

Disorders of Shared Representations

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Abstract

This chapter will begin with a focus on a particular subtopic within the shared representations research domain: imitation. Imitation occurs when the perception of another's actions causes the activation of the corresponding motor representation in the observer. Thus imitation relates to *shared representations* in that it concerns the activation of a self-related representation by an other-related representation. In this chapter I will use examples from the autism spectrum conditions (ASCs) literature to argue that if either the self- or other-related representation is atypical this can result in atypical imitation. In other words, if action observation or action execution mechanisms are atypical, then imitation will be affected. I will conclude this chapter by drawing on research that extends this logic to other socio-cognitive domains such as empathy and to conditions such as schizophrenia and alexithymia.

Imitation

The Importance of Imitation

Imitation is intricately linked with social interaction. Being imitated increases rapport (Chartrand & Bargh, 1999), altruistic behavior (van Baaren, Holland, Kawakami, & van Knippenberg, 2004) and trust (Bailenson & Yee, 2005). Furthermore, individuals imitate more when in possession of a positive social attitude (Cook & Bird, 2011, 2012; Lakin & Chartrand, 2003; Leighton, Bird, Orsini, & Heyes, 2010). For example, Leighton and colleagues (2010) asked participants to arrange five words such that they formed a grammatically-correct sentence; these sentences either comprised positive social words (e.g. friend, team, assist) or anti-social words (e.g. rebel, obstinate, distrust). Individuals who had rearranged the positive social sentences exhibited significantly higher levels of automatic imitation compared to individuals who had rearranged the anti-social sentences. Thus, imitation is bi-directionally

associated with positive social interaction and is a key component in building social relationships with others (Lakin & Chartrand, 2003; also see Lakens, Schubert, & Paladino this volume, Chapter 13). This tight link between imitation and social interaction has prompted speculation that imitation may be a core difficulty in ASC, which impacts the wider social functioning of individuals with this condition.

Defining Imitation

Automatic imitation, also known as 'simple imitation' (Heyes, 2011) and 'mimicry' (Hamilton, 2008; Tomasello, 1996), is 'a type of stimulus–response compatibility effect in which the topographical features of task-irrelevant action stimuli facilitate similar and interfere with dissimilar responses' (Heyes, 2011, p. 463). For example, Brass, Bekkering and Prinz (2001) instructed participants to perform an index or middle finger lifting movement in response to the appearance on a computer screen of either a 1 or 2. The number was superimposed over a movie of a hand that showed either the same action or the alternative action. Brass and colleagues found that finger movement reaction speeds were slow when participants observed a non-matching action and faster when the matching action was observed. This reaction time (RT) difference is considered an index of the effect of observed action congruency on action selection, i.e. there is conflict between task instruction mediated action selection and imitation mediated action selection on incongruent, but not on congruent, trials. Such automatic imitation effects have been replicated many times and can be found irrespective of effector (Bach & Tipper, 2007; Cook & Bird, 2011, 2012; Gillmeister, Catmur, Liepelt, Brass, & Heyes, 2008; Leighton & Heyes, 2010; Bardi & Brass, this volume, Chapter 8). Such 'interference effects' can also be observed for action control. When a participant is required to execute an action (e.g. horizontal sinusoidal arm movements) and simultaneously observe an incongruent action (e.g. vertical sinusoidal arm movements), the participant's movements are more variable in the direction of the observed incongruent movement compared to when she observes a congruent movement (Figure 23.1; Bouquet, Gaurier, Shipley, Toussaint, & Blandin, 2007; Chaminade, Franklin, Oztop, & Cheng, 2005; Gowen, Stanley, & Miall, 2008; Kilner, Hamilton, & Blakemore, 2007; Kilner, Paulignan, & Blakemore, 2003; Oztop, Franklin, Chaminade, & Cheng, 2005, p. 2005; Stanley, Gowen, & Miall, 2007). Action observation can therefore be said to 'interfere' with ongoing action execution.

This interference effect, defined as variance in the plane orthogonal to the participant's movement (the error plane) for incongruent compared with congruent movement observation, is greater when the observed action is made by an actor with human, rather than robot, form and motion characteristics (Kilner

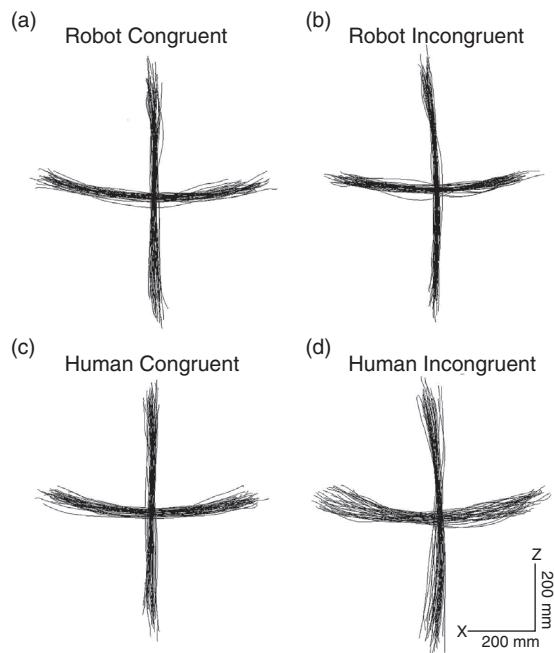


Figure 23.1 Greater interference effect for human compared to robot movements.

Notes: Data from a motion tracker on the hand of a participant whilst she conducts vertical and horizontal sinusoidal movements whilst observing (A) congruent movements conducted by a robot, (B) incongruent robot movements, (C) congruent movements conducted by a human and (D) incongruent human movements. The interference effect (variance in the plane orthogonal to the participant's movement) was greatest when the participant observed human incongruent movements (D).

Source: Image reproduced with permission from Kilner, Paulignan, and Blakemore (2003; Figure 2).

et al., 2003, 2007). With respect to form, Kilner, Paulignan and Blakemore (2003) showed that participants exhibit a greater interference effect when watching actions conducted by a real human compared to actions conducted by a robot (Figure 23.2). Similarly Press and colleagues (2005) demonstrated a greater automatic imitation effect (RT difference between incompatible and compatible actions) for human hand compared to robot hand actions. Interference effects therefore appear to be greater for observed stimuli with human form and human motion compared to stimuli with robot form (for further discussion on the biological specificity of automatic imitation, see Press 2011; see also Press, this volume, Chapter 16)).

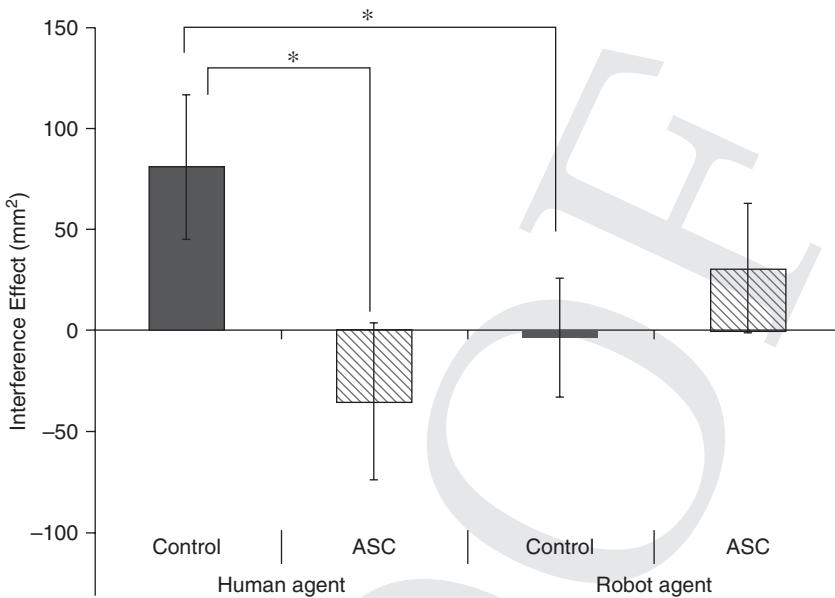


Figure 23.2 Adjusted mean (\pm SEM) interference effect (incongruent minus congruent variance) is displayed.

Notes: The control group exhibited a significant interference effect in the human agent biological motion (BM) and human agent CV conditions but not in the robot agent BM or CV conditions. In contrast, individuals with ASC did not exhibit a significant interference effect for any condition. * $p < 0.05$.

Source: Image modified from Cook, Swapp, Pan, Bianchi-Berthouze, and Blakemore (2014, Figure 3b; CC BY).

In sum, the observation of an incongruent action can result in effects on both action selection and action control. These effects are stronger for human compared to non-human stimuli.

Is the MNS Involved in Imitation?

Mirror neurons, which were originally discovered in the monkey brain (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992), fire both for execution of an action and observation of that same action. Research using a range of neuroimaging methods provides evidence for similar responses to action execution and action observation in the human motor system (e.g. Buccino et al., 2001; Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008; Iacoboni et al., 1999; Kilner, Neal, Weiskopf, Friston, & Frith, 2009; Press, Cook, Blakemore, & Kilner, 2011).

Since imitation is the execution of observed actions and the mirror neuron system (MNS) responds to both action execution and observation it can be hypothesised that the MNS plays a part in imitation. This hypothesis was supported by a fMRI study by Iacoboni et al. (1999) and by TMS studies that have demonstrated that applying repetitive TMS to disrupt activity in mirror neuron regions results in reduced imitation (Catmur, Walsh, & Heyes, 2009; Heiser, Iacoboni, Maeda, Marcus, & Mazziotta, 2003).

Imitation Summary

Imitation, the copying of the body movements of others, is bi-directionally linked with positive social attitudes: being imitated increases positive social attitudes and, in turn, being in possession of a positive social attitude makes a person more likely to imitate. Imitation can occur automatically, resulting in online interference with action execution. Such online interference may be a consequence of the automatic motoric simulation of observed action. Brain regions associated with the human mirror neuron system are active both for the execution and observation of actions, and disrupting activity in these regions can lead to imitation impairments.

Imitation in Autism Spectrum Conditions

ASCs are pervasive developmental disorders characterised by difficulties with social communication and interaction and restricted repetitive patterns of behaviour (American Psychiatric Association, 1994). A number of studies have demonstrated reduced imitation and/or MNS activity in individuals with ASCs compared to control participants (Williams, Whiten, & Singh, 2004). ~~In a recent study we employed virtual reality to investigate the integrity of interference effects (e.g. Kilner et al., 2003, 2007) in ASCs. High-functioning adults with ASCs and age- and IQ-matched healthy controls performed horizontal sinusoidal arm movements whilst observing arm movements conducted by a virtual reality agent with either human or robot form, which moved with either biological motion or at a constant velocity. In another condition, participants made the same arm movements while observing a real human. Arm movement kinematics were recorded with a motion tracking device. Observed arm movements were either congruent or incongruent with executed arm movements. An interference effect was calculated as the average variance in the incongruent action dimension during observation of incongruent compared with congruent movements. Control participants exhibited an interference effect when observing real human and virtual human agent incongruent movements but not when observing virtual robot agent movements. In contrast, individuals with ASCs showed no interference effect for real human, virtual human or virtual robot~~

movements, thus suggesting a disrupted effect of action observation on action execution in ASCs (Figure 23.2).

In 1991 Rogers and Pennington suggested that, along with emotion sharing and theory of mind, a deficit in perception–action matching might be a primary difficulty in ASCs. It was subsequently suggested that the MNS may function atypically in ASCs and that early MNS dysfunction might lead to a cascade of developmental impairments (Ramachandran & Oberman, 2006; Rogers & Pennington, 1991; Williams, Whiten, Suddendorf, & Perrett, 2001). This ‘broken MNS’ hypothesis of ASCs provides a possible explanation for the atypical interference effect that we observed: in other words, if motor neurons comprise the overlap between action observation and action execution, and if this overlap is disrupted in ASCs, this could explain the absence of an effect of action observation on action execution in our virtual reality paradigm. However, experimental evidence for a broken MNS is mixed with studies both supporting (Avikainen, Wohlschläger, Liuhanen, Hänninen, & Hari, 2003; Dapretto et al., 2006; McIntosh, Reichmann-Decker, Winkielman, & Wilbarger, 2006; Oberman et al., 2005; Rogers, Hepburn, Stackhouse, & Wehner, 2003) and opposing (Bird, Leighton, Press, & Heyes, 2007; Dinstein et al., 2010; Gowen et al., 2008; Hamilton, Brindley, & Frith, 2007; Leighton, Bird, Charman, & Heyes, 2008; Press, Richardson, & Bird, 2010; Spengler, Bird, & Brass, 2010) this hypothesis. Furthermore, clinical observations of high levels of echolalia (automatic repetition of speech patterns) and echopraxia (automatic imitation of observed actions) in individuals with ASCs (Russell, 1997; Rutter, 1974; Williams et al., 2004) are incompatible with the hypothesis that the mechanisms mediating mapping from perception to action are impaired. The broken MNS hypothesis has thus received much criticism (Southgate & Hamilton, 2008).

It is important to consider that imitation and interference effects can be decomposed into their constituent parts and that an atypicality in one component can affect the whole process. In other words, since imitation concerns the automatic activation of motor representations upon observation of another’s action, atypical imitation could be the result of atypical action observation and/or atypical motor execution. For example, an atypical interference effect could be due to atypical visual processing of the sinusoidal arm movement (i.e. atypical biological motion processing). If this arm movement is not processed typically it may not result in activation of the corresponding motor representation and thus an interference effect would not be observed. In the following section we will review the evidence for atypical biological motion processing in ASCs.

Is Biological Motion Processing Impaired in ASCs?

‘Biological motion’ refers to the movements of other animate beings. Biological motion processing has been studied using a variety of stimuli from

animations of moving people (e.g. Pelphrey et al., 2003) to single dots moving with a velocity profile that matches human movement (Dayan et al., 2007). The most common stimulus employed is the 'point-light display' (PLD) developed by Johansson (1973), whereby he attached 10 light bulbs to the joints of an actor and filmed his movements in a dark room. A number of studies employing PLD stimuli have reported difficulties with biological motion processing in children with ASCs compared to typically developing (TD) children. In a *recent* single case study, Klin and Jones (2008) showed children upright or inverted PLD videos accompanied by soundtracks. They found that, whereas TD children preferentially looked at the upright over the inverted PLD, a child with an ASC did not. In a follow-up study, Klin, Lin, Gorrindo, Ramsay, and Jones (2009) found that, whereas a TD group of two-year olds preferentially looked at the upright PLDs, an ASC group of two-year olds preferentially looked at points of audio-visual synchrony (e.g. the simultaneous collision of two dots and presentation of 'clap' sound) irrespective of the orientation of the PLD. Klin and colleagues suggest that toddlers with ASCs spend less time than TD toddlers attending to biological motion. However, it is not clear whether this study indexes a lack of attention to biological motion or a particular attentional engagement with points of audio-visual contingency in ASCs. Furthermore, the PLD videos employed in this study depicted social games (e.g. pat-a-cake); the Autism Diagnostic Observation Schedule (ADOS; Lord et al., 1989) assessment considers disinterest in these types of game a marker of ASC, hence it can be assumed that toddlers with ASCs (who have been pre-selected on the basis of ADOS assessment) spend less time than TD toddlers attending to these types of game.

A *recent* study by Annaz, Campbell, Coleman, Milne, and Swettenham (2012) investigated attention to biological motion in young children with ASCs using a task that did not feature audio-visual contingency or overtly social stimuli. They used non-social PLDs (person walking) without an accompanying soundtrack. In two separate conditions this biological PLD was presented alongside a scrambled version of the PLD (scrambled condition) or a PLD of a spinning top (spinning condition). Whereas three- to seven-year-old TD children preferentially attended to the biological PLD in both scrambled and spinning conditions, children with ASC showed no preference for the biological PLD over the scrambled PLD and they preferentially attended to the spinning top PLD over the biological PLD. Together with the work of Klin and colleagues (2009), this finding suggests that, unlike TD children, those with ASCs do not demonstrate a preference for biological motion. The spinning condition suggests that, unlike TD children, those with ASCs exhibit a preference for non-biological motion.

Reduced attention to biological motion from an early age may be causally related to atypical development of biological motion processing. Annaz and

colleagues (2010) have demonstrated that between the ages of 5 and 12 TD children improve in their ability to (1) judge whether a PLD 'moved like a person' and (b) pick, from a choice of two, the PLD in which they could see 'dots that look like a person walking'. Children with ASCs did not show this developmental improvement. In line with this, Blake, Turner, Smoski, Pozdol, and Stone (2003) report a reduced sensitivity in judging which dots 'move like a person' in 8–10-year-old children with ASCs. Koldewyn, Whitney, and Rivera (2010) have suggested that this atypical sensitivity to biological motion extends into adolescence. They used a 'direction discrimination task' in which participants were required to determine the direction of a PLD walking left or right within a field of noise dots. It is more difficult to recognise the direction of a PLD when it is embedded in a field of randomly moving noise dots compared to noise dots that move coherently. Thus the coherence of the noise dots can be adjusted to regulate the difficulty of the task. Koldewyn et al. found that, compared to TDs, adolescents with ASCs demonstrated significantly poorer direction discrimination. That is, to accurately discriminate the direction of the PLD walker, individuals with ASCs required significantly higher levels of noise dot coherence compared to controls. Atypical biological motion processing in ASCs has also been reported in adults. Kaiser, Delmolino, Tanaka, and Shiffrar (2010a) asked participants to watch scrambled or unscrambled versions of PLDs of a human actor and to say if the dots moved as if they were 'stuck' to a person; in a control condition, participants had to say whether the dots moved as if they were 'stuck' to a tractor. Whereas the control group exhibited greater visual sensitivity to human motion compared to tractor motion, individuals with ASCs exhibited equivalent sensitivity to human and tractor motion. Therefore, unlike controls, individuals with ASCs did not exhibit an enhanced sensitivity for human motion.

Behavioural reports of atypical biological motion processing in ASCs have been supported by neuroimaging studies. Freitag and colleagues (2008) used fMRI to scan adults with and without ASCs while they viewed PLDs of a walking actor and scrambled versions of these stimuli. Significant differences were found between control participants and individuals with ASCs in terms of fMRI signals relating to biological motion versus scrambled motion. In the right hemisphere reduced (hypo) activation in ASC individuals was found in the middle temporal gyrus, close to the superior temporal sulcus (STS), postcentral gyrus, inferior parietal lobe (IPL), right occipital regions and middle frontal gyrus. In the left hemisphere, hypoactivation in ASCs was found in anterior STS and fusiform gyrus, postcentral gyrus, IPL and claustrum. Similarly, Herrington and colleagues (2007) used fMRI to scan adults with and without Asperger's syndrome (AS) whilst they judged the direction of motion of PLD walkers and scrambled PLDs. Again, no behavioural differences were found. However, in the right hemisphere hypoactivation in ASC individuals was found

in a large cluster spanning the cerebellum, fusiform, middle temporal, superior temporal, middle occipital and superior occipital regions. A similar cluster was found in the left hemisphere but this cluster also included inferior temporal gyrus and the cuneus region. Hence both Herrington et al. (2007) and Freitag et al. (2008) demonstrate that, even when behavioural performance is matched, individuals with ASC exhibit hypoactivation in posterior areas, including STS and fusiform gyrus, during biological motion processing.

Work by Kaiser and colleagues (Kaiser, Delmolino, Tanaka, & Shiffra, 2010a; Kaiser et al., 2010b) demonstrates that atypical neural responses to biological motion can also be found in children and adolescents with ASCs. This group used fMRI to scan TD participants, individuals with an ASC and unaffected siblings while they viewed scrambled and intact versions of PLD movies that were similar to those employed by Klin et al. (2009). Compared to TD participants and unaffected siblings, those with an ASC exhibited hypoactivation in the left ventrolateral PFC, right amygdala, right pSTS, ventromedial PFC and bilateral fusiform gyri, hence replicating previous reports of hypoactivation in ASCs in posterior areas such as the pSTS and fusiform gyrus.

In sum, a growing body of behavioural studies suggests there is atypical attention to biological motion in ASCs in early infancy, and that this is followed by atypical biological motion processing in childhood, adolescence and adulthood (however, for conflicting findings, see Koldeewyn et al., 2010; Murphy, Brady, Fitzgerald, & Troje, 2009; Saygin, Cook, & Blakemore, 2010). These behavioural findings have been supported by neuroimaging studies showing atypical neural responses to biological motion in children, adolescents and adults.

PLDs indicate motion information with degraded form information (Johansson, 1973) and are thus often considered as 'motion' stimuli; however, they are not completely bereft of form cues. At a global level, integrating the motion of the dots that comprise a PLD provides configural human form information. In addition, at a local level, the individual point-lights follow characteristic laws of human motion. Examples of these laws of human motion include the minimum-jerk (MJ) velocity profile (Flash & Hogan, 1985) and the two-thirds power law (Lacquaniti, Terzuolo, & Viviani, 1983). The MJ velocity profile describes the bell-shaped speed profile of a straight point-to-point movement (e.g. when drawing a straight line across a page, an individual moves the pencil tip slowly at the beginning of the movement, speeds up through the middle and slows down to a stop (Abend, Bizzi, & Morasso, 1982; Flash & Hogan, 1985). Movements that obey the two-thirds power law slow down at curved relative to straight parts of motion (Lacquaniti et al., 1983). Both the MJ velocity profile and two-thirds power law agree with observations of human movement (Abend et al., 1982); for example, if an individual makes

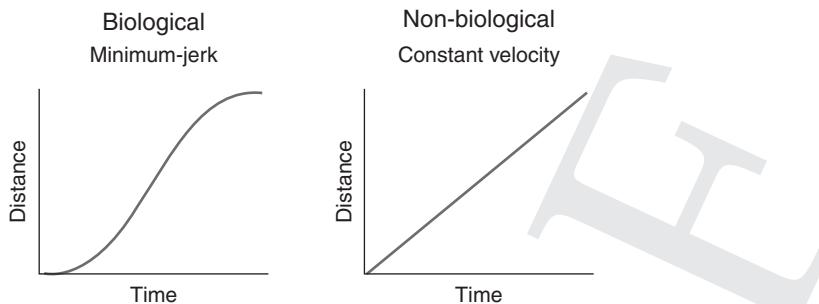


Figure 23.3 Minimum-jerk and constant velocity profiles.

Notes: The MJ velocity profile describes the bell-shaped speed profile of a straight point-to-point movement. For example, if an individual makes a vertical sinusoidal arm movement the velocity of their hand movement will comply with MJ. This stands in contrast to something like a traditional mechanical robot arm that would move at a CV.

a vertical sinusoidal arm movement (i.e. moves her arm up and down in front of her body) her movement will comply with both the MJ velocity profile and the two-thirds power law.¹ In contrast, a traditional mechanical robot arm would move at a constant velocity (CV; Figure 23.3).

In addition to biological motion perception problems, individuals with ASCs exhibit difficulties with global motion processing. A typical global motion processing task comprises a stimulus depicting a large number of randomly moving dots, of which a proportion move coherently in a given direction; participants are required to state the direction of motion (Newsome & Paré, 1988). The dependent variable is the motion coherence threshold (MCT), which represents the percentage of incoherence in dot motion directions at the point at which participants can determine the direction of global motion (left or right) on 75 percent of trials. In three independent studies, Spencer et al. (2000), Milne et al. (2002) and Pellicano et al. (2005) found that children with ASCs had significantly higher MCTs than chronological aged-matched controls: they require about 10 percent more coherent motion than do controls to report motion direction reliably. Recently, Atkinson (2009) demonstrated a correlation between MCTs and emotion recognition from PLDs in adults with ASCs (that is, high MCTs were associated with reduced accuracy in identifying emotions). Koldewyn and colleagues (2010)

¹ Due to the structure of the human shoulder joint, sinusoidal arm movements follow a more curved trajectory at the start and turning points relative to the midpoints and hence would comply with both the MJ velocity profile and the two-thirds power law.

observed a similar finding in adolescents: high MCTs were associated with poor direction discrimination from PLDs. It is therefore possible that individuals with ASCs are less able to pool motion signals across space than controls (Bertone, Mottron, Jelenic, & Faubert, 2003) and that this may relate to difficulties in biological motion processing when stimuli such as PLDs are employed.

To investigate whether biological motion processing deficits in ASCs are distinct from global motion difficulties, we investigated the integrity of the perception of simple sinusoidal hand movements that require only local, not global, motion processing. We employed stimuli in which the minimum-jerk (MJ) velocity profile was manipulated, and a novel paradigm in which participants watched pairs of animations that showed a biological stimulus (a moving hand) or a non-biological stimulus (a falling tennis ball) moving across the screen. On each trial, the velocity profile with which each animation moved was either 100 per cent natural motion (MJ in the biological condition; gravitational in the non-biological condition), or 100 per cent constant velocity (CV), or some linear combination of the two extremes. In each trial, participants were shown a 'reference' animation, which was always a combination of 85 per cent natural motion and 15 per cent constant velocity, and a 'target' animation, in which the ratio of constant velocity to natural motion varied according to performance. The task was to judge which animation was 'less natural'. A two-interval forced-choice adaptive staircase paradigm was employed to generate separate thresholds for the biological (MJ) and the non-biological (gravitational) condition. We found that, whereas typical controls were more sensitive to perturbations to biological compared to gravitational motion, individuals with ASCs did not show this same enhanced sensitivity to biological motion. Further, within the biological condition, thresholds for the ASC group were significantly worse compared to those generated by controls (Figure 23.4; Cook, Saygin, Swain, & Blakemore, 2009).

In conclusion, this section documents a growing body of evidence that suggests atypicalities in biological motion processing in ASCs. Such difficulties with processing the movements of other individuals are present both with stimuli that require global motion processing and with stimuli that require only local motion processing – such as sinusoidal arm movements. The difficulties those with ASCs experience in processing the kinematics of sinusoidal arm movements raise a potential explanation for atypical interference effects in these conditions: individuals with ASCs do not process the sinusoidal arm movements in the same way as typical controls, thus the observation of these movements does not lead to the activation of the corresponding motor representation. This hypothesis also provides a potential explanation for wider difficulties with imitation and MNS hypoactivation in ASC.

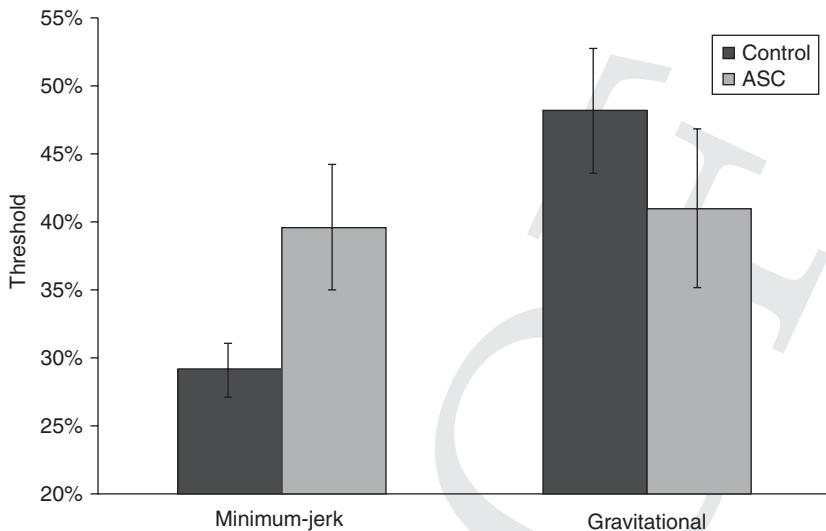


Figure 23.4 Interaction between group and condition.

Notes: There was a significant interaction between group and condition driven by lower thresholds in the MJ condition than in the G condition for the control group but not for the ASC group. Standard error bars are shown.

Source: Image modified from Cook, Saygin, Swain, and Blakemore (2009, Figure 2; CC BY).

Action Perception in ASC Summary

A growing body of studies suggests there is atypical attention to biological motion in ASCs in early infancy, and that this is followed by atypical biological motion processing in childhood, adolescence and adulthood (however, conflicting findings are described by Koldewyn et al. 2010; Murphy, Brady, Fitzgerald, & Troje 2009; Saygin et al., 2010). Such results have been reported both with point-light display stimuli, which require global motion processing, and with stimuli that require only local motion processing (Cook et al., 2009). Behavioural reports of atypical biological motion processing have been supported by neuroimaging studies showing atypical neural responses to biological motion in children, adolescents and adults with ASCs.

Is Action Execution Atypical in ASCs?

In the previous section it was suggested that action observation may be atypical in ASCs, resulting in a 'knock-on' effect on imitation. This section examines the other component of imitation: action execution.

A number of studies have reported motor atypicalities in children and adults with autism. For example, individuals with autism exhibit difficulties controlling the force and direction of a ball when throwing (Staples & Reid, 2010) and differ from typical individuals with respect to handwriting (Beversdorf et al., 2001). Furthermore, when executing motor tasks, they demonstrate atypical activation in motor-related brain areas such as the cerebellum and supplementary motor area, as well as reduced connectivity between motor nodes (Mostofsky et al., 2009). Motor difficulties in autism can be identified at both the level of gross and fine motor control (Beversdorf et al., 2001; Gowen & Hamilton, 2013; Mostofsky et al., 2006), suggesting a possible underlying problem with fundamental movement kinematics.

In a recent study we used motion tracking technology to record kinematics (velocity, acceleration and jerk) whilst adults with autism and a matched typical control group performed simple sinusoidal arm movements of the sort that participants are required to observe in an interference effect experiment. We found that individuals with autism produced horizontal sinusoidal arm movements that were more jerky than those of controls, and which proceeded with greater acceleration and velocity (Figure 23.5). The magnitude of these atypicalities was significantly correlated with autism severity, as measured by the Autism Diagnostic Observation Schedule semi-structured questionnaire (Lord et al., 1989).

Though little is known about the aetiology of atypical kinematics in ASCs, one can speculate that a lack of typical kinematics might be a consequence of peripheral factors (Todorov, 2004) such as abnormal muscle tone in autism (Maurer & Damasio, 1982) or central nervous system factors. One putative central nervous system factor is poor anticipation of the subsequent part of a motor sequence (Cattaneo et al., 2007; Fabbri-Destro, Cattaneo, Boria, & Rizzolatti, 2009). For instance, one study examined the time taken to reach for an object when it was to be subsequently placed on a large (easy condition) or small (difficult condition) target (Fabbri-Destro et al., 2009). Controls exhibited the typical pattern of a slower reach phase when the subsequent placing phase was more difficult, but the reaching movements of children with autism were not modulated by task difficulty. The authors concluded that, instead of translating their goal into a chain of motor acts, children with autism executed these acts independently. One possible explanation for the atypical kinematics that we observed is that individuals with autism have a compromised ability to predict the point at which they must change the direction of their movement, or they have difficulties with using this prediction to modulate current action kinematics. Another, potentially related, putative central nervous system factor that may contribute to atypical kinematics in autism is cerebellar neuropathology (Rogers et al., 2013). Autism has been associated with cerebellar abnormalities including reduced Purkinje cell numbers (Bauman, 1991; Courchesne,

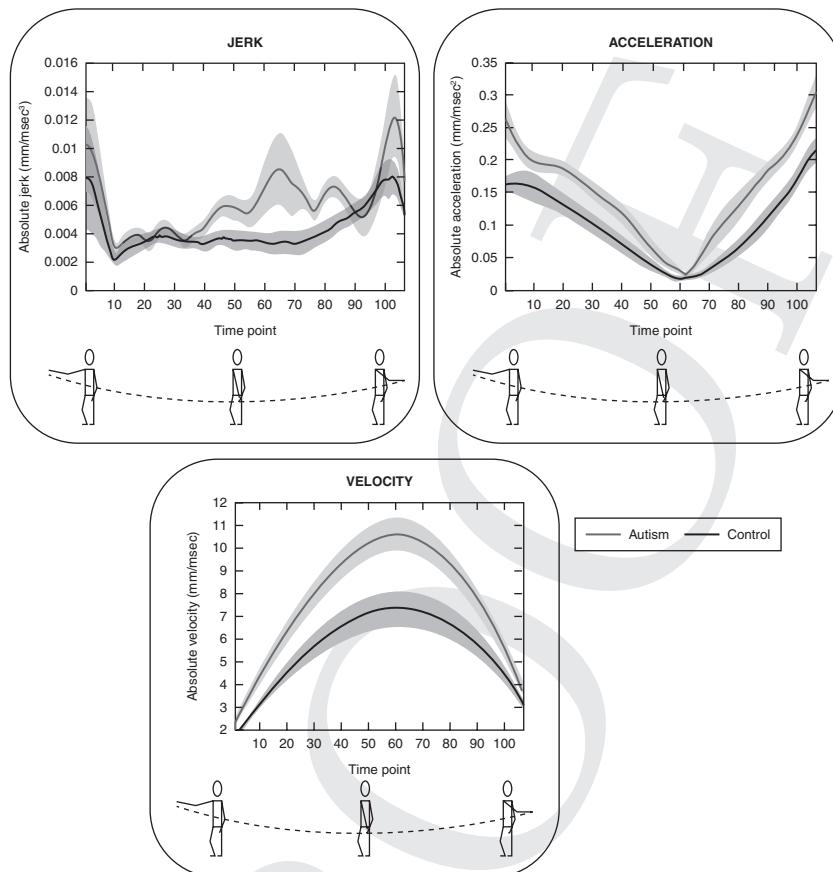


Figure 23.5 Basic kinematics of arm movements for controls and individuals with autism in the primary task.

Notes: When executing simple sinusoidal arm movements, individuals with autism made more jerky movements (left panel) and travelled with faster absolute acceleration (middle panel) and velocity (right panel). Mean movement vectors are plotted in red for the autism group and blue for the control group. Shaded regions indicate the standard error of the mean.

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1997; Courchesne, Yeung-Courchesne, Press, Hesselink, & Jernigan, 1988; DiCicco-Bloom et al., 2006; Palmen, van Engeland, Hof, & Schmitz, 2004), lower cerebellar vermal volumes (Webb et al., 2009), reductions in the size and number of cells in the cerebellar nuclei, excess Bergmann glia and active

neuroinflammatory processes within cerebellar white matter (Bailey et al., 1998; Bauman & Kemper, 2005; Vargas, Nascimbene, Krishnan, Zimmerman, & Pardo, 2005). A number of accounts suggest that cerebellar atypicalities play a key role in the development of the cognitive and behavioural profile that characterises autism (Gowen & Miall, 2007; Mostofsky et al., 2009; Rogers et al., 2013). Further studies are necessary to assess the contribution of peripheral and central factors and to investigate whether they have specific or general effects on velocity, acceleration and jerk.

Given the importance of kinematics in both gross and fine motor control, atypicalities in movement kinematics could be one reason for the difficulties with everyday motor control commonly experienced by individuals with autism (Beversdorf et al., 2001; Gowen & Hamilton, 2013). Such atypicalities may also impact upon imitation and interference effects. For example, imagine you are a participant in the interference effect experiment. Let us suppose that you execute sinusoidal arm movements in a different way from the actor you are observing: he maintains a steady pace whereas you accelerate and decelerate more, thus producing more jerky movements. You have had a lifetime's experience with simultaneously observing and executing your jerky movements so, for you, these visual and motor representations are tightly associated (Heyes, 2010; also see Catmur, this volume, Chapter 22). If you were to observe jerky vertical sinusoidal arm movements it would automatically activate your associated motor representation for vertical movements, which would create an interference effect if you were trying to execute horizontal movements. However, in this example you are watching an actor who produces steady movements. You have had very little simultaneous experience with observing steady movements and executing your own movements, thus when you watch the steady vertical movements of the actor they fail to activate your motor representation for vertical movements and there is thus there no interference effect. As demonstrated in this example, when assessing the integrity of imitation or interference effects, it is important to know whether the population of interest demonstrates imitation-independent motor difficulties.

In sum, this section presents a body of work suggesting that ASCs are associated with motor execution difficulties. Such findings raise (1) an alternative explanation for the atypical interference effect in ASCs, and (2) the hypothesis that an interference effect would be present if individuals with ASCs were shown movements that proceeded with kinematics that match their own.

Action Execution in ASC Summary

Motor difficulties in autism can be identified at both the level of gross and fine motor control (Beversdorf et al., 2001; Gowen & Hamilton, 2013; Mostofsky et al., 2006). Such difficulties may be underpinned by atypicalities in the

basic kinematics of movements in ASCs (Cook, Blakemore, & Press, 2013). Neuroimaging studies have shown that, when executing motor tasks, individuals with ASCs demonstrate atypical activation in motor-related brain areas such as the cerebellum and supplementary motor area (Mostofsky et al., 2009).

Summary and Further Directions

This chapter began by presenting a recent experiment in which we failed to find an interference effect of action observation on action execution in adults with autism (Cook, Swapp, Pan, Bianchi-Berthouze, & Blakemore, 2014). This result is compatible with the broken MNS hypothesis of ASCs. However, the broken MNS hypothesis is highly controversial given that behavioural studies have demonstrated typical imitation effects in ASCs, and clinical observations have even documented hyper-imitation in individuals with this condition. The current chapter focuses on two alternative explanations: (1) action observation is atypical in ASC, and (2) action execution is atypical in ASCs. We conclude that there is a growing body of evidence to support problems with both action observation and action execution in ASCs. Thus, even if the MNS (the link between action observation and action execution) is intact in ASCs, such individuals may demonstrate atypical performance on imitation and interference effect paradigms due to their action observation and/or execution difficulties.

Extending the Argument to Other Sociocognitive Processes

The current chapter argues that imitation relates to *shared representations* in that it concerns the activation of a self-related representation by an other-related representation. This conceptualisation can be applied to other socio-cognitive processes such as empathy. Empathy occurs 'when the perception of another's emotional state causes the empathizer to experience that state' (Bird & Cook, 2013, p. 2). Thus, like imitation, empathy concerns the activation of a self-representation (this time, emotion related) by the representation of another individual. In a recent article, Bird and Cook (ibid) argue that empathy deficits in ASCs may be due to the co-occurrence of alexithymia, which is characterised by difficulties in identifying and describing one's own emotional state. Bird et al. (2010) find a lack of empathic responses only in individuals who have this alexithymic atypicality in representing their own emotions. Individuals who have autism without co-morbid alexithymia exhibit intact empathic responses. Here, we have argued that, with respect to imitation, impairments may be due to atypical representations of one's own actions (i.e. atypical kinematics); similarly Bird and Cook argue that, with respect to empathy, impairments may be due to atypical representations of one's own emotions. They note that alexithymia has a high prevalence rate in many

clinical conditions, including schizophrenia and eating disorders; thus atypical empathic responses may also be common in these conditions.

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