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Movement interference in autism-spectrum disorder☆

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Abstract

Movement interference occurs when concurrently observing and executing incompatible actions and is believed to be due to co-activation of conflicting populations of mirror neurons. It has also been suggested that mirror neurons contribute towards the imitation of observed actions. However, the exact neural substrate of imitation may depend on task demands: a processing route for goal-directed meaningful actions may be distinct from one for non-goal-directed actions. A more controversial role proposed for these neurons is in theory of mind processing, along with the subsequent suggestion that impairment in the mirror neuron circuit can contribute to autism-spectrum disorder (ASD) where individuals have theory of mind deficits. We have therefore examined movement interference in nine ASD participants and nine matched controls while performing actions congruent and incongruent with observed meaningless arm movements. We hypothesised that if the mirror neuron system was impaired, reduced interference should be observed in the ASD group. However, control and ASD participants demonstrated an equivalent interference effect in an interpersonal condition, with greater movement variability in the incongruent compared to the congruent condition. A component of movement interference which is independent of congruency did differ between groups: ASD participants made generally more variable movements for the interpersonal task than for biological dot-motion task, while the reverse was true for the control participants. We interpret these results as evidence that the ASD participant group either rely to a greater extent on the goal-directed imitation pathway, supporting claims that they have a specific deficit of the non-goal-directed imitation pathway, or exhibit reduced visuomotor integration.

Keywords: Imitation; Autism; Mirror neurons; Facilitation

1. Introduction

1.1. The role of the mirror neuron system in action observation and imitation

In recent years it has become well established that observation of human movement influences the observer's own motor system. For example, concurrent observation and execution of a compatible action (e.g. lifting the index finger while observing index finger elevation) results in a facilitation in reaction time, whereas during incompatible observation/action combinations (e.g., lifting the index finger while observing finger depression) interference in movement initiation is indicated by increased reaction times (Brass, Bekkering, Wohlschlager, & Prinz, 2000; Brass, Bekkering, & Prinz, 2001; Craighero, Bello, Fadiga, & Rizzolatti, 2002; Vogt, Taylor, & Hopkins, 2003; see Vogt & Thomaschke, 2007 for a recent review of the perception–action system). The neural basis of such effects has been clarified with the discovery of mirror neurons, present in the pars opercularis of the ventral premotor cortex (BA 44) and inferior parietal lobe (Buccino et al., 2001; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Grezes, Armony, Rowe, & Passingham, 2003; Iacoboni et al., 1999; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Mirror neurons discharge during both observation and execution of an action, leading to the theory that facilitation and interference effects may result from co-activation of compatible or incompatible sets of mirror neurons (Blakemore & Frith, 2005).

Owing to the combined observation/execution properties of mirror neurons, Iacoboni and others have described them as core components of an imitation network (Iacoboni, 2005; Iacoboni & Dapretto, 2006; Iacoboni et al., 1999; Rizzolatti,

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Fogassi, & Gallese, 2001). However, recent evidence from neuroimaging and neuropsychological studies indicates that there are at least two different neural pathways underlying imitation, dependent on the semantic content of the action to be imitated. One is a goal directed, transitive (meaningful) route, the other a non-goal directed, intransitive (meaningless) route. There is some disagreement at present as to the exact neural areas involved in each route. One hypothesis of imitation proposes that transitive actions are associated with the inferior temporal gyrus and hippocampus and that intransitive actions have greater association with visuospatial areas such as the superior temporal lobe, parieto-occipital and occipitotemporal junctions (Rumiati et al., 2005; Tessari, Canessa, Ukmar, & Rumiati, 2007). Focussing particularly on the mirror neuron system, Molnar-Szakacs, Iacoboni, Koski, and Mazziotta (2005) proposed a functional and anatomical split within the pars opercularis of the inferior frontal gyrus whereby the ventral region processes details relating to action goals and the dorsal region guides detailed observation–execution matching in conjunction with the superior temporal sulcus (STS) and inferior parietal regions. Similarly, activation of ventral premotor mirror neurons has also been associated to a greater extent with goal-directed actions, whereas intransitive actions preferentially activated superior and inferior parietal lobes (Decety et al., 1997; Grezes, Costes, & Decety, 1998; Koski et al., 2002). However, as an alternative to this hypothesis, several authors have suggested a model whereby goals are represented in the intraparietal suclus, whereas the inferior frontal gyrus is more important in encoding the specific properties of an action (Hamilton, 2008; Hamilton & Grafton, 1996; Rizzolatti & Craighero, 2004).

1.2. The role of the mirror neuron system in theory of mind

It has been suggested that mirror neurons may contribute towards action understanding, action prediction and to theory of mind (ToM) processes by mentally reproducing or "simulating" the goals and outcomes of others' actions (Frith & Frith, 1999; Gallese & Goldman, 1998; Hamilton & Grafton, 2006; Iacoboni et al., 1999, 2005; Jeannerod, 2001; Rizzolatti et al., 2001). ToM is the ability to understand other people in terms of their intentions, beliefs and desires. Consequently, deficits in the mirror neuron system have been proposed to underlie some of the behavioural characteristics present in autistic spectrum disorder (ASD) where affected individuals fail to acquire a ToM. A number of neuroimaging studies have reported altered mirror neuron activity in ASD (Bernier, Dawson, Webb, & Murias, 2007; Dapretto et al., 2006; Hadjikhani, Joseph, Snyder, & Tager-Flusberg, 2006; Nishitani, Avikainen, & Hari, 2004; Oberman et al., 2005; Williams, Gilchrist, Perrett, Murray, & Whiten, 2006). These data support the hypothesis that many of the social impairments present in ASD may be attributed to an underlying mirror neuron system deficit.

1.3. Imitation and ASD

If mirror neuron activity is abnormal in those with ASD, one would expect to see altered movement facilitation and interference during observation of actions, as well as other effects such as impaired action understanding, prediction and imitation. However, evidence on this topic is contradictory which may be a consequence of task demands such as the effector used (face vs. hand), or the transitive versus intransitive nature of the imitation. For example, Theoret et al. (2005) reported reduced motor cortical modulation using transcranial magnetic stimulation (TMS) during observation of intransitive finger movements in ASD participants. Imitation tasks that use meaningless gestures evoke impaired performance in those with ASD (McIntosh, Reichmann-Decker, Winkielman, & Wilbarger, 2006; Williams, Whiten, & Singh, 2004), whereas those that use goal-directed actions demonstrate intact ability (Hamilton, Brindley, & Frith, 2007; Hobson & Lee, 1999; McIntosh et al., 2006; Williams et al., 2004). In addition, recent work indicates that adults with high functioning autism or Asperger syndrome are able to represent the actions of others' (Sebanz, Knoblich, Stumpf, & Prinz, 2005). Consequently, the contribution of mirror neuron dysfunction to behavioural characteristics in ASD is likely to be more complex than first suggested. On balance, one possible interpretation of these studies is that during imitation tasks, individuals with ASD have differential impairment of those circuits involved in goal-less directed imitation. A model to this effect has been put forward by Hamilton (2008), suggesting that individuals with ASD have an intact goal-directed pathway mediated by occipital–parietal connections but a deficient pathway for the mimicry of meaningless actions mediated by occipital-frontal connections.

In light of this conflicting literature and limited behavioural data concerning facilitation and interference in ASD, the current work examined movement interference in a group of ASD individuals using a previously reported paradigm (Kilner, Paulignan, & Blakemore, 2003). In this task, participants make either horizontal or vertical intransitive and continuous arm movements in time with the movements of an experimenter so that the two peoples' movements are either congruent (i.e. both moving in the same plane) or incongruent (i.e. participant moving their arm in plane perpendicular to that of experimenter). Finger tip movement variability (as measured in the orthogonal plane) is greater in the orthogonal plane for incongruent than for congruent conditions (Kilner et al., 2003; Stanley, Gowen, & Miall, 2007) and is termed the "interference effect". We predict that if the mirror neuron system was abnormal in ASD, particularly for the processing of observed meaningless actions, then the ASD participant group would demonstrate a smaller or null interference effect compared to a matched control group.

We have recently extended the interpersonal interference task by examining interference during presentation of a small dot projected onto a screen that could have either a biological (pre-recorded human arm movement) or non-biological (computer generated, constant-velocity sinusoid) motion profile (Stanley et al., 2007). Our data demonstrated that the interference effect was present if participants were instructed that both dot-motion stimuli were human generated and also uncovered a component of movement variability that was independent of congruency and agency instruction, but was driven by the higher variability of the biological as opposed to non-biological

dot-motion profiles (Stanley et al., 2007). We attributed this to a bottom-up effect of stimulus content on the ongoing arm movement. This congruency-independent or "bottom-up" interference effect may be of particular relevance for the intransitive route of action processing that is concerned with the specifics of movement detail. This is supported by data indicating that during imitation of goal-less actions more emphasis appears to be placed on effector selection and movement execution, whereas goal-directed actions are imitated correctly in respect to the goal while details regarding the movement may be ignored (Bekkering, Wohlschläger, & Gattis 2000; Franz, Ford, & Werner, 2007). Moreover, adults performing more difficult imitation tasks frequently imitate the goal of an action rather than perform an exact replication (Tessari & Rumiati, 2004; Wohlschläger, Gattis, & Bekkering, 2003). Consequently, the effect of stimulus variability may provide an indication of the degree of visuomotor coupling between the observed and executed movements. If ASD individuals rely more on abstract, goal-directed simulation, and are less able to simulate goal-less intransitive actions, then their arm trajectories should be less affected by the bottom-up increased variability in the biological dot-motion profile. Therefore, in the current study we explored the effect of stimulus presentation on our ASD participants, using these biological and not biological dot stimuli, as well as the interpersonal task.

In summary, based on the assumption that the mirror neuron system is dysfunctional in ASD, we predict less congruency-dependent motor interference ("incongruent interference") in that group than in controls, as well as less congruency-independent ("bottom-up") influence of the stimulus.

2. Methods

2.1. Participants

Participants were 12 ASD individuals (6 males) and 12 sex, age and IQ matched healthy controls. The data of three male participants from the ASD group was excluded due to one being left-handed, one being unable to maintain the correct pace of arm movement and one exhibiting consistently greater movement variability across all tasks (>2S.D.). Neuropsychological assessment of these latter two participants using the tasks documented below did not differ from the rest of the group. ASD participants had been given a diagnosis by outside clinical assessment (DSM IV criteria, American Psychiatric Association, 1994 or ICD-10, WHO, 1992) of either high functioning autism ($n=2$) or Aspergers' syndrome ($n=7$). None of the participants reported a diagnosis of developmental coordination disorder. Average age (±S.D.) of the nine ASD and control participants was 33.9 ± 13.2 and 32.0 ± 11.8, respectively. Average IQ (±S.D.) measured using the abbreviated WAIS was 117.6 ± 20.5 and 115.7 ± 14.1 for the ASD and control participants respectively. Age ($t=0.22$; $p=0.83$) and IQ ($t=0.83$; $p=0.96$) did not significantly differ between the two groups. All participants demonstrated binocular Snellens visual acuity of better than 6/9. Each participant gave written informed consent to participate and the study was approved by a local ethical committee, being performed in accordance with ethical standards laid down in the 1964 Declaration of Helsinki.

2.2. Assessment of ToM

To measure their mentalizing ability, all subjects performed false belief tasks, the results of which are shown in Table 1 in order of increasing ability. Four of these (Sally-Ann task (Wimmer & Perner, 1983), smarties, coat/ice cream story (Perner & Wimmer, 1985)) were scored as pass or fail. Responses to a penny hiding task (Baron-Cohen, 1992) were given a % score out of six repetitions and responses to Happe stories (Happe, 1994) were given a % score out of a total of 16. Each ASD participant was given a total score across these ToM tasks (Table 1). Mean autism-spectrum quotient (AQ) scores were significantly higher for the ASD group compared to the control group (ASD: 36.7 ± 6, minimum 34; control: 11.6 ± 5, maximum 18; $t=9.8$; $p<0.001$). It has been suggested that a score of 32+ distinguishes individuals who have clinically significant levels of autistic traits (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubely, 2001).

2.3. Movement recording and signal processing

Fingertip position was recorded using the Optotrak 3020 active marker system (Northern Digital Instruments, Inc.). An infrared sensor was attached to a plastic thimble on the participant's right hand index finger, and sensor position recorded at 250 Hz, with 0.01 mm spatial resolution; only data from the horizontal x-plane and the vertical z-plane were used in the analysis. The plane of instructed movement (e.g., the x-plane during a horizontal movement, and the z-plane in a vertical movement) is referred to hereafter as the "dominant" plane; the orthogonal plane is referred to as the "error" plane. The experimenter's fingertip position was also recorded for those trials where the participant moved in time with the experimenter, but is not reported here.

Following data acquisition, fingertip position data were filtered with a 20 Hz Butterworth filter (all analysis conducted in Matlab, Mathworks Inc.) prior to movement scoring. Each trial's data were split into single movement segments

Table 1
Scores for the nine ASD participants on mentalizing tasks in increasing order of ability

Subject	Smarties	Sally-Ann	Coat story	Ice cream story	Penny hiding	ToM Happé stories	Total	IQ	AQ scores
8	1	1	0	–	–	0.63	2.63	123	41
7	1	0	0	1	0.67	0.81	3.48	94	40
9	1	1	0	0	1	0.56	3.56	108	45
3	1	1	1	1	0	0.94	4.94	132	35
6	1	1	1	1	0.33	0.75	5.08	131	35
1	1	1	1	1	0.67	0.63	5.3	139	43
4	1	1	1	1	0.67	0.88	5.55	78	35
5	1	1	1	1	1	0.69	5.69	119	41
2	1	1	1	1	1	0.88	5.88	134	34
Controls ($N=9$)	1	1	1	1	1	0.92	5.92 (5.88–6)	115.7 ± 14.1 (98–136)	11.6 ± 5.0 (5–18)

Controls have been grouped together and averaged for each separate task and "total" reflects the total of these averages. 1 = pass and 0 = fail. Penny hiding and Happe stories were given a % score out of a total of 6 and 16, respectively. Final two columns display IQ and AQ score, respectively. ToM: theory of mind. Dash indicates tasks not performed.

(e.g., from extreme left to extreme right was one segment, and returning from right to left another segment). Endpoints for each segment were detected by finding the datapoints where velocity in the dominant movement plane crossed zero.

To quantify interference, the standard deviation of fingertip position (mm) was calculated within the error plane for each movement segment. The mean of these deviation scores was then calculated across all movement segments to give a single average of error-plane deviation for each trial, for each participant. As noted by Stanley et al. (2007), using S.D. of error plane variations appears preferable to using variance (as in the original Kilner et al., 2003 study) as the non-linear nature of the variance measure produces group/condition means that are inappropriately influenced by outlying data, with consequences for subsequent analysis.

2.4. Stimuli

The visual stimulus was a 1-cm diameter white dot, presented on a black background projected onto a white screen 1.9 m from the participant. The centre of the projector screen was at a height of 1.55 m; the projector refresh rate was 60 Hz. The metronome for self-pacing movements was a sequence of tones presented at 1 Hz over headphones.

The biological dot-motion stimulus was pre-recorded data of the experimenter moving his arm in time with the audio metronome. The presented trajectories therefore included variation in the plane orthogonal to the dominant movement direction (e.g., there were fluctuations in vertical position during the presented horizontal movements). Data were scaled so that 50 cm in the recorded data corresponded to 50 cm on the projection screen. Movement frequency and the amplitude of the individual movement segments varied naturally over the course of the recording (also true for trials where the participant observed the experimenter moving). The non-biological dot-motion stimulus was of a constant speed (50 cm/s) with fixed amplitude of 50 cm on the projection screen, and a fixed frequency of 0.5 Hz. The dot instantly changed direction when reaching either end of its range. For this stimulus, position orthogonal to the main plane of movement direction was invariable. The difference in the motion between the two dot trajectories was clearly visible to the participants. Both the biological and non-biological dot-motion stimuli were identical to those used by Stanley et al. (2007) where greater detail of the velocity profiles can be found.

2.5. Procedure

2.5.1. Testing dot-motion stimuli

Participants were instructed to perform movements of about 50 cm amplitude. Initially, each participant performed two practice trials (30 s duration) in time with the auditory metronome—one block of horizontal arm movements, followed by one block of vertical arm movements, while fixating a stationary circular target. Movements were timed so that the endpoints of each movement coincided with the tone.

Participants then performed the dot-motion trials that were blocked by motion profile of the observed dot stimulus (biological or non-biological), with the order of presentation counterbalanced across participants. Participants were informed that both dot stimuli were human generated (i.e. pre-recorded arm movements) and were asked to move in phase with the dot movement. At the start of each trial, the participant was instructed as to the plane in which to move his or her arm, as well as the dot-motion plane. Recordings began 2–3 s after the participant was moving in phase with the displayed dot stimulus, and lasted for 30 s. Four trials, consisting of the different combinations of congruent and incongruent arm/dot-motion conditions for the two movement planes were conducted for each dot-motion type, with order again counterbalanced across participants.

2.5.2. Testing interpersonal interference

Trial structure was identical to the dot-motion task, except that participants moved in phase with a gender-matched experimenter, who stood 190 cm away (toe-to-toe distance). The experimenter performed arm movements in time with the auditory metronome with eyes closed. The interpersonal task was always conducted last to preclude the possibility of carry over effects contaminating the dot-motion trial data (see discussion of this issue in Stanley et al., 2007).

2.6. Data analysis

Data for fingertip position standard deviation in the error plane were analyzed across both dot-motion and interpersonal movement task using a $3 \times 2 \times 2 \times 2$ ANOVA design with factors of task (biological dot-motion, non-biological dot-motion, interpersonal), direction of participant's performed movement (horizontal, vertical), congruency of observed action, and subject group (ASD, control). For significant main effects and two-way interactions, *t*-tests were performed between the appropriate levels of the factors involved, using a Bonferroni α-correction for multiple tests. Correlations between interference effects and ASD measures (ToM and ASQ scores) were conducted using Pearson's correlation.

3. Results

All of the following analyses are collapsed across movement direction. The results can be seen in Figs. 1a–b and 2a–b, for the biological, non-biological and interpersonal conditions. From the omnibus ANOVA, main effects of congruency ($F(1,16) = 18.90$, $p < 0.001$) and task ($F(2,32) = 7.78$, $p = 0.002$) were observed, along with interactions for task × congruency ($F(2,32) = 7.58$, $p = 0.02$) and task × subject

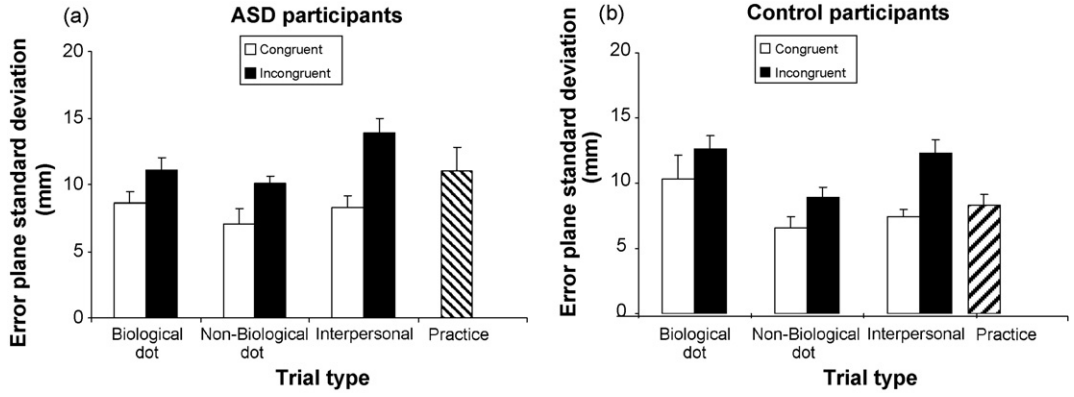

Fig. 1. Error plane standard deviation (mm) in the ASD (a) and control group (b) for congruent (white bars) and incongruent trials (black bars) during biological dot-motion trials, non-biological dot-motion trials and interpersonal trials. Hatched bar indicates error plane standard deviation for practice trials. Data is collapsed across direction. Standard error bars are shown.

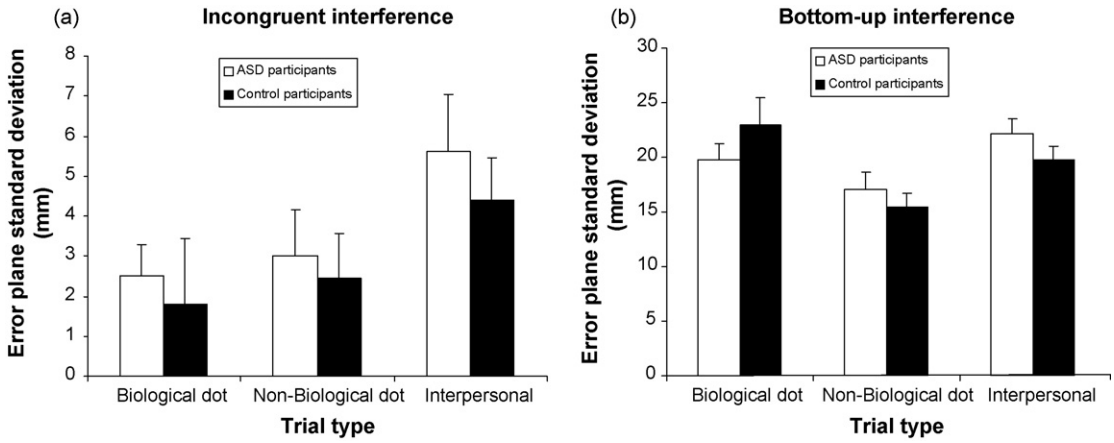

Fig. 2. Incongruent (a) and bottom-up (b) interference (mm) in the ASD (white bars) and control group (black bars) during biological dot-motion trials, non-biological dot-motion trials and interpersonal trials. Incongruent interference was calculated by subtracting error plane deviation in the incongruent plane from the congruent plane for each participant then taking the average. Bottom-up interference was calculated by summing congruent and incongruent error plane deviation for each participant, then taking the average. Data is collapsed across direction. Standard error bars are shown.

group ($F(2,32) = 3.64$, $p = 0.001$). Importantly, there was no overall significant difference between the two participant groups ($F(1,16) = 0.015$, $p = 0.9$) and no interactions between group and congruency ($F(1,16) = 0.294$, $p = 0.595$). No other interactions were significant ($F(1,16) \leq 1.99$, $p \geq 0.17$).

3.1. Main effects of congruency and task

As expected, the main effect of congruency signified greater interference for the incongruent (mean ± S.E. = 11.53 ± 0.49) compared to congruent trials (mean ± S.E. = 8.23 ± 0.65) (Fig. 1a and b). Concerning the main effect of task (on average over congruency, direction and group), error plane deviation in the biological dot profile (mean ± S.E. = 10.83 ± 0.71) and interpersonal task (mean ± S.E. = 10.4 ± 0.45) was significantly greater than in the non-biological dot profile task (mean ± S.E. = 8.45 ± 0.5) ($t(17) = 3.41$; $p = 0.003$: $t(17) = 3.1$; $p = 0.007$, respectively; Bonferroni corrected critical $\alpha = 0.0167$, for three tests). Collapsed across both groups, error plane deviation did not vary between the biological dot-motion and interpersonal tasks ($t(17) = 0.65$; $p = 0.523$).

3.2. Task × congruency interaction: greater incongruent interference in the interpersonal task

In regards to the task × congruency interaction, interference effects (incongruent trial standard deviation–congruent trial standard deviation) were calculated for each task, and three paired *t*-tests (Bonferroni corrected critical $\alpha = 0.0167$) compared these interference effects across tasks (on average over the ASD and control groups). The interpersonal task produced a greater interference effect than both the biological dot task ($t(17) = 3.61$, $p = 0.002$) and the non-biological dot task ($t(17) = 3.27$, $p = 0.005$). Interference effects in the biological and non-biological dot tasks were not significantly different ($t(17) = 0.72$, $p = 0.48$). The amount of incongruent interference for each task can be seen in Fig. 2a.

3.3. Task × group interaction: bottom-up interference differs between the biological dot-motion and interpersonal tasks according to participant group

In order to follow up the task × group interaction, difference scores were calculated for the three possible comparisons between the task conditions (biological dot, non-biological dot, and interpersonal tasks). These difference scores (Table 2) provided information on which motion type produced relatively higher error-plane deviations, independent of congruency (bottom-up interference). The unpaired *t*-test comparing the two groups on the difference between the biological dot task and the interpersonal task was significant, $t(16) = 2.69$, $p = 0.0161$ (Bonferroni corrected critical $\alpha = 0.0167$, for three tests). For control participants, fingertip position deviation was higher in the biological dot task than in the interpersonal task (Table 2); for ASD participants, the reverse was true with lower scores of fingertip position deviation in the biological dot task

Table 2
Differences in error-plane deviation scores by task, for the ASD and control groups

Difference score	ASD		Control		Between group *t*-tests	
	Mean	S.E.M.	Mean	S.E.M.	*t*(16)	*p*
Biological–non-biological	1.32	0.81	3.45	1.07	1.59	0.13
Non-biological–interpersonal	−2.54	1.00	−1.26	0.70	1.04	0.313
Biological–interpersonal	−1.22	0.76	2.19	1.02	2.69	0.016

T-tests compare difference scores between ASD and control groups.

relative to the interpersonal task. This pattern can be observed in Fig. 2b. Comparisons of the relative differences between biological/non-biological and non-biological/interpersonal task suggested no significant pattern of differences between the groups (see Table 2).

3.4. Summary

In summary, greater error plane deviation was observed during incongruent compared to congruent trials for both participant groups indicating that the ASD group also displayed incongruent interference. Less overall error plane deviation was observed in the non-biological motion condition than in the biological dot-motion or in the interpersonal conditions for both groups. Incongruent interference was greater for the interpersonal task across both subject groups. Compared to the ASD participants, control participants showed a greater degree of bottom-up, congruency-independent movement interference in the biological task relative to the interpersonal task.

3.5. Comparisons between ToM/ASQ scores and interference effects

The ASQ scores for each ASD participant were compared to the amount of incongruent interference for each task (biological, non-biological and interpersonal) using Pearson's correlation. Interference was measured as the difference in error plane variance between congruent and incongruent conditions. This was also performed for a total interference score calculated by taking the average across all 3 tasks. No significant correlations were observed for any comparison ($r \leq 0.43$; $p \geq 0.25$). Correlations were also performed between incongruent interference and ToM score. Once again, no significant correlations were observed for any comparison ($r \leq 0.32$; $p \geq 0.41$), although a larger sample size is required to fully explore this issue.

4. Discussion

Contrary to our first prediction, the ASD participants demonstrated incongruent interference effects in the interpersonal task, equivalent to the control group. Furthermore, both ASD and control participants demonstrated less error plane deviation in the non-biological dot-motion task compared to the interpersonal tasks. However, the two participant groups demonstrated a different pattern of bottom-up interference across the three tasks: the ASD group exhibited greater error plane deviation during the interpersonal task, while the control group produced greater error plane deviation during the biological dot-motion task. Overall, these results suggest that in our group of ASD individuals, the mechanisms underlying concurrent action observation and execution in a simple, apparently meaningless task were sufficient to produce equivalent incongruent interference effects as in the control participants. If co-activation of mirror neurons during the interpersonal task condition is indeed responsible for the interference effect, this would further imply that the ASD group exhibited behaviourally equivalent mirror neuron function. Nevertheless, the different pattern of bottom-up interference across the three tasks (the significant task × group interaction) does suggest potential differences in function between the two groups, which we will return to later on.

4.1. ASD individuals demonstrate incongruent interference on the interpersonal task

The finding of an equivalent incongruent interference effect for both ASD and control participants on the interpersonal task is inconsistent with the hypothesis of a global mirror neuron dysfunction in the ASD group. We suggest three possible interpretations for these findings: (1) Mirror neuron activity is not responsible for the interference effect; (2) the mirror neuron system was intact in our group of high functioning ASD participants; (3) certain components of the mirror neuron system retain function in ASD individuals.

Firstly, the incongruent interference may be a consequence of shared representational resources other than co-activation of mirror neurons, in common with more general spatial stimulus–response compatibility effects that occur with non-biological stimuli (Cho & Proctor, 2003). Indeed, facilitation and interference during stimulus–response compatibility tasks using biological stimuli can arise due to the stimulus and response sets being spatially congruent or incongruent respectively (Brass et al., 2000; Stürmer, Aschersleben, & Prinz, 2000). Both spatial compatibility and automatic imitation (the latter thought to depend on the mirror neuron system) have been shown to influence the amount of interference and facilitation during imitation (Bertenthal, Longo, &Kosobud, 2006). Although experiments have not yet been performed to directly test for mirror neuron activity during the task we used here, evidence from our previous work (Stanley et al., 2007) using the biological and non-biological dot-motion stimuli speaks to this: Interference was not observed during the two dot-motion conditions when participants believed them to be computer generated. If general spatial compatibility effects were responsible for interference one would expect interference to be present consistently for the interpersonal and dot-motion tasks. However, future work is required to directly test this suggestion.

Secondly, in regards to the high functioning ability of our participants, we believe that it will be important to assess a wider range of participants in future studies. However, those neuroimaging studies that have reported abnormal mirror neuron functioning in ASD have used participant groups equivalent to ours (Bernier et al., 2007; Dapretto et al., 2006; Nishitani et al., 2004; Oberman et al., 2005; Williams et al., 2006). Therefore, according to these studies interference should be reduced even in high functioning individuals.

Thirdly, components of the mirror system may still retain some degree of function in both children and adults with ASD, as indicated by findings of their intact abilities to imitate and represent others' actions (Hamilton et al., 2007; Hobson & Lee, 1999; McIntosh et al., 2006; Sebanz et al., 2005; Williams et al., 2004). Indeed, it has previously been suggested that individuals with ASD may have a selective impairment of the goal-less directed route of imitation, with unimpaired goal-directed imitation (Hamilton, 2008). Although the repetitive arm action in

our task appears meaningless, participants may have successfully performed the task by attributing a goal to it, or to each movement end point, hence depending more on those mirror neuron systems involved in processing transitive actions, and thus causing an interference effect.

The use of different processing strategies by individuals with ASD could help to explain the conflict between neuroimaging and behavioural findings. Those papers that have examined mirror neuron activity in the manual domain have employed simple, meaningless tasks (Oberman et al., 2005; Williams et al., 2006). So, if ASD participants were performing the imitation task in a different (but behaviourally correct) manner i.e. using a goal-directed pathway, functional activity would be expected to be different to the control group. Future studies should attempt to specifically examine transitive versus intransitive actions using a combination of both imaging and behavioural data.

4.2. ASD and control participants demonstrate different patterns of bottom-up interference

As with our previous work (Stanley et al., 2007; also see Bouquet, Gaurier, Shipley, Toussaint, & Blandin, 2007), the biological dot-motion condition created greater arm movement variability in the control participants regardless of congruency than did the non-biological dot-motion. We previously interpreted this as due to bottom-up processing of the stimulus properties as there was greater variability present in the biological as opposed to non-biological dot stimulus and because the effect was independent of agency instruction and congruency (Stanley et al., 2007). In addition, we further suggested that this congruency-independent bottom-up interference has similarities with imitation of intransitive actions and hence with processing of the specific details of movement. This differential effect of stimulus properties on action execution is also highlighted in studies of imitation style. Bekkering et al. (2000) demonstrated that transitive actions are imitated correctly in respect to the goal, but details regarding the movement may be ignored, whereas in intransitive action imitation, greater attention is paid to movement execution. In addition, during observation of goal-directed movements, observer's eye movements are predictive rather than linked reactively to the observed movement (Flanagan & Johansson, 2003), implying that the goal is identified in advance of movement execution. Furthermore, as imitation of meaningless actions becomes more familiar, functional brain activation switches from visual areas (V3, V5, MT) to more frontal and parietal areas, indicating less focus on the visual stimulus once the outcome or goal has been established (Grezes, Costes, & Decety, 1999).

The results of our current work support this interpretation as incongruent (top-down) interference was greater for the interpersonal task as opposed to both types of dot-motion task across both participant groups, suggesting that goal attribution occurred to a greater extent in the interpersonal task. However, the pattern of bottom-up interference in the biological dot and interpersonal tasks differed between the ASD participants and the control group, suggesting that attention to and subsequent processing of the visual stimuli differed between both tasks and subject groups. Perhaps due to the meaningless nature of the biological dot, visual attention towards this stimulus was higher in the control participants than for the interpersonal arm movement. In contrast, visual processing in ASD participants may have been biased towards the interpersonal task where apparent goals may have been more obvious.

Alternatively, our results may be explained by reduced visuomotor integration in the ASD participants so that the visual properties of the observed dot motion were less efficiently integrated into the executed movement and parallel previous observations that children with ASD are less precise in their imitation of action (Hobson & Lee, 1999; Vanvuchelen, Roeyers, & Weerdt, 2007). In addition, some visuomotor differences between ASD and control participants may be evident in the higher baseline variability in the ASD group, as indicated by their greater (albeit non-significant) error plane variability in both non-biological and interpersonal tasks. This makes the biological dot-motion findings potentially more revealing. Abnormal sensory motor integration deficits in ASD have previously been suggested from studies that examine visually guided actions and dorsal stream processing (Gowen & Miall, 2005; Mari, Castiello, Marks, Marraffa, & Prior, 2003; Piek & Dyck, 2004; Spencer et al., 2000). There is growing evidence that processing within occipital visual areas and the STS and subsequent connections with the inferior frontal areas may be impaired in those with ASD (Castelli, Frith, Happe, & Frith, 2002; Just, Cherkassky, Keller, & Minshew, 2004; Villalobos, Mizuno, Dahl, Kemmotsu, & Muller, 2005; Williams et al., 2006; Zilbovicius et al., 2006) which may result in altered visually guided movements and less accurate imitation.

Finally, there exists a well established literature documenting motor difficulties in ASD (Dewey, Cantell, & Crawford, 2007; Glazebrook, Elliot, & Lyons, 2006; Gowen & Miall, 2005, 2007; Green et al., 2002; Hallett et al., 1993; Miyahara et al., 1997; Ming, Brimacombe, & Wagner, 2007; Rinehart, Bradshaw, Brereton, & Tonge, 2001). As mentioned above, the ASD participants appeared to show slightly more error plane variability for all tasks except the biological dot-motion task, which suggests the presence of motor deficits within our ASD population. However, this error plane variability was not significantly different between the two participant groups and any concomitant motor deficits were not severe, which is supported by the absence of developmental coordination disorder comorbidity in our group. So while visuomotor integration differences may explain the pattern of bottom-up interference, all nine ASD participants showed a top-down incongruent interference effect, indicating that this observation is a robust finding irrespective of any motor abnormalities.

5. Conclusions

Our results demonstrate an equivalent incongruent interference effect in both ASD and control participants in all versions of the task. However, ASD participants demonstrated greater error plane deviation during the interpersonal task where incongruent interference was maximal, whereas control participants exhibited greater error plane deviation in the biological dot-

motion condition, indicating differences in way the two groups performed the tasks. We suggest two possible reasons for this difference. Firstly, in line with recent work (Hamilton, 2008), visual processing in the ASD participants may have been biased towards stimuli that were more obviously goal related, such as the arm movement compared to the dot motion, whereas control participants showed the reverse tendency. Secondly, altered visuomotor integration in the ASD participants may have reduced the impact of bottom-up stimulus variability.

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