sets to assess the likelihood that the observed scores could arise by chance without making any assumptions about the distribution of scores. In every case, we found that the pseudo-F distribution closely matched the standard F distribution, such that the same conclusion would be drawn from either the parametric ANCOVA or the non-parametric resampling procedure. For simplicity, we therefore report only the results of the standard parametric analyses in SPSS.

3. Experiment 1: goal-directed imitation

Interpreting other people's goals from their actions is crucial for social interaction and there is clear evidence that the MNS is central to this process (Fogassi et al., 2005; Hamilton & Grafton, 2006). Goal-directed imitation tasks in fMRI activate the human mirror system (Koski et al., 2002), and a similar task can be used to tap goal understanding in children. In particular, typically developing 4–6-year olds show evidence for goal understanding in a simple imitation task (Bekkering, Wohlschlager, & Gattis, 2000; Gattis, Bekkering, & Wohlschlaeger, 2002). The children were asked to copy an adult who moved her hand to cover a left or right target on the table top, and it was found that children made a high proportion of hand errors when the experimenter moved her hand across her body to cover a contralateral target (Fig. 1A, middle). This error does not reflect simply a reluctance to cross the midline because children were able to imitate crossed-hands trials. Instead, Bekkering and colleagues argue that the child represents the goal of the action, 'touch the right dot', and gives that a higher priority than the means of the action, 'use left hand'. Children imitate the goal but use the more convenient right hand, resulting in a hand error. Importantly, this contralateral error is found more frequently when goals (dots) are visible on the table top than when the table is unmarked and the action does not have a prominent goal. Thus, the presence of hand errors on contralateral movement trials provides evidence that children are able to represent and imitate the goal of an adult's action.

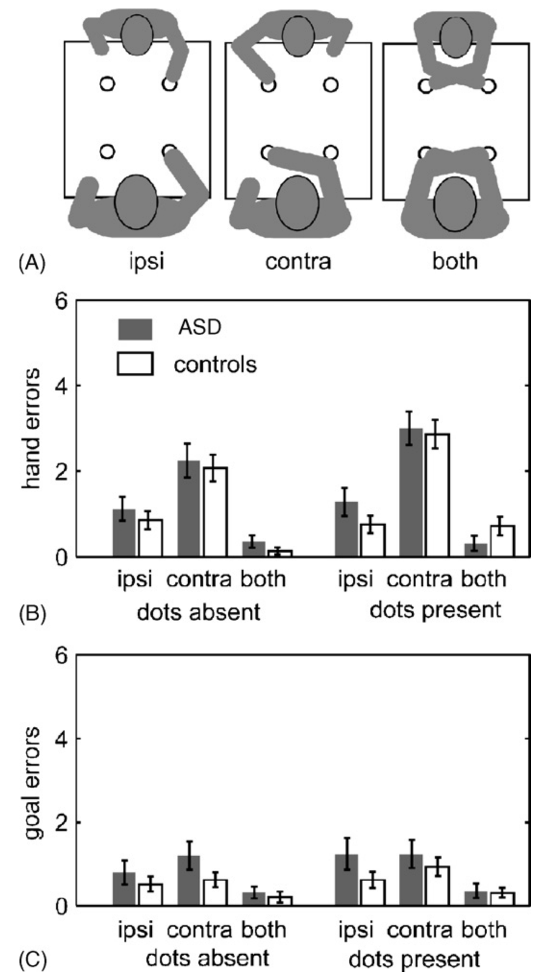

Fig. 1. Goal-directed imitation. (A) The three possible trial types are illustrated. In each case, the experimenter is represented by the larger person at the bottom, the child by the smaller person at the top and circles indicate the target locations which were (present) or were not (absent) marked by paper dots. On ipsilateral and both trials, children normally imitate correctly. On the contralateral trial, the typical hand error is illustrated; the child moves to the correct goal location but using the wrong hand. (B) Mean number of hand errors made by each group out of a maximum of six. Error bars are standard errors. (C) Mean number of goal errors made by each group, as before.

If children with ASD have a dysfunctional mirror system, they should not show this characteristic error pattern. Instead they might prefer to imitate the hand used to perform the action, or might make additional errors on the other trials. We replicated the tasks used by Bekkering and colleagues in our groups of children to test if the children with ASD are sensitive to observed goals. The AMND predicts a lack of goal-directed imitation in children with autism.

3.1. Methods

For this task, children sat opposite the experimenter at a plain table and were required to copy the experimenter's hand movement to a target location on a table top, using mirror imitation. Following previous work (Bekkering et al., 2000; Gattis et al., 2002), we used a 3×2 factorial design manipulating three possible types of movement made by the experimenter and the presence or absence of goal dots on the table. Movements could be directed towards the ipsilateral target (Fig. 1A, left), to the contralateral target (Fig. 1A, middle) or to both targets at once (Fig. 1A, right). One-handed actions could be performed with either the right or left hand and two-handed actions with arms crossed or uncrossed, giving a total of six possible trials. In one block, target locations were indicated by paper dots stuck to the table 30 cm apart and 20 cm from the edge in front of the child and experimenter, and in the other block target locations were unmarked. Block and trial order were counterbalanced across children.

Each block began with the experimenter's hands at the edge of the table close to her and the child's hands in an equivalent location. As previously (Bekkering et al., 2000; Gattis et al., 2002), children were explicitly instructed to imitate the actions of the experimenter. The experimenter told the child "All you have to do is copy me" and then performed one of the six possible movements and remained at the target location until the child responded. Then the experimenter returned to the starting posture and waited for the child to return to the same posture before beginning the next trial. Each child completed 18 trials with dots on the table and 18 trials without dots.

All trials were video-taped with a digital video camera positioned slightly behind and to the side of the experimenter, so that the table with the hands of both the experimenter and the child were fully visible on the screen. Each trial was scored for hand errors, defined as a failure to use the mirror equivalent of the experimenter's hand, and goal errors, defined as failed to touch the mirror equivalent of the experimenter's target location. Twenty-five percent of the video tapes were also scored by a second observer who was blind to the hypotheses and the children's diagnosis, and a 93 percent agreement between the two observers was obtained.

3.2. Results and discussion

Twenty-five children with ASD and 29 controls completed the task. The analysis of hand errors (Fig. 1B) revealed a main effect of movement type ($p < .001$, $F = 65.5$, $df = 2$, 102) and a main effect of the presence of dots on the table ($p = .007$, $F = 8.322$, $df = 1$, 51). Importantly, there was an interaction between dots and movement type ($p = .01$, $F = 4.75$, $df = 2$, 102), with significantly more hand errors on contralateral trials when dots where present than when they were absent. This result replicates Bekkering et al. (2000) and provides evidence for goal-directed imitation in the children tested. We did not find any differences in performance between the control and ASD groups (main effect of group, $p = .6$, $F = 2.70$, $df = 1$, 51, and all interactions with group $p > .2$), and inspection of Fig. 1B confirms the similar performance of the two groups.

As a more specific test of goal-directed imitation, we repeated the analysis of hand errors in each group separately, with chronological age as an additional covariate. The control group again showed the expected pattern of results (dots: $p = .008$, $F = 8.35$, $df = 1$, 26; movement type: $p < .001$, $F = 37.2$, $df = 2$, 52; interaction: $p < .01$, $F = 4.90$, $df = 2$, 52), and also an interaction between chronological age and performance ($p < .019$, $F = 6.3$, $df = 1$, 26). The ASD group showed a significant main effect of movement type ($p < .001$, $F = 28.44$, $df = 2$, 44) and a marginal interaction in the expected direction ($p < .094$, $F = 2.49$, $df = 2$, 44) but no interactions with VMA or CA. These results confirm that both the control and ASD groups independently show goal-directed imitation of simple hand movements.

Data were also analysed for goal errors, where the child failed to touch the appropriate target location. As illustrated in Fig. 1C, goal errors were low in both groups and all conditions. There was a main effect of movement type ($p < .001$, $F = 9.38$, $df = 2$, 102) on goal errors and an interaction between the presence of dots and VMA ($p < .01$, $F = 7.21$, $df = 1$, 51). As before there were no main effects of group ($p = .16$, $F = 2.0$, $df = 1$, 51) and no interactions with group (all $p > .2$).

In our assessment of goal-directed imitation, we found no evidence for differences in performance between the ASD group and the VMA matched control group. Both groups showed the typical pattern of hand errors on contralateral trials reported by Bekkering et al. (2000), and both groups showed an interaction between movement type and the presence of dots. Thus, we can conclude that typical and autistic children have the same tendency to imitate the goal of another person's action. This result is concordant with two studies (Aldridge, Stone, Sweeney, & Bower, 2000; Carpenter, Pennington, & Rogers, 2001) which have tested children with ASD on a task requiring imitation of failed actions (Meltzoff, 1995). Both studies found children with ASD were able to comprehend and imitate the intention of the actor even though the actor never achieved the intended goal. All these data provide clear evidence against the AMND hypothesis, which predicted that children with ASD should show poor performance in tasks requiring the understanding or imitation of goals.

4. Experiment 2: mirror imitation

Typically developing children tend to imitate movements as if they were looking in a mirror (Wapner & Cirillo, 1968). However, it has been suggested that adults with Asperger's syndrome fail to take advantage of mirroring (Avikainen, Wohlschlager, Liuhanen, Hanninen, & Hari, 2003). We aimed to test if our participants with ASD have a preference for mirror imitation over anatomical imitation, using a variation of Experiment 1.

4.1. Methods

This task used a very similar procedure to Experiment 1. The only difference was that the target locations were arranged in a single line between the child and the experimenter (Fig. 2A), which means that each dot can be reached equally well with either hand. On each trial, the experimenter moved her hand to one target location and asked the child to copy. If a child has a preference for mirror imitation, we would expect the child to use his or her right hand when the experimenter models the action with her left hand, and vice versa. Trials where the child failed to use the mirror hand were scored as hand errors. The two possible target locations were classified as 'near' or 'far' relative to the actor's body, and trials where the child failed to move to the same target as the experimenter were classified as goal errors. Children completed twelve trials (2 hands $\times$ 2 targets $\times$ 3 repetitions) with dots on the table marking the target locations, and twelve trials without dots. This task was always carried out after Experiment 1, but the order of the two blocks was counterbalanced across children. Trials were scored from video as in Experiment 1. On approximately

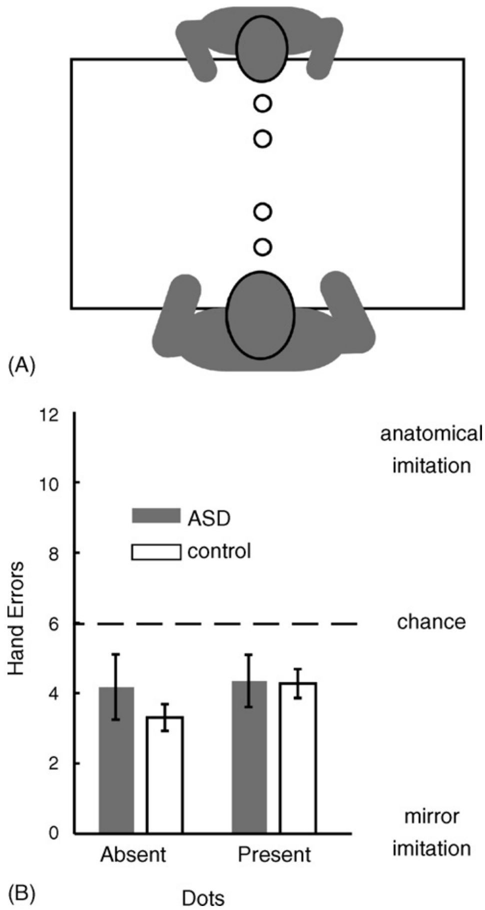

Fig. 2. The mirror imitation task. (A) This task was similar to the goal-directed imitation task, but all four target locations were arranged in a single row between the child (upper person) and the experimenter (lower person). (B) Mean number of hand errors (±*SE*) made by each group. Zero errors would indicate mirror imitation and 12 errors out of 12 would indicate anatomical imitation. On average, both groups showed a preference for mirror imitation.

four percent of trials where dots were absent, the near/far goal of the child's action was ambiguous and such trials were scored as a half error. Again, 25 percent of the tapes were scored by an independent observer and 88 percent agreement was obtained.

4.2. Results and discussion

Twenty-three ASD children and 29 controls completed the task, and both groups showed a preference for mirror imitation (Fig. 2B). There was a marginal effect of dots on hand errors ($p = .053$, $F = 3.93$, $df = 1$, 49), with more hand errors when dots were present. This result provides further evidence for goal-directed imitation in both groups of children, because the presence of a dot as a goal reduces the importance of the hand selection goal and increases hand errors. An analysis of goal errors revealed a significant effect of dots ($p = .006$, $F = 8.22$, $df = 1$, 49) with more goal errors when dots were absent. There were no effects of group on either hand errors ($p > .9$) or goal errors ($p > .5$). These data show that both control children and children with ASD have a preference for mirror imitation of hand actions.

5. Experiment 3: grasp imitation and motor planning

The human MNS is not only concerned with action understanding and imitation, it is also a motor system, concerned with planning and executing goal-directed actions. The mirror network is reliably activated by planning (Johnson-Frey, Newman-Norlund, & Grafton, 2005) and executing (Rizzolatti et al., 1996) hand actions and damage to the mirror network results in apraxia or loss of action representations (Heilman, Rothi, & Valenstein, 1982). Thus, if children with ASD have a dysfunctional MNS, they might also be expected to have difficulties with planning and performing actions.

This experiment was designed to address two related questions. First, do children with autism have difficulties with motor planning? Motor planning is a non-trivial skill which develops slowly in typical children, and some planning difficulties have been reported in children with ASD (Hughes, 1996). If motor planning impairments are common in autism, this factor might contribute to the poor imitation performance which has been reported (Williams et al., 2004). Second, can children use imitation to improve their motor planning and thus their motor performance? If an experimenter demonstrates the best way to perform a motor task, a child who has the ability to understand and imitate human actions should take advantage of the demonstration and show improved performance. We tested if control or autistic children show better motor planning when the task requirements are demonstrated manually than when the task is specified verbally. The AMND hypothesis predicts that children with ASD may show poor motor planning abilities, because the MNS is essential for motor performance. More directly, the AMND hypothesis predicts that the ASD group should not be able to take advantage of the experimenter's demonstration in the imitation condition.

5.1. Methods

To assess motor planning, we used a grip selection task which has been previously used with both normal adults (Cohen & Rosenbaum, 2004; Rosenbaum et al., 1990, chap. 10) and children with ASD (Hughes, 1996). In a series of experiments, Rosenbaum and colleagues demonstrated that typical adults plan reaching movements so as to end the movement with a comfortable grip, even if that means using a less comfortable grip at the start of the movement. For example, Fig. 3A illustrates a trial where the participant must place the red (pale) end of the bar vertically on the black target. The participant selects an awkward underhand grip at the start of the trial to achieve a comfortable vertical grip at the end of the trial. This choice of an awkward grip at the start is evidence that the participant can consider the whole movement he or she will have to make and plan accordingly. Fig. 3B illustrates the easier overhand trials, where the participant is able to place the blue (dark) end of the bar on the target using a natural overhand grip at the start and a comfortable vertical grip at the end. If children have poor motor planning abilities, we would expect them to make grip selection errors on the underhand trials which require full planning, but not on the overhand trials where a natural grip is sufficient.

Previous studies of motor planning have used verbal or graphical instructions specifying the desired end state (Rosenbaum et al., 1990), for example, 'put the red end of the bar on the black circle'. This leaves the participant to plan the best way to achieve that end state. To assess the role of action understanding in this task, we compared performance on a block of trials with verbal instruction to performance on an imitation block where the experimenter demonstrated the correct action and the end result. In these imitation blocks, the correct grip is

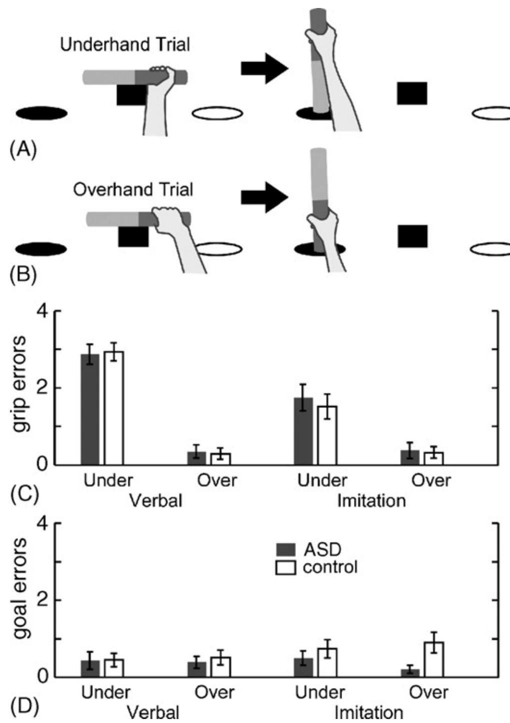

Fig. 3. The grasp imitation task. (A) The start (left) and end (right) of a correct underhand trial are illustrated. The participant's task is to put the pale end of the horizontal bar on the black target circle. This can best be accomplished using an awkward underhand grip at the start of the movement. (B) In the overhand trial the participant must put the dark end of the horizontal bar on the black target circle, which can be performed using a natural overhand grip. Note the similar end postures in both underhand and overhand trials. (C) Mean grip errors in each condition and each group of children. A grip error was scored when the child failed to use the appropriate grip at the start of a trial. Error bars are standard error and the maximum is four errors. (D) Mean goal errors in each condition for each group. A goal error was scored when the child failed to put the bar in the correct location at the end of the trial.

shown to the child, so children who have the ability to understand and imitate hand grasps should show improved performance.

For all trials, the child sat opposite the experimenter at a small desk and a video camera was positioned behind and to the side of the experimenter to record both the child's and the experimenter's hand movements. A hollow metal bar with one half painted blue and the other half painted red rested on a stand in front of the child and two paper discs, one black, one white, were fixed to the table 10 cm beyond the ends of the bar as targets. Two bar orientations and two targets give four possible trials, each presented twice in the verbal block, and twice in the imitation block. Trial order and block order was counterbalanced.

All trials began with the child sitting with his or her preferred hand on the desk in front of the bar and the other hand under the desk. For verbal trials, the experimenter asked the child "Please pick up the red end of the bar and put it on the black circle, so it looks like this," and showed a picture of the desired configuration of the bar and targets. Pictures were used to complement the verbal instructions because the children tested had low verbal abilities. The picture remained visible until the child completed the task. For imitation trials, an identical apparatus was arranged in a mirror fashion in front of the experimenter. The experimenter then asked the child to watch carefully and copy, and proceeded to demonstrate the correct starting grip and move the bar to the desired end state. The experimenter used his left hand for right handed children and vice versa, to allow the child to use mirror imitation.

After testing, performance was scored from the video tapes. For each trial, a grip error was recorded if the child used an inappropriate grip at the start of the action, and a goal error was recorded if the final position and orientation of the bar did not match the trial requirements. Some children used their non-dominant hand on some trials, in spite of the instructions not to, and these trials were recorded as hand errors.

5.2. Results and discussion

Twenty-three children with ASD and 31 controls completed this task. Fig. 3D illustrates the low level of goal errors found in all conditions. Goal errors did not differ with group ($p > .13$), indicating that all children were able to perform the task. There was a significant effect of VMA on goal errors ($p < .001$, $F = 14.25$, $df = 1, 51$) but no other significant effects.

An analysis of grip errors is presented in Fig. 3C. Children made grip errors on the majority of trials when an underhand grip was required and instructions were verbal, but made fewer grip errors when there was an opportunity to imitate. These effects where confirmed statistically, with a main effect of grip ($p < .0001$, $F = 141$, $df = 1, 51$), a main effect of instructions ($p < .001$, $F = 21.7$, $df = 1, 51$) and an interaction between these factors ($p < .001$, $F = 23.0$, $df = 1, 51$). There were no effects of group on grip errors ($p > .85$) nor interactions with group (all $p > .5$) but there was a significant effect of VMA on grip errors ($p = .045$, $F = 4.22$, $df = 1, 51$). These results show that all the children found motor planning difficult, but that they were able to take advantage of the experimenter's demonstration to improve their performance. Thus, both control and ASD children are able to understand and imitate the experimenter's grip configuration.

The results of this experiment provide further evidence against the AMND theory. Motor planning is known to rely on the fronto-parietal circuit which makes up the MNS (Johnson-Frey et al., 2005) so the AMND predicts poor performance in ASD which was not found. The children with ASD showed the same level of motor planning as the control group, and were able to understand and imitate the experimenter's grasp in the imitation trials. An unexpected result in this task was the clear effects of VMA on both goal errors and grip errors, which implies links between verbal abilities and motor planning abilities. Further research would be needed to investigate the relationship between these skills in detail.

6. Experiment 4: gesture recognition

The MNS is not only a motor system, but is also believed to support action understanding. Patients with apraxia tend to perform poorly on action understanding tasks (Buxbaum, Kyle, & Menon, 2005; Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003) and transcranial magnetic stimulation of the inferior frontal gyrus impairs action understanding in typical adults (Pobric & Hamilton, 2006). Thus, the AMND hypothesis predicts that children with ASD should have difficulties understanding the actions of other people. We used a gesture recognition task to assess this in our group of ASD children. The task was originally developed for use with patients with apraxia or aphasia (Mozaz, Rothi, Anderson, Crucian, & Heilman, 2002) and has very low motor and verbal demands. The participant is simply required to match a pictured hand posture to a cartoon drawing of an action with the hands of the actor missing. The AMND theory predicts that children with ASD should find this task particularly hard, because they should lack the ability to interpret the meaning of a gesture.

6.1. Methods

Cartoon stimuli of people performing actions with the hands missing from the cartoons were kindly provided by Professor Heilman (Mozaz et al., 2002). We created a new set of high resolution photographs of hands as targets and foils for the cartoons, matching the postures used in the original stimuli. This resulted in a set of cards depicting nine object-use gestures and nine symbolic gestures (Fig. 4A and B). All the photographs for the object-use gestures showed hands posed as if to hold a tool but with no tool present, following the stimuli developed by the Heilman group.

The task was presented to the children as a picture matching game. One card from each set was used for training trials. The child was given the card and asked to look carefully at the cartoon to see what was missing. When the child saw that the hands were missing, his attention was drawn to the photographs and he was asked "which hands fill the gap?" Errors with the training cards were corrected and explained so that the child understood the task. Then each of the 16 test cards was presented in turn, in a randomised order, and the child was required to choose the photograph which filled the gap. Responses were recorded and praise was given for all responses regardless of correctness.

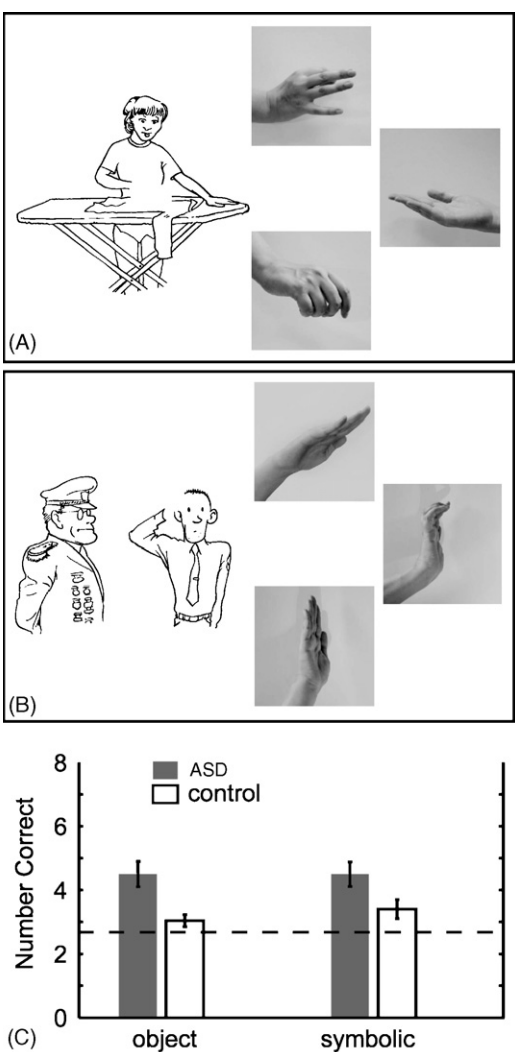

Fig. 4. The gesture recognition task. (A) An example stimulus card for an object use action. (B) An example stimulus card from a symbolic action. (C) Performance on the gesture recognition task, with chance performance indicated by the dashed line. Means and standard errors are shown for each group.

6.2. Results and discussion

Twenty-two children with ASD and 30 control children took part in this task, and results are illustrated in Fig. 4C. The ASD group performed significantly better than the control group ($p<.001$, $F=16.8$, $df=1, 49$), and children with a higher VMA also showed better performance ($p=.003$, $F=9.61$, $df=1, 49$), but there were no effects of stimulus type on performance ($p>.5$).

These data indicate that the group with ASD have no gesture recognition impairment, and in fact performed better than the VMA matched controls. This replicates the work of Smith and Byrson (1998), who found no difference in gesture recognition performance between autistic children, children with language delay and controls. These data are not compatible with the hypothesis of an action representation deficit or mirror neuron deficit in the children with ASD.

7. General discussion

We tested 25 children with an independent clinical diagnosis of autistic spectrum disorder on a variety of experiments designed to test the hypothesis of an autistic mirror neuron dysfunction (AMND), and compared their performance to 31 typically developing children matched for VMA. The autistic group of children were all significantly impaired in their ability to attribute mental states to others as assessed with standard theory of mind tests. Nevertheless, in the three action tasks, which assessed goal-directed imitation, mirror imitation and grasp planning, there were no differences between the ASD group and the control group, with both groups showing evidence of goal and grasp imitation. These results challenge the AMND hypothesis, which predicts poor imitation and poor goal understanding in children with autism who have poor theory of mind abilities. In the visual task, children with ASD performed better than controls at gesture recognition, which again was not predicted by the AMND theory. We consider now the evidence linking each of our experiments to the MNS and the relationship between our results and other studies of imitation in autism, to obtain a full assessment of the AMND hypothesis.

The tasks we used were specifically chosen because previous fMRI studies in adults have shown that these tasks involve the brain regions known as the mirror neuron system, specifically the inferior frontal gyrus and inferior parietal cortex. Goal-directed imitation involves both of these regions (Iacoboni et al., 1999; Koski et al., 2002), as does motor planning (Johnson-Frey et al., 2005) and observation of hand gestures (Lotze et al., 2006). Furthermore, lesions to the MNS in the adult brain lead to poor performance on imitation tasks (Heilman et al., 1982) and action understanding tasks (Buxbaum et al., 2005; Tranel et al., 2003). Thus, it is clear that in the typical adult brain, the MNS supports imitation and goal understanding (Rizzolatti & Craighero, 2004). If the MNS is dysfunctional in children with ASD (Williams et al., 2001), we would expect these two functions to be impaired. However, as the results indicate, we found no evidence of autism related impairments in MNS skills. The autistic children we tested showed goal-directed imitation and grasp planning skills at the level expected for their verbal mental age, and showed superior gesture recognition skills.

These results are not simply a lack of an effect due to weak statistical power. In the goal-directed imitation and grasp planning tasks, we observed a systematic pattern of errors in the control children and the same systematic pattern in children with autism. Both groups made more hand errors on contralateral goal-directed imitation trials, indicating that the children inferred the goal of the adult's action and emulated that goal without imitating the hand used by the adult (Bekkering et al., 2000). In the grasp planning task, both groups performed poorly when given verbal instructions, but both groups showed substantially better grasp planning when the experimenter demonstrated the correct action. This provides evidence that the children can interpret and imitate the adult's grasping action. Finally, in the gesture recognition task the children with autism performed even better than the controls. This task provides the purest test of MNS function because responses cannot be contaminated by motor abilities, and this task also provides the strongest evidence against the AMND hypothesis. These results provide clear evidence of a dissociation between imitation skills, where the autistic group performed normally, and the theory of mind tasks where these children were severely impaired.

Two caveats apply to these data. First, in all the imitation tasks we examined, children were explicitly instructed to copy the experimenter. Thus, our conclusions may not generalise to situations of automatic mimicry. Second, this is not a neuroimaging study and our conclusions about the neural systems underlying the behaviour we observed in children with autism is based on references to published studies, rather than direct measurement of neural activation. Nevertheless, all the tasks we used were selected because neuroimaging studies of adults have clearly demonstrated the involvement of the mirror neuron system in these behaviours. While it is possible that the children with autism show normal performance on behavioural testing but use different neural systems to pass these tasks, this is an unlikely and complex explanation of the data. We suggest instead that, when confronted with an explicit imitation or action recognition task, children with autism are able to use their mirror neuron system to achieve the same behavioural performance as typical children.

Our data are not anomalous in the context of other studies of imitation and action understanding in children with autism. Two independent groups have shown that children with autism are able to understand and imitate an adult's goal-directed action even if the action is never completed (Aldridge et al., 2000; Carpenter et al., 2001). Intact gesture recognition (Smith & Byrson, 1998) and object-directed imitation (Rogers, Hepburn, Stackhouse, & Wehner, 2003; Stone, Ousley, & Littleford, 1997) have also been reported. Children with autism recognise when they are being imitated by an adult and respond positively (Field, Field, Sanders, & Nadel, 2001). Finally, enhanced performance on meaningful imitation compared to meaningless imitation (Rogers, Bennetto, McEvoy, & Pennington, 1996; Stone et al., 1997) provides evidence against specific problems with action meaning in ASD. All these studies point to intact understanding and imitation of the goal of an object-directed action in children with autism. Our own data complement these results using tasks which are directly relevant to the MNS.

These results have important implications for the AMND hypothesis, and for our understanding of the relationship between imitation skills, the MNS and theory of mind impairment in autism. As described in Section 1, the AMND hypothesis proposed that the motor MNS, which supports imitation and goal understanding, is dysfunctional in children with autism. We suggest that the weight of evidence from our own data and the studies described above makes the AMND proposal untenable. Children with autism are able to imitate goals, plan grasps and understand gestures, despite the fact that all of these tasks are dependent on the MNS. Furthermore, this intact imitation ability was observed in children who have clear deficits on theory of mind tasks, demonstrating a dissociation between goal-directed imitation and mental state inference. This means that MNS problems cannot be a simple, single factor explanation for the theory of mind failure and other social impairments found in children with ASD.

Nevertheless, there remains a large body of evidence supporting the idea of some type of imitation deficit in ASD (Williams et al., 2004), and some neuroimaging evidence is starting to emerge indicating differences in the autistic brain during imitation (Dapretto et al., 2006) and action observation (Oberman et al., 2005) tasks. How might these results be reconciled with our rejection of the AMND?

7.1. Understanding imitation

We suggest that an understanding of imitation behaviour in autism must begin with the recognition that imitation is not a unitary cognitive component and is not dependent upon a unitary 'mirror neuron system' in the human brain. A minimal description of imitation performance must recognise the role of visual information processing, visual to motor mapping, and motor control as distinct processes which must all function correctly for imitation to occur, and much more detailed schemes have been proposed (Tessari & Rumiati, 2004). Even when low level visual and motor parameters are equated, differential brain activations have been found for meaningful compared to meaningless gesture imitation (Rumiati et al., 2005), for expressive compared to instrumental gestures (Gallagher & Frith, 2004), and for imitation of hand actions compared to emotional facial expressions (Leslie, Johnson-Frey, & Grafton, 2004). These data demonstrate that imitation behaviour cannot be localised to a single brain system, but rather different types of imitation involve different cognitive and neural systems. For example, imitation of meaningful hand actions would involve the brain regions for representing, understanding and planning goal-directed hand actions, while imitation of facial expressions would involve regions for representing, understanding and performing face movements. Thus, it would be implausible to expect a single neurocognitive mechanism to underlie imitation in either the typical or autistic brain. Rather we should examine the different roles of hand processing, face processing, emotion processing and other social-motor domains in both the perceptual and motor behaviour of children with autism.

Following this classification, we can consider the classic motor mirror system as a system for the representation of hand–object interactions and the goals of these actions. This hand-goal system is found in the inferior frontal and inferior parietal cortex (Rizzolatti & Craighero, 2004), with a left lateralisation in most object use tasks (Johnson & Grafton, 2003). Damage to this system results in impaired performance, understanding and imitation of hand actions (Buxbaum et al., 2005). However, all these skills were unimpaired in our sample of children with autism, and thus we propose that this hand-goal MNS is intact in these children.

In contrast, the tasks where autistic children do show impaired imitation are often those tasks where the children cannot rely on a hand-goal strategy. Thus, poor performance is seen on imitation of meaningless actions (Rogers et al., 1996; Stone et al., 1997) including those that involve an element of perspective taking (Ohta, 1987; Smith & Byrson, 1998). Neural responses to the observation of meaningless actions are reduced in children with autism (Oberman et al., 2005), but responses to observation of object-directed actions are normal in adults with Asperger's syndrome (Avikainen, Kulomaki, & Hari, 1999). Both of these studies used methods with low spatial resolution (EEG/MEG) and do not directly address the role of the MNS, but the data do imply a distinction between abnormal representations of meaningless actions and normal representations of meaningful actions in autism which is in line with our own results. Children with autism also show poor imitation performance in facial imitation tasks (Rogers et al., 2003). The ability to represent, understand and produce facial emotional expressions is associated with the right insula and right inferior frontal gyrus (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003). Automatic emotional mimicry seems to be impaired in people with autism (McIntosh, Reichmann-Decker, Winkielman, & Wilbarger, 2006), and differences between an autistic group and a control group in right frontal regions have been reported in an emotional imitation task (Dapretto et al., 2006). In the current paper, we do not test automatic mimicry or emotional imitation abilities, and these abilities could be impaired independent of goal-directed imitation abilities. For example, individuals with autism might fail emotional imitation tasks because of abnormal responses in the amygdala rather than the mirror neuron system (de Gelder, 2006). Overall, the imitation tasks which children with autism fail are precisely the tasks which do not rely heavily on the classic hand-goal mirror system, and which do not involve understanding the goal of the action.

Based on the present results, we suggest that it is not helpful to study imitation as a single cognitive or neural system. Further research will be needed to define whether the difficulties children with autism have on some imitation tasks are due to problems in automatic mimicry, in representing emotions or facial expressions, in parsing and planning meaningless actions or to some other factor. Our work indicates that children with autism have an intact ability to represent, understand and imitate goal-directed hand–object interactions, and thus are likely to have an intact hand-goal MNS. Defining the limits of this system and what it can do both for typical and autistic children will be an important area of research in the future.

7.2. Overall conclusion

The results of our experiments provide clear evidence against a simple mirror neuron hypothesis of autism (Williams et al., 2001), in which dysfunction of the motor mirror neuron system results in an impaired ability to understand and imitate action goals in children with ASD, leading to poor theory of mind ability. Instead we suggest that goal understanding is in fact an island of intact functioning in ASD, in contrast to these children's poor performance on theory of mind tasks. Further work will be needed to distinguish different types of imitation and the different neural systems which support them, in order to make sense of the social disabilities found in children with autism.

Acknowledgments

We thank Safina Khan, Adrian Harrison, Bhushan Joshi, Laura Wormwald and Jane Leighton for help with testing, and all the schools and children involved for their participation. We also thank Professor Heilman for providing the stimuli used in Experiment 4. This work was supported by an MRC grant to Uta Frith, no. G9617036.

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.

Avikainen, S., Kulomaki, T., & Hari, R. (1999). Normal movement reading in asperger subjects. *Neuroreport*, *10*, 3467–3470.

Avikainen, S., Wohlschlager, A., Liuhanen, S., Hanninen, R., & Hari, R. (2003). Impaired mirror-image imitation in asperger and high-functioning autistic subjects. *Current Biology*, *13*, 339–341.

Baron-Cohen, S., Leslie, A. M., & Frith, U. (1985). Does the autistic child have a "theory of mind"? *Cognition*, *21*, 37–46.

Bekkering, H., Wohlschlager, A., & Gattis, M. (2000). Imitation of gestures in children is goal-directed. *Quarterly Journal of Experimental Psychology A*, *53*, 153–164.

Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H. J., et al. (2004). Neural circuits underlying imitation learning of hand actions: An event-related fmri study. *Neuron*, *42*, 323–334.

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*, 226–239.

Carpenter, M., Pennington, B. F., & Rogers, S. J. (2001). Understanding of others' intentions in children with autism. *Journal of Autism and Developmental Disorders*, *31*, 589–599.

Carr, L., Iacoboni, M., Dubeau, M. C., Mazziotta, J. C., & Lenzi, G. L. (2003). Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas. *Proceedings of the National Academy of Sciences*, *100*, 5497–5502.

Cohen, R. G., & Rosenbaum, D. A. (2004). Where grasps are made reveals how grasps are planned: Generation and recall of motor plans. *Experimental Brain Research*, *157*, 486–495.

Dapretto, M., Davies, M. S., Pfeifer, J. H., Scott, A. A., Sigman, M., Bookheimer, S. Y., et al. (2006). Understanding emotions in others: Mirror neuron dysfunction in children with autism spectrum disorders. *Nature Neuroscience*, *9*, 28–30.

de Gelder, B. (2006). Towards the neurobiology of emotional body language. *Nature Reviews Neuroscience*, *7*, 242–249.

Devries, R. (1970). The development of role-taking as reflected by behavior of bright, average, and retarded children in a social guessing game. *Child Development*, *41*, 759–770.

Dunn, L. M., Dunn, L. M., Whetton, K., & Burley, J. (1997). *British picture vocabulary scale* (2nd ed.). Windsor: NFER-NELSON.

Field, T., Field, T., Sanders, C., & Nadel, J. (2001). Children with autism display more social behaviors after repeated imitation sessions. *Autism*, *5*, 317–323.

Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: From action organization to intention understanding. *Science*, *308*, 662–667.

Gallagher, H. L., & Frith, C. D. (2004). Dissociable neural pathways for the perception and recognition of expressive and instrumental gestures. *Neuropsychologia*, *42*, 1725–1736.

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 simulation theory of mind-reading. *Trends in Cognitive Sciences*, *2*, 493–501.

Gallese, V., Keysers, C., & Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences*, *8*, 396–403.

Gattis, M., Bekkering, H., & Wohlschlaeger, A. (2002). Goal directed imitation. In A. Meltzoff & W. Prinz (Eds.), *The imitative mind: Development, evolution and brain bases*. Cambridge, UK: Cambrigdge University Press.

Hamilton, A. F., & Grafton, S. T. (2006). Goal representation in human anterior intraparietal sulcus. *Journal of Neuroscience*, *26*, 1133–1137.

Heilman, K. M., Rothi, L. J., & Valenstein, E. (1982). Two forms of ideomotor apraxia. *Neurology*, *32*, 342–346.

Howell, D. (2001). *Statistical methods for psychology* (5th ed.). Wadsworth.

Hughes, C. (1996). Brief report: Planning problems in autism at the level of motor control. *Journal of Autism and Developmental Disorders*, *26*, 99–107.

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, *286*, 2526–2528.

Johnson-Frey, S. H., Newman-Norlund, R., & Grafton, S. T. (2005). A distributed left hemisphere network active during planning of everyday tool use skills. *Cerebral Cortex*, *15*, 681–695.

Johnson, S. H., & Grafton, S. T. (2003). From 'acting on' to 'acting with': The functional anatomy of object-oriented action schemata. *Progress in Brain Research*, *142*, 127–139.

Keysers, C., Wicker, B., Gazzola, V., Anton, J. L., Fogassi, L., & Gallese, V. (2004). A touching sight: Sii/pv activation during the observation and experience of touch. *Neuron*, *42*, 335–346.

Koski, L., Wohlschlager, A., Bekkering, H., Woods, R. P., Dubeau, M. C., Mazziotta, J. C., et al. (2002). Modulation of motor and premotor activity during imitation of target- directed actions. *Cerebral Cortex*, *12*, 847–855.

Leslie, K. R., Johnson-Frey, S. H., & Grafton, S. T. (2004). Functional imaging of face and hand imitation: Towards a motor theory of empathy. *Neuroimage*, *21*, 601–607.

Lotze, M., Heymans, U., Birbaumer, N., Veit, R., Erb, M., Flor, H., et al. (2006). Differential cerebral activation during observation of expressive gestures and motor acts. *Neuropsychologia*, *44*, 1787–1795.

Luckett, T., Powell, S. D., Messer, D. J., Thornton, M. E., & Schulz, J. (2002). Do children with autism who pass false belief tasks understand the mind as active interpreter? *Journal of Autism and Developmental Disorders*, *32*, 127–140.

McIntosh, D. N., Reichmann-Decker, A., Winkielman, 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*, 295–302.

Meltzoff, A. (1995). Understanding the intentions of others: Re-enactment of intended acts by 18-month-old children. *Developmental Psychology*, *31*, 838–850.

Mozaz, M., Rothi, L. J., Anderson, J. M., Crucian, G. P., & Heilman, K. M. (2002). Postural knowledge of transitive pantomimes and intransitive gestures. *Journal of the International Neuropsychological Society*, *8*, 958–962.

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*, 190–198.

Ohta, M. (1987). Cognitive disorders of infantile autism: A study employing the wisc, spatial relationship conceptualization, and gesture imitations. *Journal of Autism and Developmental Disorders*, *17*, 45–62.

Pobric, G., & Hamilton, A. F. (2006). Action understanding requires the left inferior frontal cortex. *Current Biology*, *16*, 524–529.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*, 169–192.

Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D., et al. (1996). Localization of grasp representations in humans by pet. 1. Observation versus execution. *Experimental Brain Research*, *111*, 246–252.

Rogers, S. J., Bennetto, L., McEvoy, R., & Pennington, B. F. (1996). Imitation and pantomime in high-functioning adolescents with autism spectrum disorders. *Child Development*, *67*, 2060–2073.

Rogers, S. J., Hepburn, S. L., Stackhouse, T., & Wehner, E. (2003). Imitation performance in toddlers with autism and those with other developmental disorders. *Journal of Child Psychology and Psychiatry*, *44*, 763–781.

Rosenbaum, D. A., Marchak, F., Barnes, H. J., Jonathan, V., Slotta, J. D., & Jorgensen, M. J. (1990). Constraints for action selection: Overhand versus underhand grips. In M. Jeannerod (Ed.), *Attention and performance 13: Motor representation and control* (pp. 321–342). Hillsdale, NJ, USA: Lawrence Erlbaum Associates, Inc.

Rumiati, R. I., Weiss, P. H., Tessari, A., Assmus, A., Zilles, K., Herzog, H., et al. (2005). Common and differential neural mechanisms supporting imitation of meaningful and meaningless actions. *Journal of Cognitive Neuroscience*, *17*, 1420–1431.

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*, 1157–1162.

Smith, I. M., & Byrson, S. E. (1998). Gesture imitation in autism i: Nonsymbolic postures and sequences. *Cognitive Neuropsychology*, *15*, 747–770.

Stone, W. L., Ousley, O. Y., & Littleford, C. D. (1997). Motor imitation in young children with autism: What's the object? *Journal of Abnormal Child Psychology*, *25*, 475–485.

Tessari, A., & Rumiati, R. I. (2004). The strategic control of multiple routes in imitation of actions. *Journal of Experimental Psychology: Human Perception and Performance*, *30*, 1107–1116.

Tranel, D., Kemmerer, D., Adolphs, R., Damasio, H., & Damasio, A. R. (2003). Neural correlates of conceptual knowledge for actions. *Cognitive Neuropsychology*, *20*, 409–423.

Wapner, S., & Cirillo, L. (1968). Imitation of a model's hand movements: Age changes in transposition of left-right relations. *Child Development*, *39*, 887–894.

Wellman, H. M., & Liu, D. (2004). Scaling of theory-of-mind tasks. *Child Development*, *75*, 523–541.

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*, 655–664.

Williams, J. H., Whiten, A., & Singh, T. (2004). A systematic review of action imitation in autistic spectrum disorder. *Journal of Autism and Developmental Disorders*, *34*, 285–299.

Williams, J. H., Whiten, A., Suddendorf, T., & Perrett, D. I. (2001). Imitation, mirror neurons and autism. *Neuroscience and Biobehavioural Reviews*, *25*, 287–295.