Action observation and imitation in the healthy brain and in high-functioning adults with Autism Spectrum Conditions.

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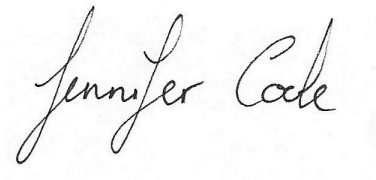
Thesis submitted for Doctor of Philosophy Degree in Neuroscience

I, Jennifer Cook, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.



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Abstract

Accurate action perception plays an important role in social interaction enabling us to identify and appropriately respond to the behaviour of others. One such response is automatic imitation, the reflexive copying of observed body movements. Action perception is associated with activity in posterior brain areas, which feed into the Mirror Neuron System (MNS), a network of regions that has been associated with imitation and which is under the regulatory control of frontal brain areas.

The fMRI study described in Chapter 2 demonstrated that in healthy adults, action perception can be subdivided into objective and subjective components which are primarily associated with activity in different brain areas. Chapter 3 demonstrated that activity in MNS areas, as measured by MEG, comprises an automatic motoric simulation of the kinematics of observed actions. Chapters 2 and 3 therefore enhance knowledge of the neural mechanisms of action perception in the typical brain.

Previous studies have linked Autism Spectrum Conditions (ASC) with action perception and imitation impairments. Chapters 4 and 5 demonstrated that adults with ASC exhibit atypical action perception which is likely due to difficulties with subjective processing (i.e. knowing what a 'natural' human movement should look like) rather than with objective visual processing of human motion. Chapter 6 reported a lack of imitation in ASC: whereas typical adults imitated human movements more than robot movements, individuals with ASC failed to imitate. Chapter 7 suggested that problems with imitation in ASC may relate to difficulties with the control of imitation: whereas control participants show increased levels of imitation when in a positive social frame-of-mind individuals with ASC did not.

Chapters 4 to 7 have implications for ASC. They suggest that atypical imitation may be due to atypical sensory input to the MNS (i.e. impaired action perception) and/or atypical control of imitation.

Contents

Figure legends

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Abbreviations

Anterior cingulate cortex (ACC)
Asperger's syndrome (AS)
Autism Diagnostic Interview – Revised (ADI-R)
Autism diagnostic observation schedule (ADOS)
Autism Spectrum Conditions (ASC)
Constant velocity (CV)
Dorsomedial prefrontal cortex (dmPFC)
Electroencephalography (EEG)
Electromyography (EMG)
Functional Magnetic Resonance Imaging (fMRI)
Inferior frontal gyrus (IFG)
Inferior parietal lobe (IPL)
Intraparietal sulcus (IPS)
Magnetoencephalography (MEG)
Medial prefrontal cortex (mPFC)
Milliseconds (ms)
Minimum-jerk (MJ)
Motor evoked potentials (MEPs)
Reaction time (RT)
Region of Interest (ROI)
Superior temporal sulcus (STS)
Temporoparietal junction (TPJ)
Transcranial magnetic stimulation (TMS)
Typically developing (TD)
Ventromedial prefrontal cortex (vmPFC)

Chapter 1. Introduction

NB. Due to copyright issues most of the figures have been removed from the electronic version of the introduction of this thesis

1.1 SOCIAL COGNITION AND THE SOCIAL BRAIN

Over the past two decades, research has begun to elucidate the neural correlates of the functions that allow humans to understand and interact with each other. These functions include action perception, mental state attribution, action prediction and social communication. These social cognitive processes have been associated with a network of brain regions, referred to as the 'social brain' (Brothers, 1990; Frith and Frith, 2010), which includes the medial prefrontal cortex (mPFC), the temporoparietal junction (TPJ), the anterior cingulate cortex (ACC), the inferior frontal gyrus (IFG), the inferior parietal lobe (IPL), the intraparietal sulcus (IPS), the superior temporal sulcus (STS), the amygdala and the anterior insula (Blakemore, 2008; Figure 1).

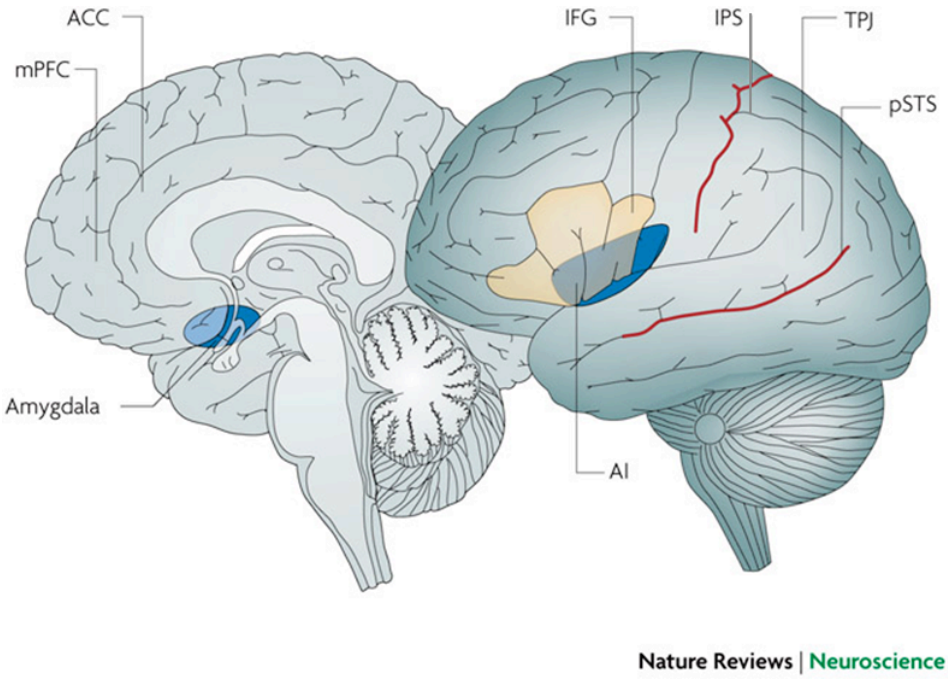

Figure 1. The social brain. Regions that are involved in social cognition include the medial prefrontal cortex (mPFC) and the temporoparietal junction (TPJ), which are involved in thinking about mental states, and the posterior superior temporal sulcus (pSTS), which is activated by observing faces and biological motion. Other regions of the social brain include the amygdala, anterior cingulate cortex (ACC), anterior insula, inferior frontal gyrus (IFG) and the inferior parietal lobe (IPL: between the intraparietal sulcus (IPS) and TPJ on the above figure). Image from Blakemore (2008).

The social brain regions have been associated with various cognitive functions. The pSTS and cortical

regions on the ventral surface of the brain, such as the fusiform and lingual gyri, have been associated with action perception (Peelen and Downing, 2007). Also involved in action perception are classic Mirror Neuron System (MNS) areas IFG and IPL (Rizzolatti and Craighero, 2004) which are active in response to both action observation and execution of the same action. This thesis will focus on these action perception related areas and their functions which will be discussed in detail in sections 1.2.3 and 1.3.3. With respect to social cognition, the mPFC and TPJ regions have principally been associated with 'mentalising' or 'theory of mind' – the ability to attribute goals, desires and beliefs to others (Fletcher et al., 1995; Castelli et al., 2000; Saxe and Kanwisher, 2003; den Ouden et al., 2005). The amygdala has been associated with the processing of social and emotional cues and learning to fear signs of potential danger (Adolphs et al., 2002; Skuse et al., 2003). The ACC is thought to play an important role in the assessment of emotional and motivational information and the regulation of emotional responses (Allman et al., 2001). Lastly, the insula has been linked to the experience of one's own and others' emotions and subjective states (Craig, 2009; Singer et al., 2009).

The different brain regions that comprise the social brain are often discussed as having distinct cognitive functions. However, these brain areas are highly interconnected (Adolphs, 2001). Communication between regions is likely very important in effective sociocognitive functioning. Impairment in a higher-level function such as social reasoning could be due to a difficulty with a lower-level process such as detailed sensory processing. Conversely impaired feedback from higher-level processing areas (also known as 'atypical top-down modulation') may manifest as atypical lower-level processing (Adolphs, 2003).

Although the influence of higher-level social cognitive processes will be referred to, this thesis will focus on the lower-level sociocognitive processes of action perception and automatic imitation. Action perception can be argued to comprise a number of sub-components including the ability to represent the movements of other animate beings (also known as biological motion processing), to identify these movements, and to categorise sequences of movements as discrete actions. Accurate action perception plays an important role in social interaction enabling us to identify and appropriately respond to the behaviour of others. One such response is automatic imitation, the reflexive copying of the topography of observed body movements. Automatic imitation is bi-directionally linked with positive social attitudes (Lakin and Chartrand, 2003; Leighton et al., 2010) and, as such, plays an important role in the development of reciprocal social interactions.

The main aims of this thesis are two-fold. The first is to investigate outstanding questions regarding the

neural mechanisms that underpin biological motion perception and automatic imitation in the typical brain. The second aim relates to Autism Spectrum Conditions (ASC) – developmental disorders characterised by difficulties with, amongst other things, reciprocal social interactions. It has been suggested that these difficulties may be traced back to lower-level sociocognitive processes such as perceptions of, and responses to, actions (Kaiser and Pelphrey, in press). This thesis will investigate whether biological motion perception and automatic imitation are atypical in ASC.

1.2 BIOLOGICAL MOTION PERCEPTION

1.2.1 What is biological motion?

'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., 2003a) 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). This stimulus class was developed in 1973 by Johansson who attached 10 light bulbs to the joints of an actor and filmed his movements in a dark room.

Although PLDs indicate motion information with degraded form information (Johansson, 1973) they are not completely bereft of form cues: at a global level integrating the motion of the 10 to 13 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 and Hogan, 1985) and the $2/3^{rds}$ power law (Lacquaniti et al., 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 et al., 1982; Flash and Hogan, 1985). Movements that obey the $2/3^{rds}$ power law slow down at curved relative to straight parts of motion (Lacquaniti et al., 1983). Both the $2/3^{rds}$ power law and MJ velocity profile agree with observations of human movement (Abend et al., 1982); for example, if an individual makes a vertical sinusoidal arm movement (i.e. moves their arm up and down in front of their body) their movement will comply with both the MJ velocity profile and the $2/3^{rds}$ power law[1]. In contrast a traditional mechanical robot arm would move at a constant velocity (CV; Figure 1.1)

[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 $2/3^{rds}$ power law.

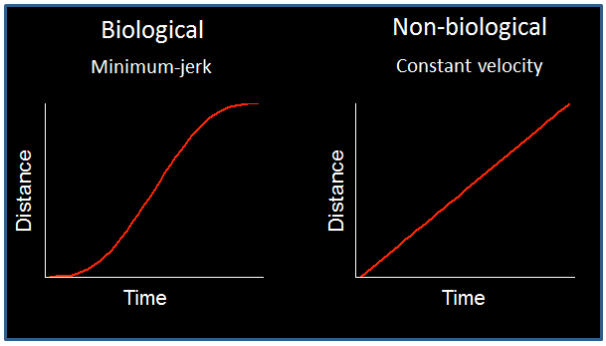

Figure 1.1. Minimum-jerk and constant velocity profiles. The MJ velocity profile describes the bell-shaped speed profile of a straight point-to-point movement. For example, if an individual makes a vertical sinusoidal arm movement the velocity of their hand movement will comply with MJ. This stands in contrast to something like a traditional mechanical robot arm which would move at a CV

1.2.2 The importance of biological motion perception

Biological motion perception may be evolutionarily important for activities such as detecting predators, selecting prey (Ewert, 1987) and courtship behaviour (Morris, 1954; Nuechterlein and Storer, 1982). Bodily and facial movements are important for social communication in monkeys and humans (Darwin, 1872; Andrew, 1963; Adolphs, 2001) and it is thought that the early development of biological motion processing abilities may be important for typical social cognitive development through the direction of attention to appropriate learning resources (Spelke, 2003; Vallortigara, Regolin, and Marconato, 2005).

Behavioural studies have demonstrated that 2 day old infants preferentially attend to upright compared to inverted PLDs (Simion et al., 2008) and 4 day old infants are able to discriminate a single dot moving with 2/3^{rds} power law motion from one moving at a CV (Méary et al., 2007). Studies of real-life interactions have demonstrated that the ability to direct attention according to biological motion signals, such as eye gaze or pointing, at the age of 9 to 10 months, is significantly correlated with referential language at 12 months of age (Carpenter, Nagell, and Tomasello, 1998) indicating that early biological motion abilities may be important for later development.

By adulthood humans are able to recognise biological movements accurately and robustly (Johansson, 1973) and can derive a wealth of information from PLDs including facial expression (Bassili, 1978), complex hand and arm movements (Poizner et al., 1981; Pollick et al., 2001), actions (Dittrich, 1993), emotional states (Dittrich et al., 1996; Pollick et al., 2001), gender (Kozlowski and Cutting, 1977), identity (Cutting and Kozlowski, 1977) and even the weight of a lifted object (Runeson and Frykholm, 1981).

1.2.3 The neural correlates of biological motion

Responses to biological motion as depicted in PLDs, single dot studies, and animations of whole body movements, have been reported in numerous brain areas including the posterior STS (pSTS: (Bonda et al., 1996; Grèzes et al., 2001; Vaina et al., 2001; Pelphrey et al., 2003a, 2005; Santi et al., 2003; Saygin et al., 2004; Peuskens et al., 2005; Peelen et al., 2006; Thompson et al., 2007; Safford et al., 2010), lingual gyrus (Vaina et al., 2001; Servos et al., 2002; Pelphrey et al., 2003a; Santi et al., 2003; Dayan et al., 2007), hMT/V5 (Vaina et al., 2001; Peuskens et al., 2005), inferior occipital cortex (Bonda et al., 1996; Vaina et al., 2001; Pelphrey et al., 2003a; Santi et al., 2003; Peelen et al., 2006; Dayan et al., 2007) and anterior regions such as premotor cortex (Saygin et al., 2004; Saygin, 2007; Dayan et al., 2007). It has been suggested that these different brain areas play distinct roles in biological motion processing with dorsal visual cortical regions such as hMT/V5 primarily responding to motion cues and ventral visual cortical regions responding to form cues (such as the configural form information in PLDs: Giese and Poggio, 2003; Vangeneugden, 2011). The most commonly discussed, and most thoroughly researched, area with respect to biological motion processing is the pSTS. This region has been suggested to play a key role in integrating both form and motion cues to provide a comprehensive visual representation of biological motion (Giese and Poggio, 2003; Vangeneugden et al., 2009, 2011).

1.2.3.1 Monkey studies of the STS

Single and multiple cell recording from the monkey brain have shown that neurons in the STS respond to biological motion signals such as eye gaze direction (De Souza et al., 2005); body orientation (Wachsmuth et al., 1994); particular combinations of body movements and postures (e.g. walking forwards but not bending forwards or walking backwards (Oram and Perrett, 1996; Jellema et al., 2004) and to static ‘snapshots’ of body postures (Perrett et al., 1985; Oram and Perrett, 1994; Nelissen et al., 2006; Vangeneugden et al., 2011). Many of these cells respond in a size, position and viewing condition invariant manner (Jellema and Perrett, 2006) and will respond to many different presentation modes (e.g. live action, movies, stick figures, PLDs: (Bruce et al., 1981; Oram and Perrett, 1994). Therefore, in the monkey brain, cells in the pSTS respond to both form (e.g. static snapshots) and motion (e.g. walking forwards versus backwards) components of biological motion. Indeed, this region is ideally located for this function as it receives convergent information from dorsal areas associated with motion processing (MT / MST) and ventral areas associated with form processing (inferotemporal cortex) (Payne and Bachevalier, 2009).

1.2.3.2 Human studies of the pSTS

Numerous studies that have employed fMRI have reported elevated levels of pSTS activity when human participants view biological motion as depicted in animations of moving humans (Pelphrey et al., 2003a, 2005; Thompson et al., 2007), dots that move with $2/3^{rds}$ power law (Dayan et al., 2007) and PLD stimuli (Bonda et al., 1996; Grèzes et al., 2001; Vaina et al., 2001; Santi et al., 2003; Saygin et al., 2004; Peuskens et al., 2005; Peelen et al., 2006; Safford et al., 2010) compared to when participants view non-biological motion displays.

The pSTS is particularly responsive to the articulated global motion of the human limbs. Beauchamp and colleagues (2002) demonstrated that the human pSTS responds more strongly to images of humans moving with articulated motion compared to humans moving with unarticulated motion (i.e. rotating about their centre-of-mass). Similarly, Pelphrey and colleagues (2003a) compared pSTS activity profiles when participants viewed a) a moving person b) a robot, which was matched in terms of articulated motion but which differed in form, and c) a grandfather clock which was matched to the human in terms of familiarity, meaningfulness and local motion (the pendulum moved with 2/3rds power law) but differed in articulated motion. Results showed that pSTS activity did not differentiate the human and robot conditions, suggesting that the pSTS is insensitive to detailed form cues (although it should be noted that the robot had torso, legs, arms and head and so in a configural sense represented the human body). pSTS activity for human and robot conditions was significantly greater than for the grandfather clock condition suggesting that it is articulated biological motion per se, and not just familiar and meaningful motion that drives the pSTS response.

More recent work has suggested that not only does the pSTS respond to articulated biological motion but that this region is sensitive to local motion cues which indicate characteristic human movement. Dayan and colleagues (2007) used stimuli similar to those employed by Méary and colleagues (2007; **Error! Reference source not found.**). These stimuli comprised a cloud of dots which traced the outline of an ellipse with either $2/3^{rds}$ power law or CV. The pSTS region, amongst others, was more active in response to biological ($2/3^{rds}$ power law) motion compared to CV motion. In a further control condition Dayan and colleagues (2007) showed that the pSTS was more active in response to $2/3^{rds}$ power law motion compared to inverted $2/3^{rds}$ power law motion. For inverted $2/3^{rds}$ power law motion velocity is greatest at maximally curved parts of the trajectory and least for the straightest parts of the trajectory. Comparing $2/3^{rds}$ power law motion and inverted $2/3^{rds}$ power law motion therefore controls for variability in the velocity profile; thus the pSTS responds to local motion cues that are characteristic of biological motion even when the variability of the velocity profile is matched.

A number of studies, which have employed sophisticated fMRI designs and analysis techniques (e.g. fMR-repetition suppression, multi-voxel pattern analysis), suggest that the pSTS is not merely a "biological motion detector" that responds to the presence or absence of biological motion but that activity in this area may comprise higher-level representations of actions. In a repetition suppression design fMRI experiment Grossman and colleagues (2010) asked participants to watch pairs of animations in which the first animation comprised a PLD depicting one of twenty-five unique action sequences (e.g. walking, running, jumping) and the second animation was either (a) the same animation repeated (b) a PLD of a different action or (c) the same animation mirror reversed. fMRI repetition suppression is based on the observation that repeated activation of the same neuronal population results in reduced haemodynamic responses as compared to activation of a different neuronal population (Buckner et al., 1998; Grill-Spector and Malach, 2001). Hence Grossman and colleagues (2010) predicted that repetition suppression would be evident in the pSTS when the same animation is repeated and - if pSTS activity comprises a viewing-perspective-invariant higher-level representation of action - when the mirror reversed but nevertheless matching animation is shown but not when different actions are shown. Results demonstrated significant repetition suppression for repeated actions in bilateral pSTS: left pSTS and right pSTS exhibited significant and marginally significant repetition suppression for mirror reversals. Further experiments demonstrated that the pSTS action representation was size and position invariant (Grossman et al., 2010). These results suggest viewing perspective invariant visual representation of action in pSTS and similar results from others groups (Kable and Chatterjee, 2006; Wiggett and Downing, 2011) confirm this role for the pSTS.

1.2.3.3 The pSTS in subjective judgments

The studies discussed above provide convincing evidence that the human pSTS represents biological motion and may comprise a high-level representation of action. In addition, there is accumulating evidence that the pSTS appears to be involved with more than just the visual representation of biological motion. This region also exhibits elevated levels of activity when participants imagine biological motion compared to fixation (Grossman and Blake, 2001); when participants listen to walking human footsteps compared to noise (Bidet-Caulet et al., 2005), during animacy judgements (Castelli et al., 2000; Schultz et al., 2004, 2005; Santos et al., 2010) and during intention attribution (Saxe et al., 2004).

Robust activity has been observed in the pSTS to seemingly animate movements of simple shapes (Castelli et al., 2000; Schultz et al., 2004, 2005; Santos et al., 2010). Castelli and colleagues (2000)

showed participants videos of shapes that moved around the screen with either random motion or with motion that elicited the attribution of mental states, intentions or beliefs (mentalising animations). Castelli and colleagues (2000) found that activity in the pSTS was greater when participants viewed the mentalising animations compared to the random animations. Similarly, Santos and colleagues (2010) scanned participants whilst they watched animations of two dots which varied parametrically in terms of interaction; participants were required to judge animacy on a four-step scale. Santos and colleagues (2010) found that animacy judgements were positively correlated with pSTS activity.

'Animate' movements such as those employed by Castelli and colleagues (2000) and by Santos and colleagues (2010) encourage cognitive processes such as mental state, intention and belief attribution as well as the categorisation of the stimulus as an animate, self-propelled, agent. Saxe and colleagues (2004) focused on one particular aspect of animate movement – intention attribution. Saxe and colleagues (2004) showed participants videos of people passing behind a bookcase. In a 'short occlusion' condition the sequence was continuous, in a 'long occlusion' condition the actor paused behind the bookcase. pSTS activity was significantly greater in the second condition compared to the first. This difference did not arise when the actor glided, rather than walked and hence is not a result of a pause in motion. They argue that in the long occlusion condition participants reasoned about the actor's intentions for stopping behind the bookcase and hence that the pSTS plays a role in representing intentional actions. In line with the idea that the pSTS represents the intentions of others, Winston, Strange O'Doherty and Dolan (2002) found pSTS activity when participants made judgements about the trustworthiness of faces compared to judgements about age. They suggest that trustworthiness judgements may evoke reasoning about an individual's intentions.

In sum, it has been suggested that activity in pSTS is associated with the visual representation of biological motion and also with subjective, animacy-judgement or intention based, processing of motions (Pelphrey et al., 2003a; Jastorff and Orban, 2009). Figure 1.2 shows coordinates from PLD studies of biological motion and also from studies of imagined biological motion (yellow spheres), animacy judgements (blue spheres) and intention attribution (green spheres). From this figure it can be seen that these three study types active overlapping regions in pSTS (outlined in red; Ono et al., 1990). Also plotted on this figure are visual cortical regions human MT/V5 (blue border; Hadjikhani et al., 1998), LO (green border; Tootell and Hadjikhani, 2001) and the right pSTS region of interest (ROI) employed in the experiment described in Chapter 2 (black border). These regions are further discussed in section 1.2.4.1.

fMRI studies of biological motion processing typically contrast intact and scrambled PLDs. Intact PLDs evoke a visual representation of biological motion *and* would be judged to be 'animate'; scrambled PLDs do not evoke a visual representation of biological motion and would not be judged as 'animate'. Hence PLD studies have confounded these two interpretations of pSTS activity. Whether activity in pSTS reflects the 'objective' visual representation of biological motion, or the subjective judgement of a stimulus as 'animate' comprises an unanswered question which will be investigated in Chapter 2 of this thesis.

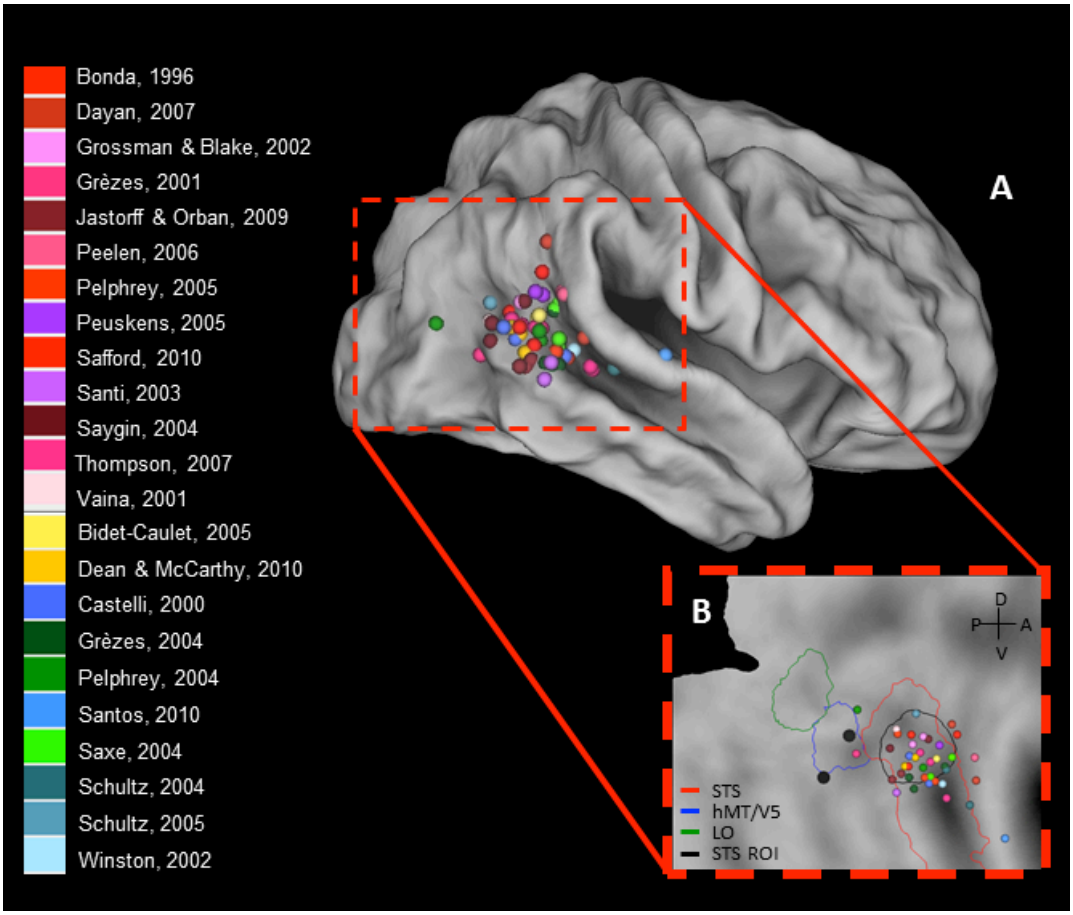

Figure 1.2. Foci of activity for studies of the visual perception of biological motion, animacy judgments and intention attribution. **A.** Previous studies of biological motion perception have frequently reported pSTS activity (red/pink/purple spheres). pSTS activity has also been reported for imagined biological motion (yellow spheres), animacy judgements (blue spheres) and intention attribution (green spheres). Coordinates plotted on the right hemisphere 3D (fiducial) surface of the PALS brain using Caret Software (Van Essen, (2005): http://www.nitrc.org/projects/caret/). Note left hemisphere coordinates have been projected through to the right hemisphere. **B.** pSTS coordinates from previous studies on flattened cortical surface of the PALS brain. The red border outlines the STS (Ono et al., 1990), the blue border outlines human MT/V5 (Hadjikhani et al., 1998), the green border outlines LO (Tootell and Hadjikhani, 2001) and the black border shows the right pSTS ROI employed in the experiment described in Chapter 2. To indicate the location of the extrastriate body area (EBA) the peak EBA coordinates from Kontaris, Wiggett and Downing (2009) and Urgesi, Calvo-Merino, Haggard and Aglioti (2007) are plotted as large black circles. Anatomical axes are indicated: dorsal (D), ventral (V), posterior (P), anterior (A).

1.2.4 Other cortical areas associated with biological motion processing

1.2.4.1 Posterior regions

Human fMRI studies have demonstrated activity related to biological motion processing in areas also active in response to non-biological motion. For example, the lingual gyrus is associated with speed discrimination (Orban et al., 1998) but activity in this area has been reported in at least five studies of PLD biological motion (Howard et al., 1996; Servos et al., 2002; Ptito et al., 2003; Pelphrey et al., 2003a; Dayan et al., 2007). Biological motion related activity has also been reported in motion area human MT/V5 (hMT/V5: Zeki et al., 1991; Vaina et al., 2001; Peuskens et al., 2005) and in the kinetic-occipital (KO) region (Vaina et al., 2001) an area, thought to extend over visual areas V3 and V3A (Larsson and Heeger, 2006), which is sensitive to motion-defined boundaries (Orban et al., 1995; Dupont et al., 1997; Figure 1.3). These areas most likely respond to local motion cues (i.e. changes in the velocity profile of biological motion) and to global cues (e.g. the opponent motion of the limbs) that are present in most biological motion stimuli.

Inferotemporal and occipitotemporal regions, which are selective for static human bodies, are also frequently discussed with reference to biological motion processing (Figure 1.6 inset). Cortical regions selective for static human bodies include the fusiform face area (FFA: Kanwisher et al., 1997), occipital face area (OFA: Rotshtein et al., 2005) and STS (Grill-Spector et al., 2004) for face representations and extrastriate body area (EBA: Downing et al., 2001, 2006a) and fusiform body area (FBA: Peelen and Downing, 2005; Schwarzlose et al., 2005; Peelen et al., 2006) for body representations. It is thought that these areas are not active in response to biological motion per se but rather form-from-motion that results from biological motion stimuli such as PLDs (Peelen et al., 2006). These areas may play an important role in biological motion processing by representing snapshots of biological motion which can be integrated by other neural areas (e.g. pSTS) to form a representation of a motion sequence (Giese and Poggio, 2003; Downing et al., 2006b).

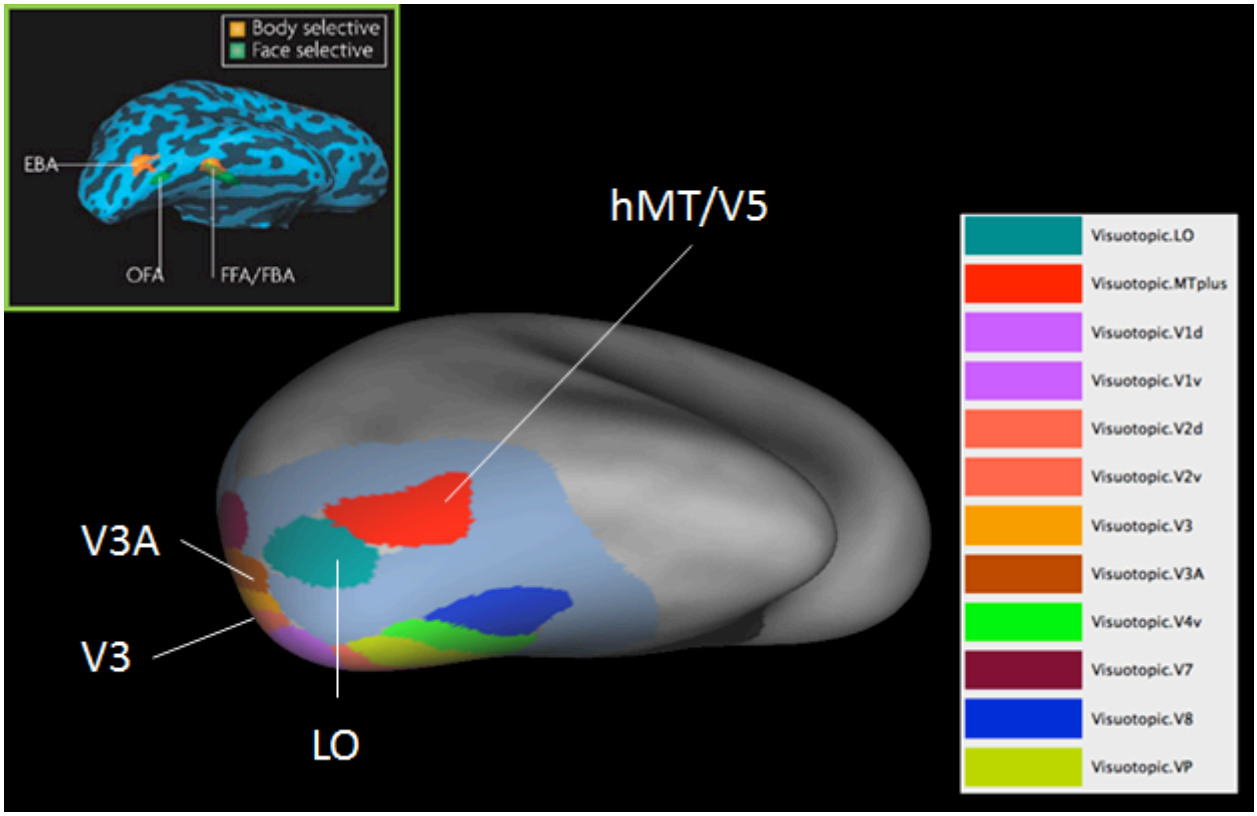

Figure 1.3. Visual cortex. Ventral view of a fully inflated human brain right hemisphere. Note that hMT/V5 is shown in red and visual area LO in teal. KO is thought to extend over V3 and V3A which are highlighted in orange and brown. Areas illustrated on the right hemisphere fully inflated surface of the PALS brain using Caret Software (Van Essen, (2005): http://www.nitrc.org/projects/caret/). Inset (top-left) shows body- and face-selective regions of the human visual cortex, in a ventral view of the right hemisphere of one individual, rendered on an inflated anatomical scan from the same individual. Orange indicates body-selective regions (bodies versus tools); green indicates face-selective regions (faces versus tools). Bodies and faces activate similar regions of the fusiform gyrus (the fusiform body area (FBA), and fusiform face area (FFA), respectively). Posterior to this region are nearby but distinct body-selective (EBA) and face-selective (occipital face area (OFA)) regions. Inset from Peelen and Downing (2007).

1.2.4.2 Anterior regions

Areas of the frontal cortex have been found to be active in response to biological motion. Right lateralised frontal activation was reported in Brodmann area (BA) 47 extending into BA 45 (**Error! Reference source not found.**) in a study in which participants were required to discriminate biological and scrambled PLDs (Vaina et al., 2001). Santi and colleagues (2003) also reported activation in right BA 47 during biological motion perception. Using a scanning protocol designed to maximise signal in the frontal cortex Saygin and colleagues (2004) found activity in the inferior frontal sulcus when participants watched PLD walkers compared to scrambled PLDs. The location of this cluster of activity was close to parts of the IFG which are considered part of the classic MNS (Rizzolatti and Craighero,

2004). Indeed the STS is reciprocally connected to the parietal MNS (Luppino et al., 1999), which in turn is reciprocally connected to the frontal MNS (Harries and Perrett, 1991; Seltzer and Pandya, 1994). Activity in pSTS can therefore impact on frontal MNS regions. In a follow-up study Saygin (2007) demonstrated that, of a group of unilateral stroke patients, those with ventral premotor and superior temporal lesions exhibited the greatest impairment on a test of biological motion perception. Saygin (2007) argues that superior temporal and premotor areas are not only involved in biological motion perception, but are necessary for accurate biological motion perception.

1.2.5 Action perception summary

Accurate and efficient action perception is important for social interactions. The pSTS is considered a key brain region for biological motion processing. Activity in this area is commonly discussed in terms of the visual representation of biological motion. However, pSTS also responds to auditory representations of biological motion, to seemingly animate movement of simple shapes and during complex social judgements and intention attribution. *Chapter 2 of this thesis will investigate the question of whether activity in pSTS reflects the 'objective' visual representation of biological motion, or the subjective judgement of a stimulus as 'animate'.*

1.3 IMITATION

Accurate action perception and biological motion processing is not only important for social perception and evolutionary reasons, such as detecting prey and predators, but also forms the basis for another important social behaviour: imitation.

1.3.1 The importance of imitation

Imitation is intricately linked with social interaction. Being imitated increases rapport (Chartrand and Bargh, 1999), altruistic behavior (van Baaren et al., 2004) and trust (Bailenson and Yee, 2005). Furthermore, individuals imitate more when in possession of a positive social attitude (Lakin and Chartrand, 2003; Leighton et al., 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 that had rearranged the positive social sentences exhibited significantly higher levels of automatic imitation compared to individuals that 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 and Chartrand, 2003).

1.3.2 Defining imitation

Imitation can be broadly defined as copying the body movements of others. However, an individual may show impairment in one type of imitation and preserved abilities with another type (see Hamilton (2008) for a discussion of this point with respect to ASC). It is therefore important to consider that there may be different types of imitation and that these may be underpinned by different mechanisms. Imitation can be subdivided into two categories: simple imitation and complex imitation (Heyes, in press). Simple imitation is also known as 'mimicry' (Tomasello, 1996; Hamilton, 2008), 'automatic imitation' (Heyes et al., 2005), 'priming' and 'response facilitation' (Byrne and Russon, 1998). It occurs when an observer copies body movements of an actor that are already in that individual's behavioural repertoire (Heyes, in press). For example, two individuals often copy body movements such as ear-touching and foot-waggling when engaged in conversation (Chartrand and Bargh, 1999).

Complex imitation has also been referred to as 'imitation learning' (Tomasello, 1996), 'true imitation' (Zentall, 2006), 'observational learning' (Carroll and Bandura, 1982) and 'programme-level imitation' (Byrne and Russon, 1998). It occurs when an observer copies body movements of an actor that are not already in that individual's behavioural repertoire (Heyes, in press). For example, copying a novel sequence of semaphore-like movements of the hand and arm (Carroll and Bandura, 1982).

This thesis is primarily concerned with simple imitation, therefore the terms imitation and automatic imitation should be considered synonymous with simple imitation. Furthermore, imitation will be considered distinct from emulation (Tomasello, 1996). To emulate is to copy the effects of body movements on environmental objects. If I see you tip a bucket by rotating it in your hands I would be imitating if I copied the rotating movement of your hands, whereas I would be emulating if I tipped a bucket using a different method (e.g. kicking with my foot; example adapted from Heyes, (2011)).

Automatic imitation 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) … For example, Brass, Bekkering and Prinz (2001a) 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 which showed either the same action or the alternative action. Brass and colleagues (2001a) 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. For instance, automatic imitation effects have been reported for foot movements (Bach and Tipper, 2007; Gillmeister et al., 2008), whole-hand movements (Press et al., 2005) and mouth movements (Leighton and Heyes, 2010).

There is therefore a significant body of evidence to suggest that action observation interferes with action selection. Such 'Interference Effects' are not only observed in the action selection domain but 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 they observe a congruent movement (Kilner et al., 2003a, 2007a; Oztop, E et al., 2005; Chaminade et al., 2005; Bouquet et al., 2007; Stanley et al., 2007; Gowen et al., 2008). Action observation can therefore be said to 'interfere' with ongoing action execution.

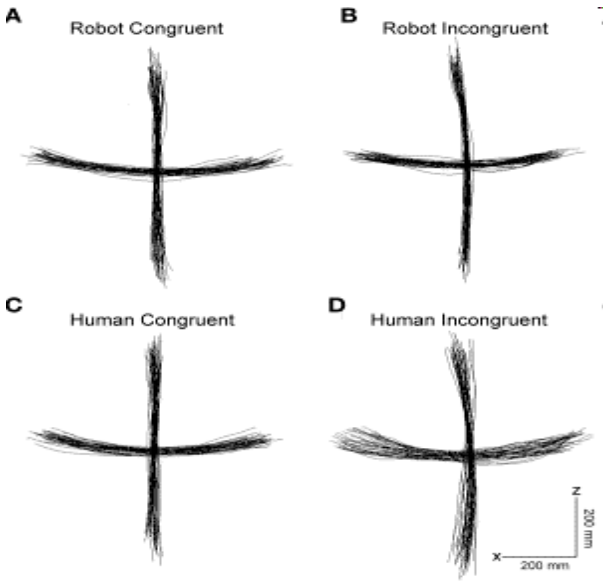

Figure 1.4. Greater Interference Effect for human compared to robot movements. Data from a motion tracker on the hand of a participant whilst he/she conducts vertical and horizontal sinusoidal movements whilst observing, A) congruent movements conducted by a robot, B) incongruent robot movements, C) 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). Image from Kilner, Paulignan and Blakemore (2003a).

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 et al., 2003a, 2007a). With respect to form, Kilner, Paulignan and Blakemore (2003a) showed that participants exhibit a greater Interference Effect when watching actions conducted by a real human compared to actions conducted by a robot (Figure 1.4). 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. With respect to motion, Kilner, Hamilton and Blakemore (2007a) demonstrated that videos in which arm movements made by a human actor had been manipulated such that the finger-tip moved with CV (Figure 1.1) resulted in a reduced Interference Effect compared to videos in which the finger-tip moved with typical biological motion (MJ velocity profile: Figure 1.1). Interference Effects therefore appear to be greater for observed stimuli with human form and human motion compared to stimuli with robot form (see Press (2011) for further discussion on the biological specificity of automatic imitation).

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.

1.3.3 Neural mechanisms of imitation

It is suggested that, by automatically motorically simulating observed actions, MNS activity comprises the neural basis of the aforementioned automatic effects of action observation on action execution (Blakemore and Frith, 2005). Mirror Neurons fire both for execution of an action and observation of that same action. These neurons were originally discovered in the monkey brain in ventral premotor cortex (PMv) of the IFG (area F5: di Pellegrino et al., 1992; Gallese et al., 1996) and rostral inferior parietal lobule (IPL / area PF / parietal frontal: Gallese et al., 2002; Fogassi et al., 2005). Krascov and colleagues (2009) recently showed that although Mirror Neurons in area F5 fired more for object directed actions (i.e. picking up a peanut with a precision-grip), firing was also significantly greater than baseline during observation of non-object related actions (i.e. a precision-grip with no object present).

Research using a range of neuroimaging methods including fMRI, transcranial magnetic stimulation (TMS), magnetoencephalography (MEG) and electroencephalography (EEG) provides strong evidence

for similar responses to action execution and action observation in the human motor system.

A number of studies have recorded the effects of single-pulse TMS to primary motor cortex on peripheral motor system responses during the observation of action. TMS induces an electrical current by rapid oscillation of a magnetic field. This electrical current can depolarize cortical neurons underlying the electromagnetic coil, elevating cortical motor system activity and consequently enhancing cortico-spinal motor excitability (Pascual-Leone et al., 1998). TMS studies of the MNS typically record motor evoked potentials (MEPs) from muscles as a peripheral motor system correlate of MNS activity. These studies have shown that observation of arm, hand and finger movements results in the activation of the same muscles involved in the production of the movements (Fadiga et al., 1995; Maeda et al., 2002; Aziz-Zadeh et al., 2006; Catmur et al., 2007). For example, Fadiga and colleagues (1995) stimulated motor cortex and recorded MEPs whilst participants, a) observed an object-grasping action, b) viewed the same objects with no grasp action, c) observed an arm elevation action, d) detected a dimming light. They found significantly greater MEPs for action conditions ((a) and (c)) relative to non-action conditions ((b) and (d)). Furthermore, the patterns of MEPs reflected the MEP pattern recorded when participants executed the same actions: for example, opponens pollicis MEPs were greater during grasping relative to arm elevation in both execution and passive observation conditions.

fMRI and positron emission tomography (PET) experiments have looked for areas of overlap for the execution of action (without visual feedback) and passive observation of the same action, hence investigating whether overlapping cortical areas are active during action observation and execution. Areas of overlap have been identified in the IFG e.g. (Iacoboni et al., 1999; Kilner et al., 2009a), the IPL, (Grèzes et al., 2003; Aziz-Zadeh et al., 2006), ventral and dorsal premotor cortex (Buccino et al., 2001; Gazzola et al., 2007), anterior IPS (Shmuelof and Zohary, 2006; Dinstein et al., 2007) and the STS (Gazzola et al., 2006). These areas are considered to comprise the human MNS. However, measuring overlapping clusters of activity does not necessitate that the same neuronal population is active during the observation and execution conditions. For example, it could be that within the same voxel there are neurons that respond to action execution and different neurons that respond to action observation. As previously discussed, repetition suppression is based on the observation that repeated activation of the same neuronal population results in reduced haemodynamic responses as compared to activation of a different neuronal population (Buckner et al., 1998; Grill-Spector and Malach, 2001). Cross-modal repetition suppression, where a reduced response is seen for observation following execution or vice-versa, would comprise evidence for mirror neurons; such a response would only be observed if the same neurons are active during both observation and execution. Kilner and colleagues

(2009) compared the magnitude of repetition suppression for trials in which participants observed and executed the same action (either precision grip or index finger pull) with trials in which participants observed and executed different actions. Kilner and colleagues hypothesised that, if the IFG contains mirror neurons, cross-modal repetition suppression should be observed in this area. In line with their predictions Kilner and colleagues observed cross-modal repetition suppression effects in IFG. Cross-modal repetition suppression for action observation and execution has also been demonstrated in the parietal MNS (Chong et al., 2008). fMRI studies have therefore provided evidence, at the level of neuronal populations, for a human MNS.

Studies using MEG and EEG have also provided evidence for comparable neural responses to action execution and observation. Such studies have shown that sensorimotor oscillatory activity in both the 8-12 Hz (μ) and 15-30 Hz (β, *beta*) ranges is attenuated both when observing and executing actions (Cochin et al., 1998, 1999; Hari et al., 1998; Babiloni et al., 2002; Caetano et al., 2007; Kilner et al., 2009b). However, electrical activity is not simply suppressed during action execution: Kilner and colleagues (2000, 2003b) have demonstrated that β power is modulated dynamically during action execution. For instance, when participants moved a lever with their finger and thumb the power of *beta* oscillations was more greatly attenuated at the midpoints of this action relative to the endpoints of the action. If, indeed, MNS activity comprises an automatic motor simulation of observed action, *beta* power over MNS regions should be dynamically modulated during action observation as it is during action execution.

In sum, converging evidence from fMRI, MEG and EEG studies supports the existence of a human MNS. In addition, peripheral effects of MNS activity, as investigated using TMS, show that the same muscles are active during action execution and observation. However, the view that MNS activity comprises an automatic motor simulation of observed actions would predict that the timecourse of activity for observed and executed actions is also matched. Whether MNS activity is dynamically modulated according to the timecourse of the observed action is investigated in Chapter 3 of this thesis.

1.3.4 Is the MNS involved in imitation?

Since imitation is the execution of observed actions and the MNS responds to both action execution and observation it can be hypothesised that the MNS plays a part in imitation. To investigate this proposition Iacoboni, Woods, Brass, Bekkering, Mazziotta and Rizzolatti (1999) used fMRI to scan participants while they viewed three stimulus types: an animated hand, for which the fingers lifted in sequence; a static hand, for which the fingers acquired crosses in sequence; or a sequence of dots that appeared in

different spatial locations. In different conditions participants were required to passively observe the sequence or to observe and execute the sequence. The only condition comprising imitation is observation and execution of the animated hand. Activity in frontal and parietal MNS regions (specifically left frontal operculum, right anterior parietal region and right parietal operculum), was greater during the imitation relative to non-imitation conditions, demonstrating imitation-specific elevated MNS activity.

Not only is imitation thought to activate MNS regions but TMS studies have suggested that typical MNS function is *necessary* for accurate imitation. Catmur, Walsh and Heyes (2009) demonstrated that applying repetitive TMS (rTMS) to disrupt IFG activity resulted in a reduced automatic imitation RT effect (i.e. a reduced RT difference between incompatible and compatible conditions), whereas rTMS over a control region did not (Catmur et al., 2009). Similarly Heiser, Iacoboni, Maeda, Marcus and Mazziotta (2003) found that rTMS over IFG resulted in higher error rates on a conscious effortful imitation task relative to rTMS over a control region. Error rates on a non-imitative control task were not affected. Together this evidence suggests that the IFG is critically involved in imitation of non-object-related actions.

In sum, there is evidence to suggest that the MNS comprises the neural mechanism underpinning imitation. If, indeed, the MNS supports imitation it may be hypothesised that MNS activity represents motoric simulation of observed actions. Chapter 3 tests this hypothesis by investigating whether MNS activity is dynamically modulated according to the timecourse of observed actions.

1.3.5 Why don't we imitate all the time?

Although the MNS may automatically respond to observed actions, and likely supports imitation, we do not imitate every action we observe. A recent set of studies implicate other, non-MNS, brain regions in the control of imitative responses. Following on from observations that individuals with mPFC lesions exhibit heightened levels of imitation (Lhermitte, 1986; Brass et al., 2003) Brass, Spengler and colleagues (Brass et al., 2001b, 2003, 2005; Spengler et al., 2009, 2010c) have used fMRI to show that inhibition, compared to execution, of imitative responses elicits activity in key nodes in the social brain network (Figure 1): the mPFC and temporo-parietal junction (TPJ). They suggest that the mPFC and TPJ play key roles in the control of imitation. This suggestion has received support from a set of studies by Wang and Hamilton. In an initial behavioural study they showed that direct eye contact increases the RT difference between incongruent and congruent hand movement conditions of an automatic imitation paradigm (Wang et al., 2011a). In a subsequent fMRI paradigm they demonstrated that the interaction

between automatic imitation and eye-contact was associated with mPFC, STS and IFG activity (Wang et al., 2011b). Furthermore using Dynamic Causal Modelling they were able to show that eye-contact enhanced mPFC to STS connectivity and this subsequently impacted on connectivity between STS and IFG, suggesting that mPFC controls automatic imitation by enhancing sensory processes in the STS which then feed-forward to MNS regions.

To investigate the function of the mPFC and TPJ at the individual subject level Spengler and colleagues (2009) used fMRI to record neural activity whilst participants completed 4 different tasks: 1) imitation inhibition – participants were required to execute a finger movement in response to the presentation of a number, a video of a finger movement was shown simultaneously and participants had to inhibit imitating the video, 2) mentalising – participants had to read stories which required the attribution of a mental state to the actor, 3) self-referential thinking – participants had to read statements (e.g. "I like Leipzig") and decide whether they agreed with the statement and 4) agency attribution – participants had to judge whether the appearance of a visual stimulus was a consequence of their own action or the actions of the experimenter. Spengler and colleagues (2009) found that mPFC activity during imitation-inhibition overlapped with activity related to self-referential thought and mentalising. TPJ activity during imitation inhibition was found to overlap with activity related to mentalising and to agency. Individual differences in the responsivity of mPFC during mentalising correlated with imitation-inhibition such that individuals with a high mPFC response during mentalising showed better imitation-inhibition performance (Spengler et al., 2009).

The four tasks employed by Spengler and colleagues all relied on the ability to separate representations of (or information about) the self from representations of others. Spengler and colleagues have therefore suggested that self-other discrimination and the control of imitation share common mechanisms. In support of this hypothesis Bird, Spengler and Brass (2010a) recently showed that individuals who performed poorly on a mentalising task - which required distinguishing one's own mental state from the mental state of another agent – also showed poor inhibition of imitation. Furthermore, Santiesteban and colleagues (under review) recently found that training imitation-inhibition enhanced performance on a perspective-taking based mentalising task – presumably because training imitation-inhibition enhances self-other distinction, facilitating the discrimination of own perspective from the perspective of another agent.

The hypothesis that self-other distinction and control of imitation share common mechanisms receives further support from experiments which have demonstrated increased imitation following positive social

priming compared to anti-social priming (Leighton et al., 2010; see section 1.3.1 for further details) and following ostensive cues such as direct eye-gaze (Wang et al., 2011a). It is possible that pro-social priming and direct eye-gaze serve to blur self-other distinctions hence temporarily reducing the ability to inhibit imitation.

In sum, it is important to consider that imitative behaviour does not depend solely on MNS activity but also on the functioning of other cortical regions, such as mPFC and TPJ, which may increase or decrease imitation levels.

1.3.6 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. MNS regions are active both for the execution and observation of actions, and disrupting activity in these regions can lead to imitation impairments. If, indeed, MNS activity comprises a motoric simulation of observed actions the timecourse of MNS activity during action observation should be comparable to the timecourse expected for execution of the action. *Chapter 3 investigates this hypothesis.*

1.4 IMITATION IN AUTISM SPECTRUM CONDITIONS

ASCs are pervasive developmental disorders, characterised by a triad of impairments: verbal and non-verbal communication problems, difficulties with reciprocal social interactions, and unusual patterns of repetitive behaviour (American Psychiatric Association, 1994). A number of studies have demonstrated reduced imitation and MNS activity in individuals with ASC compared to control participants (Williams et al., 2004). It has been hypothesised that a 'broken MNS' and corresponding imitation impairment is a core feature of ASC. However, experimental evidence both supports (Avikainen et al., 2003; Rogers et al., 2003; Oberman et al., 2005; Dapretto et al., 2006; McIntosh et al., 2006) and opposes (Hamilton et al., 2007; Bird et al., 2007; Gowen et al., 2008; Leighton et al., 2008; Dinstein et al., 2010; Press et al., 2010; Spengler et al., 2010a) the presence of an imitation impairment in ASC. Furthermore, clinical observations of high levels of echolalia (automatic repetition of speech patterns) and echopraxia (automatic imitation of observed actions) in individuals with ASC (Rutter, 1974; Russell, 1997; Williams et al., 2004) are incompatible with an imitation deficit, and instead suggest problems with control of imitation. The following section will evaluate the evidence for and against a broken MNS and corresponding imitation impairment in ASC.

1.4.1 Is the MNS 'broken' in ASC?

1.4.1.1 Evidence from EEG and MEG studies

Using EEG, Oberman, Hubbard, McCleery, Altschuler, Ramachandran and Pineda (2005) monitored electromagnetic oscillations in the frequency range 8–13 Hz (Mu) in both controls and individuals with ASC whilst participants either observed a hand open and close video or executed this action. Suppression of Mu oscillations are considered an index of motor system activity therefore Mu suppression during observed hand actions is considered an index of MNS activity (Hari, 2006). Control participants demonstrated significant Mu wave suppression from baseline (white noise) for electrodes over sensorimotor cortex during both the observation and execution of hand open and close actions. Individuals with ASC exhibited significant Mu suppression for the execute condition but not the observe condition, suggesting that the motor system response to action observation differs between controls and individuals with ASC.

Attempts to replicate this finding have, however, had mixed success. Bernier, Dawson, Webb and Murias (2007) used a similar paradigm to record EEG while participants, with and without ASC, executed, observed or imitated a manipulandum grip. They reported no main effect of group (ASC or control) or interaction between group and condition (execute, observe or imitate). Using MEG, Avikainen, Kulomäki and Hari (1999) found comparable motor system activity during observation and

execution in individuals with and without ASC. Similarly, Raymaekers et al. (2009) found significant suppression of Mu rhythm to executed and observed hand movements in both children (8-13 years) with ASC and control children. Oberman, Ramachandran and Pineda (2008) reported typical Mu suppression in individuals with ASC for observation of actions conducted by familiar others. In sum, although there is some evidence of atypical motor system responses to action observation in ASC, attempts to replicate this finding, using the MEG or EEG methodology, have had mixed success.

1.4.1.2 Evidence from fMRI studies

A number of studies have used fMRI to investigate MNS function in individuals with ASC. Dapretto and colleagues (2006) presented participants (10 children with ASD and 10 control children) with faces depicting either a neutral expression or 1 of 4 emotions: anger, fear, happiness, or sadness. Participants either imitated or passively observed the faces. There were no differences between the groups in quality of facial expression imitation, or in eye-gaze. However, during imitation (versus null events) children with ASC failed to activate a key MNS region: the pars opercularis of the IFG (**Error! Reference source not found.**). In contrast, control children showed bilateral IFG activity. Furthermore, when passively observing faces, activity in the right pars opercularis was significantly greater for control children relative to children with ASC. Controlling for intelligence quotient (IQ), pars opercularis activity during the imitation condition significantly correlated with scores on the social subscales of the Autism Diagnostic Observation Schedule (ADOS) – Generic (Lord et al., 1989) and Autism Diagnostic Interview – Revised (ADI-R: Lord et al., 1994), which are considered gold-standard ASC diagnostic instruments. This work therefore suggests that low levels of pars opercularis activity are associated with reduced social functioning.

The work of Dapretto and colleagues (2006) has been considered a key study supporting the broken MNS hypothesis of autism and has been discussed in the context of anatomical MNS atypicalities in ASC. Using an automated technique to estimate cortical thickness, Hadjikhani, Joseph, Snyder and Tager-Flusberg (2006) found local decreases of grey matter in the pars opercularis in individuals with ASC relative to controls. Pars opercularis cortical thickness was correlated with combined social and communication scores on the ADI-R (Lord et al., 1994) such that thinner cortex was associated with reduced social and communication scores. Similarly, using voxel-based morphometry, Abell and colleagues (1999) found decreases of grey matter density in the left IFG. Using manual tracing techniques, Yamasaki and colleagues (2010) found a significant bilateral grey matter reduction of pars opercularis and the adjacent pars triangularis in ASC relative to a control group.

Although the study by Dapretto and colleagues (2006) demonstrates different levels of activity in a key MNS region in control children and those with ASC, this difference may not directly reflect atypical MNS function per se. One possibility is that children with ASC may veridically imitate the facial expressions but not 'feel' the emotion to the same extent as controls; in other words, the atypical pars opercularis activity may be a correlate of atypical emotional contagion. Indeed Grézes, Wicker, Berthoz, and de Gelder (2009) report that, during observation of dynamic relative to static actions, adults with and without ASC activate a similar network of brain regions including the pSTS, IPS, precentral gyrus and the dorsal part of the IFG (BA 6 and BA 44; **Error! Reference source not found.**). Group differences emerged when responses to emotional (i.e. fearful) and neutral actions were contrasted. To rule out this alternative explanation for weak MNS activity in ASC a number of studies have employed non-emotional stimuli. These studies investigate MNS function independent from emotion processing and emotional contagion.

Dinstein and colleagues (2010) used a repetition suppression fMRI paradigm to investigate selectivity for action execution and observation in individuals with ASC and control participants. The observation phase of this experiment compared the magnitude of repetition suppression for trials in which participants *observed* pairs comprising the same action (e.g. scissors hand gesture repeated) with trials in which participants *observed* pairs comprising different actions (e.g. scissors followed by thumbs-up hand gesture) . The execution phase of this experiment compared the magnitude of repetition suppression for trials in which participants *executed* pairs comprising the same action with trials in which participants *executed* pairs comprising different actions. For control participants greater repetition suppression for 'same' compared to 'different' trials was observed in part of the parietal MNS, the bilateral anterior IPS, in both the observation and execution phases. The repetition suppression data for individuals with ASC was indistinguishable in location and magnitude from that exhibited by control participants. This result does not comprise evidence of the existence of mirror neurons (for which cross-modal repetition suppression would be expected) for either control participants or individuals with ASC. However, this result does show that individuals with ASC have distinct neural populations that respond selectively to actions and that exhibit repetition suppression when a movement is repeatedly observed or executed; in this respect individuals with ASC do not differ from control participants.

Williams and colleagues (2006) employed the fMRI paradigm of Iacoboni and colleagues (1999) to investigate MNS function in adolescents with ASC. The experiment comprised an execute phase and an observe phase. In both phases participants viewed videos that depicted a) fingers lifting in sequence, b) a static hand on the fingers of which crosses appeared in sequence, or c) a sequence of dots that appeared

in different spatial locations. On each trial participants either observed the sequence or observed and simultaneously executed the sequence. Only observation and execution of (a) fingers lifting in sequence constitutes imitation. Imitation compared to non-imitative observation and execution resulted in less extensive IPL activation for individuals with ASC relative to controls. The authors suggest a weak MNS response. However, individuals with ASC also showed greater activity compared to controls in part of the motor system, the dorsal premotor cortex, and also in dorsal prefrontal cortex. Hence a weak response was only seen in the parietal, not frontal, component of the MNS. Activity differences between the groups in TPJ, amygdala and somatosensory cortices led the authors to suggest that abnormal patterns of integration of areas serving visual, motor, proprioceptive and emotional components of imitation may characterise ASC.

A recent fMRI study suggested that mPFC hypoactivity in ASC may be related to action understanding (Marsh and Hamilton, 2011). Participants passively observed videos of hand grasping actions which followed a rational or irrational trajectory towards a target; in a control condition participants watched videos of moving shapes. The authors found that mPFC activity differentiated between rational and irrational actions for control participants; this effect was not seen for the ASC group, suggesting atypical mPFC activity during action understanding in ASC.

Lastly, rather than finding a weaker MNS response in ASC, Martineau and colleagues (2010) found that, compared to observation of a static hand, observation of hand opening and closing actions resulted in *greater* left and right pars opercularis activity for adults with ASC relative to control participants. There were no differences between the groups in activity related to execution of hand open-close actions.

In sum, Dapretto and colleagues (2006) reported atypical MNS activity in ASC using an emotional face imitation task. However, fMRI studies have largely failed to replicate atypical MNS responses using stimuli that are unrelated to emotion processing and have even reported increased activity in MNS areas in individuals with ASC relative to control participants.

Adding to the inconsistency in neuroimaging results Théoret and colleagues (2005) recorded TMS-induced-MEPs whilst participants (10 adults with ASC and 10 control adults) observed movies of index finger or thumb movements. Movies were either oriented away from (egocentric view point) or towards (allocentric viewpoint) the participant. They found that, for control participants, irrespective of movie viewpoint, observation of index finger movements elicited greater MEPs from the muscle controlling index finger movements compared to the muscle controlling thumb movements and vice versa. The

ASC group exhibited muscle-specific MEPs that were comparable to those exhibited by the control group for observation of actions directed towards the participant. However, MEPs for actions directed away from the participant were significantly reduced relative to those exhibited by control participants. This data suggests typical MNS activity in ASC: like controls, when individuals with ASC observed actions from an allocentric viewpoint they exhibited muscle-specific activation of the motor system. However, this data can also be interpreted as evidence of an atypical MNS: individuals with ASC did not exhibit typical MEPs for actions viewed from an egocentric perspective. The authors suggest that this latter effect is related to faulty self-other representations. However, further work is required to replicate this effect and understand the underlying mechanism.

1.4.1.3 Evidence from behavioural studies: EMG, motion tracking and reaction time analysis

McIntosh, Reichmann-Decker, Winkielman and Wilbarger (2006) used electromyography (EMG) to record electrical activity from facial muscles during the observation of facial expressions in individuals with and without ASC. In an initial automatic imitation session participants were first required to 'just watch' images of happy and angry facial expressions. Subsequently, in a voluntary imitation session participants were asked to 'make the faces on the screen'. During the automatic imitation phase control participants activated facial muscles corresponding to the observed expression (zygomaticus major, which lifts the cheeks, in response to happiness, and corrugator supercilii, which furrows the brows, in response to anger). In contrast, individuals with ASC showed a non-specific pattern of spontaneous EMG activity. During the voluntary imitation task both groups showed comparable, expression-specific muscle activations. The authors suggest atypical automatic imitation in ASC.

A similar EMG study by Oberman, Winkleman and Ramachandran (2009), which measured automatic facial mimicry in children with and without ASC, failed to replicate this result. In agreement with McIntosh and colleagues (2006) no group differences in voluntary imitation were found. However, in contrast to McIntosh's (2006) findings, Oberman and colleagues (2009) also reported no group differences in the amplitude or selectivity of emotion related EMG activity during an automatic imitation phase: EMG activations were found to be temporally delayed but nevertheless present.

A study by Cattaneo and colleagues (2007) has raised an important issue for the interpretation of delayed imitative muscles activations in ASC. This study showed that control children activated the jaw muscle when they observed a model bring food to the mouth and that children with ASC were delayed in this response. However, in a second experiment Cattaneo and colleagues (2007) showed that children with ASC are also delayed in *non-imitative* muscle activations: when children with ASC bring food to

their own mouth they exhibit delayed activation of the jaw muscle relative to the control children. This result shows that, in both control children and those with ASC, observation of action results in motoric simulation of the action; however, a group difference arises because the action would be executed differently by the two groups.

In sum, facial EMG studies have failed to reliably report problems in ASC in the amplitude or selectivity of imitative EMG activity. Although it has been suggested that imitative muscle activations are temporally delayed in ASC, this effect likely reflects delayed execution related activity in ASC. This set of studies highlights an important point: difficulties with behavioural imitation may arise in the presence of intact observation–execution links due to atypical processing in one of the components of this link (execution in the above example but this argument could also be applied to atypical observation).

One suggestion in the literature is that, although individuals with ASC may imitate, they fail to do this in a typical way. Avikainen, Wohlschläger, Liuhanen, Hänninen, and Hari (2003) asked participants to copy an action sequence comprising putting a pen, with the left or right hand, into a green or blue cup, using one of two possible grips (the 'pen and cups task'). Participants were asked to imitate the experimenter's movements using the anatomically matching hand (anatomical imitation) or the mirror hand (mirror imitation). The two groups did not differ in errors on the anatomical imitation task. However the groups differed on the mirror image imitation task with individuals with ASC making more errors than controls. The finding of impaired mirror-image imitation has, however, been called into question. Firstly, this result has proved difficult to replicate. Hamilton, Brindley and Frith (2007) tested 25 children and 30 verbal mental age matched controls on a battery of imitation tasks. They found that children with ASC were just as likely as control children to make use of mirror imitation. Secondly, Leighton and colleagues (2008) argue that poor performance of individuals with ASC on this 'pen and cups task' may not reflect an imitation impairment per se but rather difficulties in more general processes such as attention or working memory. Leighton and colleagues (2008) have shown that although adults with ASC make more errors, relative to control participants, on the pen and cups task, they also make comparable amounts of errors on a geometric and on a verbal version of the task. In the geometric version the hands, pen and cups are replaced with symbols; in a verbal version of the task participants have to describe the model's actions; neither version requires imitation. Leighton and colleagues (2008) point out that good performance on the pen and cups task involves perceptual processing of complex stimuli, attentional control, executive function, motor control, theory of mind, language, and the comprehension of social cues. Difficulties, in ASC, with these non-imitative

components of the task may manifest as 'atypical imitation'.

A number of studies have demonstrated that ASC and control groups do not differ, in terms of imitation, on tasks with minimal attention, working memory and social cognition demands. Gowen and colleagues (2008) required participants to execute sinusoidal arm movements whilst observing congruent and incongruent movements depicted by either a real human, a two-dimensional animation of a dot that moved with biological motion, or a dot animation that moved at CV. They found that high-functioning adults with ASC did not differ from control participants in the magnitude of the Interference Effect resulting from observation of real human, biological dot or non-biological dot movement. Bird and colleagues (2007) used a block paradigm in which participants were instructed to execute a pre-specified response (open or close hand) upon perception of the movement of a stimulus. The stimulus depicted either a congruent or incongruent action. Both control participants and individuals with ASC exhibited significant automatic imitation effects (greater RTs for incongruent relative to congruent trials); there were no differences between the groups. Using a similar paradigm but with observation of face (eyebrow raise or mouth open), rather than hand, actions Press and colleagues (2010) replicated the finding of typical automatic imitation RT effects in adults with ASC. The online nature of these paradigms placed little demand on working memory. Furthermore, the stimuli comprised disembodied representations of hand and face actions that were relatively non-social and unemotional in comparison to stimuli employed in other imitation and MNS studies (e.g. Avikainen et al., 2003; Dapretto et al., 2006). These studies therefore suggest that automatic imitation is preserved in ASC and that findings of impaired imitation may be due to task-specific features such as high attention demands, working memory load and social cognition requirements.

In sum, both neuroimaging and behavioural studies have reported inconsistent findings with respect to the integrity of imitation in ASC. The pattern of results across behavioural studies suggests that the extent to which a task places demands on non-imitative functions - such as planning or working memory - and on social or emotional processing, is an important factor in the resulting degree of imitation. On tasks that minimise these demands individuals with ASC exhibit typical automatic imitation.

1.4.2 Atypical modulation of imitation in ASC?

In response to the inconsistent literature it has been hypothesised that, rather than an imitation deficit *per se*, individuals with ASC may have difficulties with appropriately controlling levels of imitation (Hamilton, 2008; Kana, Wadsworth, and Travers, 2011; Spengler et al., 2010); in other words individuals with ASC may exhibit *atypical modulation of imitation*. As previously discussed, a number

of studies have suggested a key role for mPFC and TPJ in the control of imitation (Brass et al., 2001b, 2003, 2005; Spengler et al., 2009, 2010c). Although no studies have directly tested the atypical modulation of imitation hypothesis, it is consistent with studies of ASC that report hypoactivity, relative to controls, in the mPFC and TPJ (Castelli, Happé, Frith, and Frith, 2000; Spengler, Bird and Brass, 2010, Marsh and Hamilton, 2011).

MPFC hypoactivity in ASC has been documented by Castelli, Happé, Frith, and Frith (2002) using a PET paradigm in which participants observed moving shapes that encouraged mentalising. Comparing activity during mentalising with activity elicited by watching random motion revealed reduced mPFC activity in individuals with ASC, relative to controls.

A recent fMRI study suggested that mPFC hypoactivity in ASC may be related to action understanding (Marsh and Hamilton, 2011). Participants passively observed videos of hand grasping actions which followed a rational or irrational trajectory towards a target; in a control condition participants watched videos of moving shapes. The authors found that mPFC activity differentiated between rational and irrational actions for control participants; this effect was not seen for the ASC group, suggesting atypical mPFC activity during action understanding in ASC.

Finally, work by Spengler et al., (2010a) suggests a functional association between mPFC function and control of imitation in ASC. This study consisted of three phases 1) participants were scanned whilst watching animations that evoked mentalising (Castelli et al., 2000); 2) participants completed a behavioural measure of mentalising in which they had to answer questions about stories which required them to infer the mental states of others (Happé et al., 1999); 3) participants completed a behavioural measure of imitation-inhibition. The imitation-inhibition task required participants to lift their index finger in response to a number 1 and middle finger in response to a number 2. In a ‘congruent condition’ the video showed a lifting action of the matching finger. In an ‘incongruent condition’ the video showed a lifting action of the non-matching finger. The number of errors (lifting the wrong finger) for incongruent minus congruent trials was labelled the ‘interference score’ and considered an index of imitation-inhibition. A high interference score corresponded to poor imitation-inhibition.

Spengler and colleagues (2010a) found that control over imitation (ability to inhibit the tendency to imitate) was associated with reduced behavioural mentalising scores and reduced social interaction ADOS scores. Furthermore, mPFC and TPJ activity during the fMRI mentalising task was correlated with imitation-inhibition such that individuals with low mPFC activity exhibited poor imitation-

inhibition.

In addition, recent functional connectivity MRI (fcMRI) studies have suggested that connectivity between social brain regions such as the mPFC and classic MNS areas is atypical in ASC. Intrinsic fcMRI detects the temporal correlation between spatially discrete low-frequency fluctuations of the BOLD signal. Shih, Shen, Öttl, Keekn, Gaffrey and Müller (2010) used fcMRI to investigate the intrinsic connectivity of brain areas associated with imitation: the IFG, IPL and STS. Functional MRI data was collected while participants performed a non-imitative task (semantic decision / letter detection). Although there was a trend towards a reduced effect of IPL on IFG in the ASD group there were no significant differences between the groups in a simple network model of imitation that included IPL, IFG and STS. If PFC was included as a moderator of this simple imitation network, the ASD group showed a significantly increased effect of PFC on IFG and a reduced effect of IPL on IFG in comparison to the control group. These data show that although communication between MNS regions is typical, the influence of PFC on MNS activity is atypical in ASC. Given the importance of appropriate levels of imitation for positive social interaction (Lakin and Chartrand, 2003) the atypical modulation hypothesis may go some way towards explaining difficulties with social interaction in individuals with ASC.

1.4.3 Imitation in ASC summary

Difficulties with imitation and findings of atypical MNS function led to the 'broken MNS' hypothesis of ASC. However, neuroimaging studies finding atypical MNS responses in ASC have proved difficult to replicate; delayed EMG activity has been suggested to reflect atypical action execution rather than atypical observation-execution links; and behavioural studies suggest that evidence of poor imitation in ASC may be due to task specific features such as high social processing demands. It has been hypothesised that the difficulty may lie in the modulation of imitation, rather than imitation per se. Although there is no empirical evidence in support of this hypothesis to date, functional connectivity MRI suggests a reduced influence of 'control' brain regions on MNS brain regions. *Whether individuals with ASC exhibit atypical modulation of imitation will be investigated in Chapter 7 of this thesis.*

1.5 ACTION PERCEPTION IN ASC

Action perception and biological motion processing comprise important inputs to the MNS. In principle,

atypical imitation could be the result of atypical biological motion processing rather than atypical action observation-execution links. Biological motion processing, as previously discussed, is also important in social communication and in learning about the social environment. For these reasons, whether biological motion processing is atypical in ASC has recently received much attention.

1.5.1 Is biological motion processing impaired in ASC?

A number of studies employing PLD stimuli have reported difficulties with biological motion processing in children with ASC 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 sound tracks. They found that, whereas TD children preferentially looked at the upright over the inverted PLD, a child with ASC did not. In a follow-up study Klin, Lin, Gorrindo, Ramsay and Jones (2009) found that, whereas a TD group of 2-year-olds preferentially looked at the upright PLDs, an ASC group of 2-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 (2009) suggest that toddlers with ASC 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 ASC. Furthermore, the PLD videos employed in this study depicted social games (e.g. pat-a-cake); the ADOS (Lord et al., 1989) assessment considers disinterest in these types of games a marker of ASC, hence it can be assumed that toddlers with ASC (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 (2011) investigated attention to biological motion in young children with ASC using a task that did not feature audio-visual contingency or overtly social stimuli. Annaz and colleagues (2011) used non-social PLDs (person walking) without an accompanying sound-track. In two separate conditions this biological PLD was presented alongside a scrambled version of the PLD (condition 1) or a PLD of a spinning top (condition 2). Whereas 3 to 7 year old TD children preferentially attended to the biological PLD in conditions 1 and 2, children with ASC showed no preference for the biological PLD over the scrambled PLD in condition1 and in condition 2 they preferentially attended to the spinning top PLD over the biological PLD. Together with the work from Klin and colleagues (2009) this finding suggests that, unlike TD children, those with ASC do not demonstrate a preference for biological motion. Condition 2 suggests that, unlike TD children, those with ASC exhibit a preference for non-biological (spinning top) 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 a) 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 ASC did not show this developmental improvement. In line with this, Blake and colleagues (2003) report a reduced sensitivity in judging which dots '*move like a person*' in 8 – 10 year old children with ASC. 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. The coherence of the noise dots was adjusted to regulate the difficulty of the task. Koldewyn and colleagues (2010) found that for adolescents with ASC, when they were responding correctly on 75% of trials (75% correct threshold) the noise dot coherence level was significantly higher than that for TD adolescents, indicating poorer direction discrimination for adolescents with ASC relative to TD adolescents. Atypical biological motion processing in ASC 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 for human motion compared to tractor motion, individuals with ASC exhibited equivalent sensitivity to human and tractor motion. Therefore, unlike controls, individuals with ASC did not exhibit an enhanced sensitivity for human motion.

Behavioural reports of atypical biological motion processing in ASC have been supported by neuroimaging studies. Freitag and colleagues (2008) used fMRI to scan adults with and without ASC while they viewed PLDs of an actor walking to the left or right. The within-scanner behavioural task was to indicate if the stimulus showed a walker or scrambled dots. On this task there were no behavioural differences between the groups: participants with ASC responded slower on average but there was no significant interaction between group and condition on RTs or errors. However, differences were found between control participants and individuals with ASC in terms of fMRI signal relating to biological motion versus scrambled motion. In the right hemisphere hypoactivation in ASC individuals was found in middle temporal gyrus, close to the STS, postcentral gyrus, IPL, right occipital regions, and the middle frontal gyrus. In the left hemisphere, hypoactivation in ASC 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 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 and colleagues (2007) and Freitag and colleagues (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 (2010b) demonstrates that atypical neural responses to biological motion can also be found in children and adolescents with ASC. This group used fMRI to scan TD participants, individuals with ASC and unaffected siblings while they viewed scrambled and intact versions of PLD movies that were similar to those employed by Klin and colleagues (2009). Compared to TD participants and unaffected siblings, those with ASC exhibited hypoactivation in left ventrolateral PFC, right amygdala, right pSTS, ventromedial PFC, and bilateral fusiform gyri. Hence replicating previous reports of hypoactivity in ASC in posterior areas such as pSTS and fusiform gyrus.

In sum, a body of behavioural studies suggests there is atypical attention to biological motion in ASC in early infancy, and that this is followed by atypical biological motion processing in childhood, adolescent and adulthood. These behavioural findings have been supported by neuroimaging studies showing atypical neural responses to biological motion in children, adolescents and adults.

In opposition to this body of evidence is a contrasting set of studies showing typical biological motion processing in ASC. Murphy, Brady, Fitzgerald and Troje (2009) tested adults with and without ASC on a task which required discrimination of the direction of movement of either an intact or scrambled PL walker in a field of noise dots. For both ASC and control groups, RT and error decreases, and sensitivity increases, were observed for the intact compared to scrambled walker. Hence, like the control participants, individuals with ASC were able to make use of the biological form-from-motion in order to determine the direction of movement. This result contrasts with studies suggesting atypical biological motion processing in ASC and stands in direct contrast to the study, reported above, conducted by Koldewyn and colleagues (2010), which reported atypical direction discrimination in adolescents with ASC. An obvious difference between these studies is the age of participants: it is possible that the older participants had developed compensatory strategies that were not available to adolescent participants.

Another difference, which may explain the discrepant results, is the masking procedure employed. Koldewyn and colleagues (2010) employed an atypical procedure for masking the PL walker wherein the same amount of noise dots were present on every trial; at easy levels dot coherence was high, at more difficult levels dot coherence was low. This mask was identical to the stimulus that they employed to measure global motion processing in the same participants. In contrast Murphy and colleagues (2009) used a more typical method: at easy levels there were only a few noise dots, at more difficult levels there were many noise dots; these noise dots always moved in an incoherent fashion. It may be the case that individuals with ASC have particular difficulties with the global motion mask employed by Koldewyn and colleagues (2010; see section 1.5.3); this difficulty may masquerade as biological motion processing problems when this type of mask is employed. On this basis it is possible that individuals with ASC exhibit typical direction discrimination from PLDs. One of the aims of Chapter 4 of this thesis is to further investigate the hypothesis that direction discrimination from PLDs is typical in ASC.

Moore, Hobson and Lee (1997) also demonstrated typical performance in individuals with ASC on a task requiring biological motion processing. Moore and colleagues (1997) showed children with and without ASC PLDs depicting either a person or an object and asked them to "*describe what you see*"; participants had an unlimited amount of time in which to complete the task. Children with ASC did not differ from controls in their ability to describe actions or subjective states such as tired or bored; however, they were relatively impaired in their ability to describe depictions of emotion. This finding of intact descriptions of actions and subjective states and atypical descriptions of emotion has been replicated in adolescents (Parron et al., 2008) and adults (Hubert et al., 2007; Atkinson, 2009) with ASC. These studies suggest that biological motion perception in ASC functions at a level that enables the direction of motion to be determined and the description of actions and subjective states. Difficulties with description of emotions requires further investigation; it may, for instance, be the case that this constitutes a non-specific impairment in emotion processing that is not directly related to the visual processing of biological motion.

1.5.2 Sources of variability

1.5.2.1 Age

It has previously been suggested that findings of typical performance on biological motion perception tasks are more likely in adult than in child populations and may be indicative of developmental improvement (Kaiser and Pelphrey, in press). However, within each stage of development (i.e. childhood, adolescence, adulthood) there are mixed findings. For instance, Blake and colleagues (2003) report reduced sensitivity to PLD biological motion in children with ASC relative to controls whereas

Moore and colleagues (1997) show that children with ASC do not differ from controls in their descriptions of actions and subjective states. Similarly, Murphy and colleagues (2009) show typical direction discrimination from PLDs in adults with ASC but Kaiser and colleagues (2010a) show that, unlike controls, individuals with ASC do not exhibit an enhanced sensitivity for human motion. A developmental improvement cannot account for all of the variance in experimental findings in this field.

1.5.2.2 Task

Another source of variability is the task. Three main tasks have previously been employed:

1) Judging whether the PLD represents a person (as opposed to scrambled dots)
2) Judging the direction of motion of the PLD
3) Describing the visual display.

There are two dominant designs for task type 1: one alternative forced choice (1AFC) or two alternative forced choice (2AFC). For the 1AFC design, on a single trial, one stimulus is presented comprising either an intact or scrambled PL walker. Participants are forced to respond yes or no to the question 'do the dots move like a person?' (or a similar variant of this question). For the 2AFC design two stimuli are displayed comprising an intact and a scrambled PL walker typically these are embedded in noise dots and the task is to determine which stimulus (1 or 2) contains dots that 'move like a person'. For task type 2 the dominant task design is that a single trial comprises an intact PL walker embedded in noise dots and participants are forced to decide the direction of motion (left or right).

It has previously been demonstrated that different components of the PLD are differentially informative to different tasks. For instance, the 'opponent motion' of the limbs is particularly informative in detecting a PL walker in an array of noise dots with the walker being most easy to detect when the limbs are crossing the midline of the body (Thurman and Grossman, 2008). For detecting the direction of motion of a PL walker, the foot dots have been suggested to be maximally informative (Saunders et al., 2010). Hence although all task types feature PLDs they may promote different attentional foci.

In addition these tasks differ in the extent to which they require stored knowledge about human movement. Task 1, judging whether a PLD moves like a person, presumably requires knowledge of how a person typically moves. Task 3, describing PLDs, may or may not require such stored knowledge depending on the marking criteria – for instance, if the marker is seeking the response that the PLD moves 'like a sad person' this likely requires a stored representation of how a person typically moves when they are in a 'sad' emotional state. In contrast Task 2 does not require stored representations of

human movement.

1.5.2.3 Dependent variable

Another source of variability is the dependent variable. Task type 3, measures verbal responses. Using this task type Moore and colleagues (1997) suggest that children with ASC can name simple biological motion displays. However, as highlighted by Annaz and colleagues (2010), this does not rule out the possibility that individuals with ASC are less *sensitive* to biological motion stimuli. To address the question of sensitivity task types 1 and 2 have typically employed either signal detection theory (SDT) to derive *d'* - an unbiased estimate of sensitivity (e.g. Blake et al., 2003) - or have estimated the psychophysical function and derived a threshold which indicates the noise to signal ratio (i.e. number of noise dots in the mask) at the point at which the participant responds correctly with a high (typically 75% correct) degree of accuracy.

1.5.3 The relationship between biological motion processing and global motion processing

In addition to biological motion perception problems individuals with ASC 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 and 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% of trials. In three independent studies, Spencer et al. (2000), Milne et al. (2002) and Pellicano et al. (2005) found that children with ASC had significantly higher MCTs than chronological aged-matched controls: they require about 10% 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 ASC (that is high MCTs were associated with reduced accuracy in identifying emotions). Koldewyn and colleagues (2010) observed a similar finding in adolescents: high MCTs were associated with poor direction discrimination from PLDs. It is therefore possible that individuals with ASC are less able to pool motion signals across space than controls (Bertone et al., 2003) and that this may relate to difficulties in biological motion processing. However, the extent to which this is a robust finding has been called into question. Del Viva and colleagues (2006) found no significant difference in MCTs between their ASC group and chronological age or verbal mental age matched control groups. Furthermore, in a follow-up study Milne et al. (2006) found that only a sub-group of their ASD sample (about 20%) had MCTs that significantly differed from those produced by control participants.

In sum, this literature suggests that individuals with ASC may have difficulties with global motion processing. Given that PLDs require the integration of the motion of multiple points across space it is currently unclear whether the deficit in perceiving biological motion from PLDs is distinct from the global motion processing deficit that has also been observed in ASC.

1.5.4 Action perception in ASC summary

Many studies have reported difficulties, in individuals with ASC, in detecting whether a PLD moves 'like a person'. However, individuals with ASC do not differ from control participants on some biological motion tasks such as describing the actions of PLDs and discriminating the direction of motion from PLDs. Furthermore it is unclear whether difficulties with biological motion processing in ASC are distinct from global motion processing problems. *Chapters 4 and 5 will investigate this issue. Chapter 5 will also question why individuals with ASC show poor biological motion processing on some tasks and typical performance on others.*

It has been suggested that biological motion processing difficulties in ASC may be related to hypoactivity in posterior brain regions such as pSTS. However, to better predict the behavioural correlates of pSTS hypoactivity further work needs to be conducted with control participants to gain more insight into the function of this region: *Chapter 2 focuses on this aim*.

1.6 SUMMARY AND THE CURRENT THESIS

The literature that has here been discussed can be considered to comprise a basic neural model of action perception and imitation as shown in Figure 1.11.

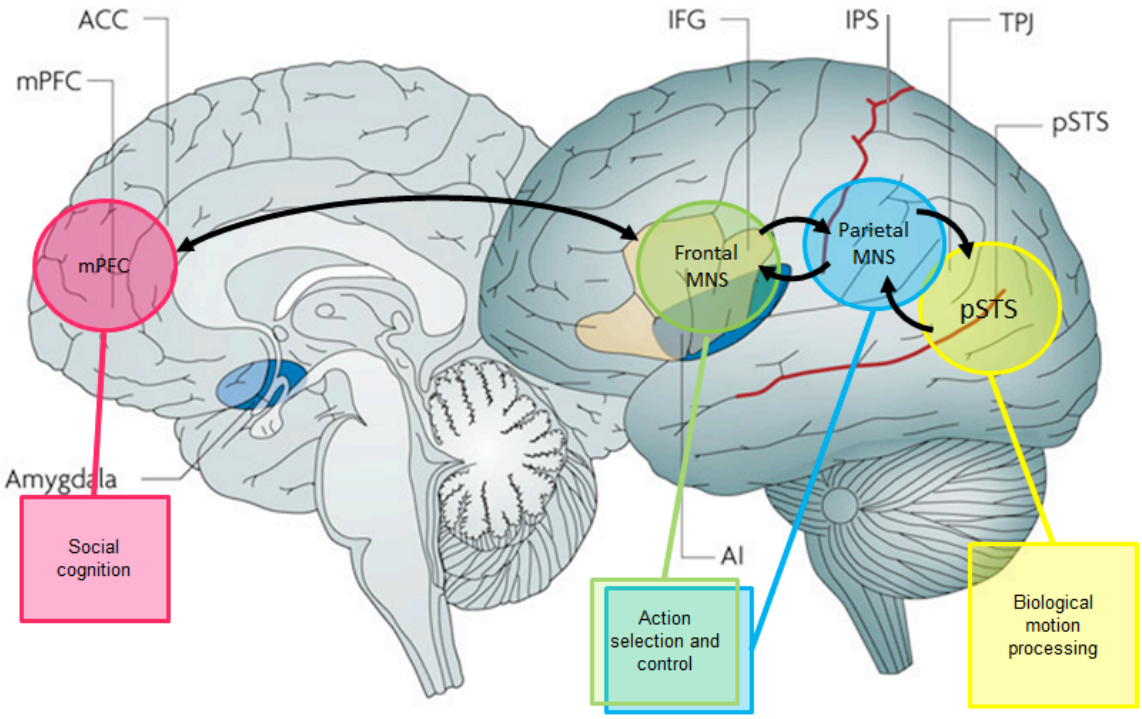

Figure 1.5. Basic neural model of action observation and execution. Adapted from Blakemore (2008). Based on the previous literature this basic model suggests that biological motion signals are processed in pSTS and fed-forward to the parietal and frontal MNS regions where this visual information about actions activates corresponding motor codes for execution of the action. Activity in this system is modulated by mPFC, an area known to play a role in the control of imitation (Brass et al., 2005, 2009; Wang et al., 2011b).

Based on the previous literature this basic model suggests that biological motion signals are processed in pSTS and fed-forward to the parietal and frontal MNS regions where this visual information about actions activates corresponding motor codes for execution of the action. Automatic motor system activity may interfere with on-going selection and control of actions (Blakemore and Frith, 2005). Activity in this system is modulated by mPFC, an area known to play a role in the control of imitation (Brass et al., 2005, 2009; Wang et al., 2011b).

Knowledge of connections in the brain makes this an anatomical plausible model. The pSTS is known to be reciprocally connected with the parietal MNS (Luppino et al., 1999), which feeds into the frontal

MNS (Harries and Perrett, 1991; Seltzer and Pandya, 1994); and mPFC has been shown to be reciprocally connected with the frontal MNS (Carmichael and Price, 1995; Luppino et al., 1999; Gong et al., 2009).

This thesis will address outstanding questions about these neural mechanisms that underpin action perception and imitation in the typical brain and will investigate atypical imitation and action perception in adults with ASC.

1.6.1 The neural basis of action perception in the typical brain.

As demonstrated in Figure 1.2 previous studies have implicated posterior areas such as pSTS in the visual representation of biological motion. However pSTS also responds to imagined or auditory representations of biological motion, to seemingly animate movement of simple shapes and during complex social judgements. *An unanswered question is whether activity in pSTS reflects the extent to which a stimulus objectively depicts, or is subjectively judged to depict, human motion.* **Chapter 2** describes a novel fMRI paradigm that aimed to address this question. Participants watched animations in which the velocity profile was either MJ human motion, or CV, or a 'motion-morph' comprising a linear combination of these extremes (e.g. 80% MJ: 20% CV). Participants were subsequently required to judge whether the dot motion looked 'human' or 'robot'. This paradigm therefore manipulated the amount of objective biological motion in the stimuli (percentage human motion) and measured the subjective perception of biological motion (percentage of 'human' judgements). Regions of Interest (ROIs) were identified by conducting a meta-analysis to establish the areas mostly commonly associated with biological motion processing. An ROI based analysis was employed to investigate whether activity in posterior regions associated with biological motion processing is associated with the 'objective' visual representation of biological motion, or the 'subjective' judgement of a stimulus as human.

A number of studies have shown that, in addition to posterior regions, the observation of biological motion activates anterior areas such as ventral premotor cortex which is considered a classic MNS region (Saygin et al., 2004; Saygin, 2007; Dayan et al., 2007). Although it has been suggested that these MNS activations during action observation are evidence for motoric simulation of observed action (Saygin, 2007) this hypothesis has never been directly tested. In addressing this hypothesis **Chapter 3** focuses on the MNS response to MJ biological motion (compared to CV motion) in typical adults. As previously discussed a number of studies have demonstrated that sensorimotor oscillatory activity in the *beta* range is modulated dynamically during action execution (Kilner et al. 2000, 2003b). *An*

unanswered question is whether activity in the MNS is modulated dynamically during action observation. **Chapter 3** describes a novel MEG paradigm in which *beta* range oscillatory activity over sensorimotor cortex was recorded whilst participants observed MJ and CV movements with either human form or dot form.

1.6.2 Action perception and the modulation of imitation in ASC

Imitation can occur automatically resulting in online interference with action execution. Such online interference may be a consequence of the automatic simulation of observed action in the observers own MNS and is greater for actions with human kinematics and human form relative to robotic, non-human actions. Such automatic imitation is part of a bi-directional relationship with positive social attitudes and hence is important for smooth, harmonious social interactions.

It has been suggested that a core impairment in ASC lies in the mechanisms that underpin imitation – the MNS. However, direct evidence for a 'broken MNS' in ASC is mixed. The neural model of action perception and imitation, that provides a starting point for the work in this thesis (Figure 1.5), suggests that atypical imitation in ASC may result, not only from MNS problems but also from difficulties with biological motion processing and the modulation of the output from the MNS (modulation of imitation). Chapters 4 to 7 will therefore establish whether these cognitive functions are intact in ASC.

Chapters 4 and 5 focus on action perception in individuals with ASC with the aim of investigating *whether biological motion processing deficits in ASC are distinct from global motion processing problems.* **Chapter 4** investigated perceptual thresholds for motion detection from PLDs in three conditions: Biological Motion (BM), in which we used a point-light walker; Structured Object (SO), in which we used a non-biologically moving, coherent, recognizable shape (a rectangle); and Unstructured Object (UO), in which we used a non-biologically moving, less coherent, unfamiliar shape (inverted single frame from BM condition). On this task a biological motion processing deficit in ASC that is distinct from general form-from-motion processing would be indicated by low thresholds, relative to those generated by control participants, in the BM but not SO or UO conditions.

Chapter 5: Experiment 1 took a different approach in investigating *whether biological motion processing deficits in ASC are distinct from global motion processing problems.* As in **Chapter 2** participants watched animations in which the velocity profile was either MJ human motion, or CV, or a 'motion-morph' (e.g. 80% MJ: 20% CV). Two animations were shown and participants were required to

'pick the less natural'. Whereas good performance in **Chapter 4** requires ignoring noise dots, good performance in **Chapter 5: Experiment 1** depends on sensitivity to perturbations to MJ motion. Crucially this judgement requires only local, not global, motion processing hence poor performance on this task cannot be a result of more general difficulties with global motion processing. Reflecting the emphasis of **Chapter 2** on objective and subjective components of biological motion processing, **Chapter 5: Experiment 2** considers that the effect reported in **Chapter 5: Experiment 1** could reflect a difficulty in perceiving the difference between the two animations or, alternatively, could be due to atypical conceptions of 'natural' human motion. To investigate whether individuals with ASC have an inability to perceive the difference between the two animations employed in **Chapter 5: Experiment 1** the same animations are employed in **Chapter 5: Experiment 2** however participants are asked whether the two animations look the 'same' or 'different'.

Atypical biological motion perception may constitute atypical sensory input to the MNS possibly resulting in imitation impairments. Control participants exhibit greater interference when observing movements with human motion (MJ biological motion) versus CV movements. Likewise form plays an important role: control participants exhibit greater interference in response to movements with human as opposed to robot form. **Chapter 6** investigates the effect of manipulating motion (MJ biological motion versus CV) and form (human versus robot) on the automatic interference of observed actions on on-going action execution in ASC.

Atypical imitation performance may occur as a result of atypical modulation of imitation: for instance control participants imitate more when in a positive social frame-of-mind but it is not known whether this is also true for individuals with ASC. **Chapter 7** employs a previously validated task (Cook and Bird, 2011) to investigate the social modulation of imitation in ASC. Participants 'primed' with either a pro-social or a non-social attitude are compared with respect to the effect of this attitude on the magnitude of automatic imitation.

Chapter 2. Dissociable processing of subjective and objective components of biological motion

Previous studies have implicated posterior areas such as pSTS in the visual representation of biological motion. However pSTS also responds to imagined or auditory representations of biological motion, to seemingly animate movement of simple shapes and during complex social judgements. This chapter investigated whether activity in posterior brain regions commonly implicated in biological motion processing is associated with the extent to which a stimulus objectively depicts human motion, or the extent to which participants subjectively judge a stimulus to move with human motion. Healthy adult human participants were scanned using fMRI whilst watching and making judgements about dot stimuli in which biological motion was parametrically modulated. Stimuli comprised a dot that moved with 100% MJ (biological) motion, or 100% CV, or some linear combination of these two extremes. Activity in the dorsomedial PFC correlated with objective measures of the extent to which the stimulus accurately depicted human motion. Activity in pSTS was not significantly correlated with objective perceptual features, but rather represented the difference between subjective judgements and the objective sensory data. We speculate that pSTS compares the incoming sensory data to a category exemplar (i.e. stored representation of 100% human motion). In short, our data suggest that pSTS plays an important role in judgement-based processing of biological stimuli.

2.1.1 INTRODUCTION

Perception of human movements is important for the interpretation of others' actions (Dittrich, 1993), intentions (Troje, 2002) and emotions (Dittrich et al., 1996; Pollick et al., 2001). However, observers' subjective judgements of the sensory world do not necessarily parallel the underlying objective data (Runeson, 1974). For example, a single dot moving at constant velocity (CV) is perceived to move with high velocity at the start, end and turning points, relative to midpoints of motion (Piaget et al., 1958; Goldstein and Wiener, 1963; Cohen, 1964) and a stimulus that moves with a sinusoidal (MJ) velocity profile is perceived to move at CV (Johansson, 1950; Viviani and Stucchi, 1992).

FMRI studies have shown a number of brain areas, including posterior regions such as lingual gyrus, fusiform gyrus and posterior STS (pSTS) (see section 2.2.3.2 and Table 2 for references), and anterior regions such as premotor cortex (Saygin et al., 2004; Dayan et al., 2007) are activated when participants watch biological motion stimuli such as PLDs. Activity in posterior areas such as the pSTS is commonly

discussed in terms of visual processing (Grossman and Blake, 2002; Giese and Poggio, 2003; Puce and Perrett, 2003), implying that activation in these areas reflects the objective sensory data. However, pSTS may be involved with more than just the visual processing of biological motion stimuli, since it also responds to imagined (Grossman and Blake, 2001) or auditory representations of biological motion (Bidet-Caulet et al., 2005), to seemingly animate movement of simple shapes (Castelli et al., 2000; Schultz et al., 2004, 2005; Santos et al., 2010) and during complex social judgements (Winston et al., 2002: see Figure 1.2 for review of previous studies activating pSTS). Therefore, activity in posterior areas may reflect subjective, judgement based, processing of biological motion rather than objective properties (Pelphrey et al., 2005; Jastorff and Orban, 2009). The aim of the current study was to investigate whether activity in posterior areas commonly associated with biological motion processing is correlated with the extent to which a stimulus objectively depicts, or is subjectively judged to depict, human motion.

2.1.2 METHODS

2.1.3 Participants

16 neurologically healthy adults (M:F ratio = 9:7; mean age = 27.57 years) took part in this study. All participants had normal or corrected-to-normal vision and were screened for exclusion criteria (dyslexia, epilepsy, and any other neurological or psychiatric conditions) prior to taking part. All participants were right-handed and gave informed consent. The study was approved by the local ethics committee and performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All participants were reimbursed for their time at a rate of £7.50 per hour. Four volunteers did not successfully complete the practice task and were subsequently excluded from the study. Data from one further participant had to be excluded due to excessive drowsiness in the scanner. Data from 11 participants (M:F ratio = 6:5; mean/SD age = 26.82/4.60) were included in the final analyses.

2.2 Stimuli

Previous fMRI studies of biological motion processing have typically employed PLDs (Johansson, 1973; Grossman et al., 2000; Saygin et al., 2004), which can be considered to comprise two sources of information. At a global level, the overall formation provides configural human form information. At a local level, the individual point-lights follow characteristic laws of human motion such as the MJ velocity profile (Flash and Hogan, 1985) which describes the bell-shaped speed profile of a straight point-to-point movement (e.g. drawing a straight line across a page: Abend et al., 1982; Flash and Hogan, 1985).

Our stimuli were animations of a single dot making 2 horizontal sinusoidal movements across the screen at a frequency of 0.8 Hz. The velocity profile of the stimulus was generated by motion-morphing between two movement prototypes:

(1) Human motion (MJ biological motion – Figure 2, 100% MJ): we used a constrained MJ model (Todorov and Jordan, 1998) which assumes that if $\mathbf{r}(s) = [x(s), y(s), z(s)]$ is a 3D curve describing the path of the hand during a particular trial, where s is the distance along the path, and tangential speed is $\dot{s}(t)$ ($\dot{s}$ is a time derivative, $\mathbf{r}'$ is the derivative with respect to s, and boldface signifies vector quantities) the temporal profile of the movement will minimise the scalar function:

$$J = \int_0^T \left\| \frac{d^3}{dt^3} r[s(t)] \right\|^2 dt$$

(2) Non-human motion (CV – Figure 2, 0% MJ)

A series of new 'motion-morph' velocity profiles was created by linear combinations of the prototype velocity profiles using the following equation:

Motion-morph = p_1(MJ) + p_2(CV)

where the weights p_i determine the proportion of the morph described by the individual prototype. Therefore, in each condition, stimuli were either 100% human motion (MJ) or 0% human motion (100%CV), or some linear combination of the two.

We employed 11 motion-morph stimulus types in total: 0%, 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90%, 100% human motion (Figure 2). For the 100% human motion condition, the velocity profile of the dot was comparable to that produced during a point-to-point human arm movement. We considered the percentage human motion in each motion-morph an index of Objective biological motion.

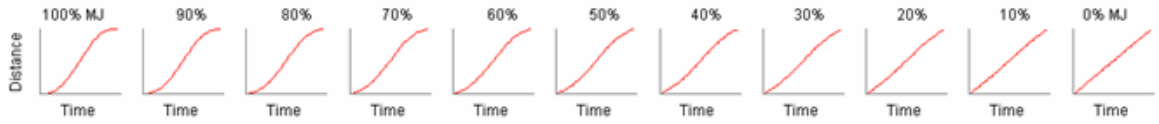

Figure 2. Motion-morph stimuli. On each trial the participant viewed a dot make 2 horizontal sinusoidal movements across the screen and was required to judge the motion as 'human' or 'robot'. We employed a parametric design with 11 levels of velocity profile of the dot stimulus. Distance/time graphs illustrate the velocity profile for each motion-morph. For the 0%MJ condition, distance is linearly related to time. For the 100%MJ condition, there is a sinusoidal relationship between distance and time. As the percentage human motion in the animation decreases the relationship between distance and time approaches a linear function.

2.2.1 Procedure

Participants lay in the scanner and viewed a projection screen, at the foot of the scanner bed, via a mirror. On each trial the participant saw one motion-morph stimulus (duration 2.5 s), followed by a 2 s response interval, followed by an inter-trial-interval (duration range 2 - 4 s; mean 3 s). During the response interval a question mark appeared on the screen and the participant was required to judge whether the dot moved like a 'human' or a 'robot'. Half the participants used their index finger to press a button on a response box to indicate 'human' and their middle finger to indicate 'robot'; for the other participants key assignments were reversed. There were 20 trials of each of the 11 motion-morph conditions (220 trials in total). In addition there were 15 rest trials in which participants fixated a central cross for 10 s. The scanning session was subdivided into 2 functional runs of 78 trials and 1 run of 79 trials. Condition order was pseudo-randomised within runs such that no more than two identical trials were presented in succession. A different randomisation schedule was employed for each participant. The duration of the fMRI session was approximately 30 minutes. Before scanning, participants completed a practice task in which they viewed examples of 100% MJ and 0%MJ movements and were required to judge successfully the movement as human or robot within a 2 s time limit.

2.2.2 MRI data acquisition

A 1.5 Tesla Siemens Avanto MRI scanner with a 32-channel head coil was used to acquire T2* echo-planar images using a sequence sensitive to blood oxygen level dependent contrast (30 slices, resolution 3.5x3.5x3.5mm, TR = 2.55 s, TE = 50 ms) and a 3D T1-weighted fast-field echo structural image (176 slices, resolution 1x1x1mm, TR = 2.73 s, TE = 3.57ms). The first 6 volumes of each session were discarded to allow for T1 equilibrium effects. Stimulus presentation began after the sixth volume.

2.2.3 Data analysis

2.2.3.1 Behavioural data

To acquire an index of subjective biological motion we calculated the percentage of 'human' judgements across all 20 trials for each of the 11 stimulus types for each participant. Binomial logistic regression curves were fitted to each individual's data set and the beta value was compared to zero. A beta value that is significantly greater than zero indicates that the probability of a 'human' judgement varies as a function of motion-morph stimulus type.

Reference	Contrast	STS				Lingual gyrus				Fusiform gyrus			
Safford et al., 2010	Attend to biological motion vs. attend to tool motion	±	50	-47	20								
Dayan et al., 2007	Dot motion that complies with human kinematics vs. dot motion that violates human kinematics	±	67	-57	28	±	22	-78	2	±	43	-75	-10
						±	13	-81	4	±	45	-62	-2
Thompson et al., 2007	Animated face motion vs. radial motion	±	48	-34	2								
		±	54	-48	12								
	Animated hand motion vs. radial motion	±	56	-54	14								
Peelen et al., 2006	Biological vs. scrambled motion	±	66	-39	27					±	42	-37	-19
										±	40	-67	-16
Peuskens et al., 2005	Biological vs. scrambled motion	±	57	-41	21								
Pelphrey et al., 2005	Eye movement vs. [mouth + hand + no movement]	±	46	-58	11								
	Mouth movement vs. [eye + hand + no movement]	±	53	-47	4					±	35	-51	-25
		±	60	-44	7								
	Hand movement vs. [eye + hand + no movement]					±	7	-79	0				
Saygin et al., 2004	Biological vs. scrambled motion	±	60	-44	7								
		±	61	-57	19								
Santi et al., 2003	Biological vs. scrambled motion	±	73	-42	5	±	9	-55	20	±	35	-52	-11
						±	8	-65	17	±	41	-43	-20
Servos et al., 2003	Biological vs. scrambled motion					±	7	-67	13				
Grezes et al., 2001	PLD walker vs. rotating PL cube	±	38	-62	4								
		±	34	-74	10								
		±	52	-60	6								
Vaina et al., 2001	Decide whether PLD depicts biological motion	±	51	-67	16	±	14	-92	0	±	26	-63	-5
		±	51	-73	16	±	24	-73	-7	±	29	-73	-11
	Decide direction of PLD	±	53	-65	16	±	24	-69	0	±	51	-60	-10
						±	22	-73	-2				
Bonda et al., 1996	Hand motion vs. random motion	±	54	-59	23								
	Body motion vs. random motion	±	65	-52	12					±	34	-37	-20
	Average coordinates	±	**55**	**-54**	**13**	±	**15**	**-73**	**5**	±	**38**	**-56**	**-14**

Table 2 Coordinates averaged to create peak coordinates for pSTS, fusiform gyrus and lingual gyrus regions of interest.

2.2.3.2 Meta-analysis

Previous fMRI studies were identified using pubmed (www.pubmed.com) with the search terms "fmri biological motion" and "fmri kinematics of human motion". Results were filtered to include studies conducted with healthy adults that contrasted biological motion with a control motion stimulus. Studies contrasting different types of biological motion stimuli (e.g. goal directed versus non-goal directed) and those that focused on the effects of learning were not included. Studies that employed only ROI analyses were also excluded. Fourteen studies satisfied these criteria. These previous studies reported activity in response to biological motion displays in 24 different brain areas (identified on the basis of labels in the

reviewed papers). ROIs only included areas reported in five studies or more. This resulted in three ROI areas: pSTS (reported in 11 studies); fusiform gyrus (reported in six studies) and lingual gyrus (reported in five studies). ROIs were defined by calculating the average of coordinates resulting from the contrast of interest in the reviewed papers (Table 2, Figure 2.2) resulting in peaks in pSTS at ±55 -54 13; Lingual gyrus at ±15 -73 5; and Fusiform gyrus at ±38 -56 -14.

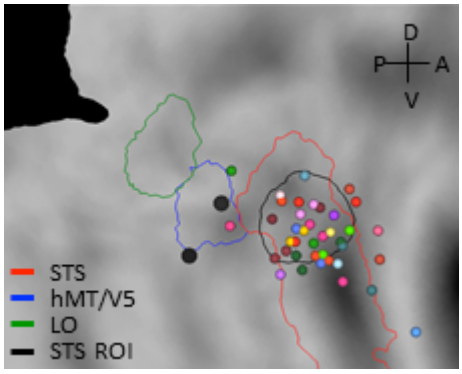

Figure 2.1. Location of pSTS ROI in relation to hMT/V5, LO EBA, and the STS

A12 mm radius sphere provided the best compromise between encompassing the critical region without also encompassing other cortical regions. This is illustrated for pSTS in Figure 2.1, whereby 12 mm allows inclusion of pSTS but not hMT/V5 nor nearby superior or middle temporal gyrus. ROIs were created using WFUpickatlas (Maldjian et al., 2003). pSTS and fusiform gyrus coordinates correspond well with those reported in a recent Activation Likelihood Estimation (ALE: Turkeltaub et al., 2002; Laird et al., 2005) meta-analysis which included 21 biological motion studies (contrast: Human Motion > Non-Human Motion, pSTS -52 -50 4, 54 -54 10; Fusiform gyrus, 42 -54 -20, -40 -48 -20; Grosbras et al., 2011). Whereas the current meta-analysis includes the lingual gyrus, Grosbras and colleagues (2011) do not report activity in lingual gyrus for the comparison between human and non-human motion. This discrepancy is likely due to the different keywords employed: the lingual gyrus has been implicated in kinematic processing (Orban et al., 1998) and unlike Grosbras and colleagues (2011) our search terms included “fmri kinematics of human motion”.

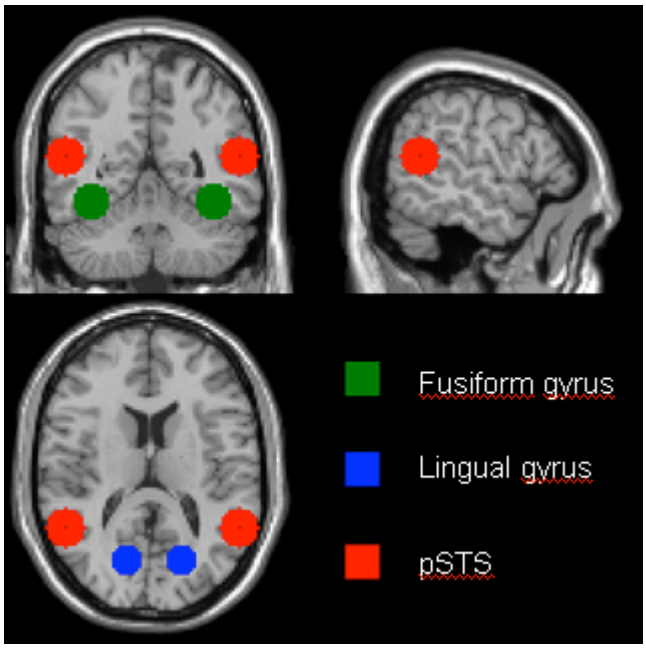

Figure 2.2. ROIs.12mm radius spheres centred at pSTS at ±55 -54 13; Lingual gyrus at ±15 -73 5; Fusiform gyrus at ±38 -56 -14. Displayed on SPM single subject T1 image at ±55 -54 13 MNI coordinates.

2.2.3.3 fMRI data

fMRI data were analyzed using statistical parametric mapping implemented in SPM8 (Wellcome Department of Imaging Neuroscience, London; http://www.fil.ion.ucl.ac.uk/spm) using Matlab 7.11.0. During preprocessing, functional images were re-aligned to the first volume and unwarped, spatially normalized to an EPI template based on the Montreal Neurological Institute (MNI) reference brain with a resampled voxel size of 3 x 3 x 3 mm and spatially smoothed with a 4 mm, full- width, half-maximum Gaussian kernel.

After preprocessing, functional images were analysed in an event-related fashion (Worsley and Friston, 1995). The volumes acquired during the three runs were treated as separate time series. For each series, the variance in the BOLD signal was decomposed with a set of regressors in a general linear model (Friston et al., 1995). To create regressors of interest, each trial was modelled by convolving a delta function at each trial onset (presentation of the dot stimulus) with a canonical haemodynamic response function over the duration of the event (2.5 s). At the individual subject level two regressors were created representing: 1) all trials parametrically modulated by a vector coding for the objective percentage of human motion in each of the 11 stimulus types (Objective biological motion model); 2) all trials parametrically modulated by a vector coding for the percentage of 'human' judgements for each of the 11 stimulus types (Subjective biological motion model). Two additional separate analyses were also conducted. For the first additional analysis (subjective-objective difference) a single regressor was

created at the individual subject level that represented the difference between subjective and objective models. For the second (all motion versus rest) a single regressor was created at the individual subject level that represented every dot motion trial. The data and models were high-pass filtered with a cut-off of 128 s. Parameter estimates calculated from the least mean squares fit of the model to the data were used in contrasts coding for the various different regressors at the individual subject level. First level contrasts from all participants were spatially smoothed with an 8 mm, full-width half-maximum Gaussian kernel and entered into separate one-sample t-test second level analyses, where 'subject' was treated as a random effect. Main effects were determined using the t-statistic on a voxel by voxel basis.

Regions of Interest analysis

Activations are reported if they survive a peak and cluster level threshold of $p \leq 0.05$ (small volume correction (FWE) at each ROI).

Whole brain analysis

In order to investigate whether activity in brain areas outside these previously defined ROIs correlated with either the Subjective or Objective model, an exploratory whole brain analysis was conducted using a cluster-level threshold of $p<0.05$.

2.3 RESULTS

2.3.1 Behavioural data

The mean percentages of 'human' judgements across all 20 trials for each of the 11 conditions were calculated for each participant and are depicted in Figure 2.3. Note that participants gave more 'human' responses for stimuli that tend towards 100% human motion compared to those that tend towards 0% human motion. For each participant binomial logistic regression was used to predict the probability of a 'human' judgement as a function of percentage human motion. For all participants the resulting beta value was significantly different from zero (all $p \leq 0.0002$) demonstrating that the probability of a 'human' response significantly increased as a function of percentage human motion.

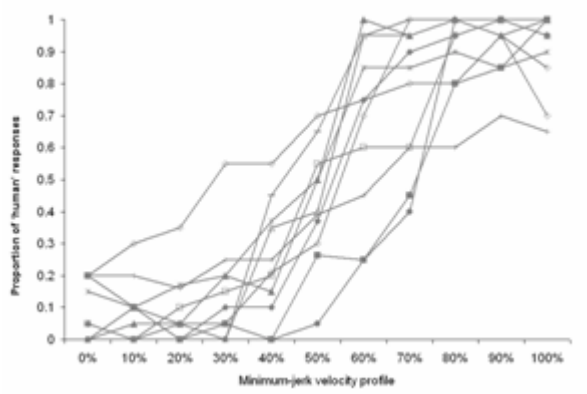

Figure 2.3. Mean 'human' responses for each of the 11 stimulus types. Each line represents data from one individual participant.

2.3.2 fMRI data

2.3.2.1 Subjective biological motion model

Analysis of the Subjective biological motion model revealed brain areas where the BOLD response increased as the extent to which the stimulus was judged to depict human motion increased.

ROI analysis

Activity in two of the six ROIs, the right pSTS and left Lingual Gyrus, correlated significantly with the Subjective model (Figure 2.4**,** Table 2.1). There was no significant correlation between fusiform gyrus activity and the Subjective model. The pattern of significance was the same if the ROIs were defined as 12mm radius spheres around the peak pSTS (-52 -50 4; 54 -54 10) and fusiform gyrus (42 -54 -20; -40 -48 -20) coordinates from the human motion versus non-human motion contrast of a recent ALE meta-analysis by Grosbras and colleagues (2011) (Table 2.3).

Whole brain analysis

There were no suprathreshold voxels for the whole brain analysis.

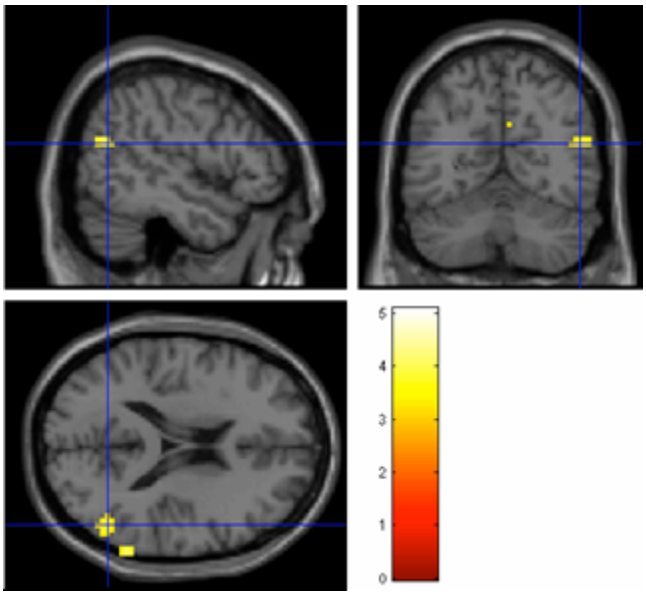

Figure 2.4. Subjective biological motion. BOLD response in the pSTS significantly correlates with subjective biological motion. Data from ROI analysis thresholded at (*p (uncorr)* < 0.005) and displayed on SPM single subject T1 image, crosshairs at peak coordinate 51 -61 19. Note that the most anterior locus of activity did not reach significance.

Region	**Coor-dinates**	**Contrast**	**Z**	**Cluster level $P_{FWE\text{-}corr}$ (SVC)**	**Peak level $P_{FWE\text{-}corr}$ (SVC)**	**K_E**
L Inferior lingual gyrus	-21 -76 -5	Subjective model	3.34	0.04	0.02	6
R pSTS	51 -61 19	Subjective model	3.01	0.05	0.05	3
L Inferior lingual gyrus	-21 -76 -5	Subjective-objective difference	2.98	0.055	0.056	2
R pSTS	51 -64 19	Subjective-objective difference	3.25	0.04	0.03	6
R pSTS	51 -61 4	All motion > rest	3.64	0.02	0.01	25
R lingual gyrus	9 -67 7	All motion > rest	5.00	0.000	0.000	257
L lingual gyrus	-6 -79 4	All motion > rest	5.08	0.000	0.000	257
R fusiform gyrus	36 -64 -8	All motion > rest	3.71	0.001	0.01	107
L fusiform gyrus	-39 -64 -11	All motion > rest	4.45	0.002	0.001	91

Table 2.1 ROI analysis. MNI coordinates, Z value of peak voxels, family wise error (FWE) corrected p values of small volume (12mm radius), cluster extent (K_E) from ROI analysis.

2.3.2.2 Objective biological motion model

Analysis of the Objective biological motion model revealed brain areas where the BOLD response increased as the extent to which the stimulus accurately depicted human motion increased.

ROI analysis

No suprathreshold voxels were found in any of the three ROIs.

Whole brain analysis

BOLD signal in the dorsomedial PFC (dmPFC) was significantly correlated with objective biological motion (Figure 2.5**,** Table 2.2.). This activity survived cluster-level multiple-comparison correction at $p<0.05$ false discovery rate (FDR).

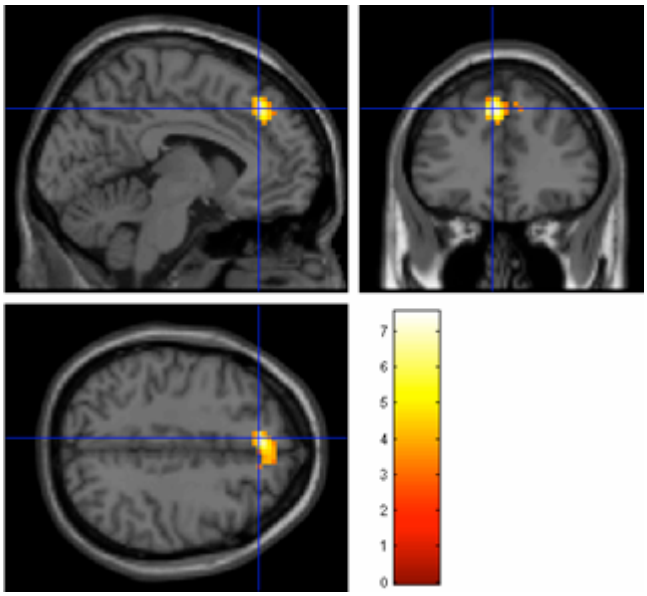

Figure 2.5. Objective biological motion. BOLD response in dmPFC significantly correlates with objective biological motion. Data from whole-brain analysis thresholded at (*p (uncorr)* < 0.005) and displayed on SPM single subject T1 image, crosshairs at peak coordinate -6 35 43.

Region	Coordinates	Contrast	Z	Cluster level $q_{FDR\text{-}corr}$	K_E
Medial prefrontal cortex: superior frontal gyrus	-6 35 43	Objective model	4.27	0.03	58
	3 41 37	Objective model	4.08	Part of above cluster	Part of above cluster
R middle occipital gyrus	27 -88 10	All motion > rest	5.46	0.00	4891
L postcentral gyrus	-39 -31 61	All motion > rest	5.33	0.00	4878

Table 2.2 Whole-brain analysis.MNI coordinates, Z value of peak voxels, false discovery rate (FDR) corrected p value, cluster extent (K_E) from whole-brain analysis.

2.3.2.3 Subjective-objective difference

The Subjective-objective difference analysis revealed brain areas where the BOLD response increased as the difference between subjective judgements and objective biological motion increased.

ROI analysis

Right pSTS activity correlated significantly with the Subjective-objective difference model. The correlation between the difference model and left Lingual Gyrus activity was marginally significant (Figure 2.6, Table 2.1). There was no significant correlation between activity in the fusiform gyrus and the Subjective-objective difference model. The pattern of significance was the same if the ROIs were defined as 12 mm radius spheres around the peak pSTS (-52 -50 4; 54 -54 10) and fusiform gyrus (42 -54 -20; -40 -48 -20) coordinates from the human motion versus non-human motion contrast of the meta-analysis by Grosbras and colleagues (2011; Table 2.3).

Whole brain analysis

There were no suprathreshold voxels for the whole brain analysis.

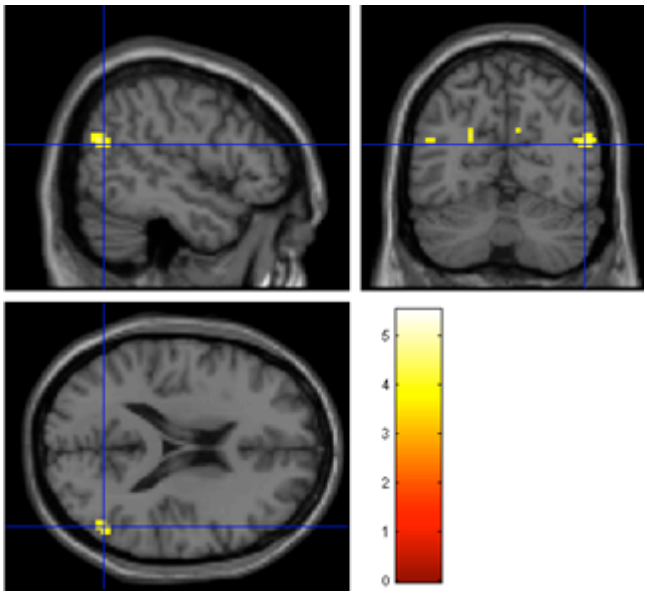

Figure 2.6. Subjective-objective difference model. BOLD response in the pSTS significantly correlates with the difference between subjective and objective measures of biological motion. Data from ROI analysis thresholded at (*p (uncorr)* < 0.005) and displayed on SPM single subject T1 image, crosshairs at peak coordinate 51 -64 19. Note that the left hemisphere activity did not reach significance.

Region	**Coordinates**	**Contrast**	**Z**	**Cluster level $P_{FWE-corr}$ (SVC)**	**Peak level $P_{FWE-corr}$ (SV**	**K_E**
R pSTS	51 -61 19	Subjective model	3.01	0.05	0.05	2
R pSTS	51 -61 19	Subjective-objective difference	3.13	0.055	0.04	2
R pSTS	48 -61 4	All motion > rest	3.86	0.008	0.007	47
R fusiform gyrus	42 -55 -14	All motion > rest	3.60	0.004	0.02	72
L fusiform gy	-36 -52 -11	All motion > rest	4.29	0.009	0.002	43

Table 2.3 Grosbras et al. (2011) defined ROI analysis. MNI coordinates, Z value of peak voxels, family wise error (FWE) corrected p values of small volume (12mm radius), cluster extent (K_E) from ROI analysis defined on the basis of the Grosbras meta-analysis contrast: Human Motion > Non-Human Motion, pSTS -52 -50 4, 54 -54 10; Fusiform gyrus, 42 -54 -20, -40 -48 -20; Grosbras et al. (2011).

2.3.2.4 All motion versus rest

ROI analysis

Suprathreshold activity was observed in the right pSTS, right lingual gyrus, right fusiform gyrus, left lingual gyrus and left fusiform gyrus but not in left pSTS (Table 2.1). The pattern of significant was the

same if the ROIs were defined as 12mm radius spheres around the peak pSTS (-52 -50 4; 54 -54 10) and fusiform gyrus (42 -54 -20; -40 -48 -20) coordinates from the human motion versus non-human motion contrast of a recent ALE meta-analysis by Grosbras and colleagues (2011; Table 2.3).

Whole brain analysis

Clusters of activity were also observed in middle occipital gyrus and postcentral gyrus (Table 2.2).

2.4 DISCUSSION

Participants were scanned whilst making judgements about moving dot stimuli in which biological motion information was parametrically modulated. ROI analyses investigated whether activity in pSTS, lingual gyrus and fusiform gyrus correlated with a vector coding for: 1) percentage human motion in each stimulus type (Objective model); 2) percentage 'human' judgements for each stimulus type (Subjective model). Activity in pSTS and lingual gyrus correlated with the Subjective model. A Subjective-objective difference analysis supported and expanded this finding demonstrating that pSTS represents the difference between subjective judgements and the objective sensory data. Given that many brain regions e.g. cerebellum (Bonda et al., 1996; Vaina et al., 2001; Ptito et al., 2003; Dayan et al., 2007), premotor cortex (Saygin et al., 2004; Saygin, 2007; Dayan et al., 2007) and cingulate cortex (Grèzes et al., 2001; Dayan et al., 2007; see Grosbras et al. 2011 for review) have been associated with biological motion, a whole brain analysis was conducted to identify any areas outside the ROIs in which activity correlated with Objective or Subjective models. This analysis showed that activity in dmPFC correlated with the Objective model.

2.4.1 Objective biological motion

Surprisingly, the ROI analysis showed no evidence that activity in posterior brain regions commonly associated with biological motion correlated with the extent to which a stimulus objectively depicted biological motion. A significant correlation was only observed in dmPFC [MNI coordinates -6 35 43, BA8 extending rostrally into BA9]. Three previous studies have found activity in this location during observation of biological motion (Grèzes et al., 2001 [-6 42 40]; Pelphrey et al., 2005 [4 30 39]; Ptito et al., 2003 [4 63 14]). Unlike these previous experiments, which do not feature a parametric modulation of biological motion, we were able to demonstrate that activity in dmPFC correlates with the objective extent to which the stimulus depicted biological motion. That is, activity correlated with the degree to which the dot moved with a velocity profile characteristic of human motion.

A recent ALE meta-analysis found a cluster of activity in dmPFC, overlapping our cluster (peak MNI

coordinates 2 38 46: Sperduti, Delaveau, Fossati, and Nadel, 2011), which was associated with external agency attribution. Sperduti and colleagues (2011) focused on experiments in which the visual feedback of an executed action was perturbed resulting in the belief that the observed motion was externally generated. It is possible that the correlation found in the current study between dmPFC activity and Objective biological motion is related to an increase in external agency attribution as the kinematics of the observed dot motion tend towards veridical human motion. In other words, when the dot moves with a high, compared to low, degree of human motion participants may be more likely to process the dot as being driven by the actions of another agent.

dmPFC has also been associated with response conflict and executive function (Barch et al., 2001; Neumann et al., 2008) and with representing mental states (mentalising or Theory of Mind: Van Overwalle, 2009; Amodio and Frith, 2006). Although areas active for response conflict (e.g. task irrelevant information versus task relevant information) are typically posterior to the location of activity from the current study (e.g. Peak MNI coordinates from the current study [-6, 35, 43], peak coordinates from the Barch meta-analysis [4, 23, 39]) more anterior coordinates have been observed (Milham, Banich, and Barad, 2003 [5, 38, 42]; Steel et al., 2001 [-3, 41, 28]; Roelofs, van Turennout, and Coles, 2006 [-4, 34, 40]; de Zubicaray, Wilson, McMahon and Muthiah, 2001 [28, 47, 21]). Likewise, although mentalising studies often report coordinates anterior to our peak, activations from this type of study can extend quite posteriorly (Fletcher et al., 1995 [-13, 41, 39]; Platek, Keenan, Gallup and Mohamed, 2004 [7, 38, 63]; Goel, Grafman, Sadato and Hallett, 1995 [-13, 42, 40]). Overlapping activations for mentalising and response inhibition have led to the suggestion that this brain region may be well suited for inhibiting information pertaining to the self in order to attribute information to another individual (Amodio and Frith, 2006). Similarly, it has been argued that processes involved in mentalising, such as self/other distinctions are also involved in inhibition of imitation (Spengler et al., 2009, 2010b, 2010a) and rely on similar brain regions (Brass et al., 2009; Spengler et al., 2010c). In particular a recent set of studies by Wang and Hamilton have shown that the enhancement of automatic imitation by direct gaze (Wang et al., 2011a) is mediated by a cluster of activity in dmPFC which is close to the cluster here reported (Wang, Ramsey and Hamilton, 2011 [6 44 34]; coordinates from the current study, -6 35 43). One possibility is that the correlation found in the current study between dmPFC cortex activity and objective biological motion relates to the inhibition of the automatic tendency to imitate the movement of the dot. Since the tendency to imitate movements can be greater for stimuli that comply with human kinematics than for those that do not (Kilner et al., 2007a), imitation inhibition may correlate with the extent to which the stimulus objectively depicts human motion. Given that this area is activate for both agency attribution and the modulation of automatic imitation by eye-contact another possibility is that

this region is involved in the processing of behaviourally relevant information about biological stimuli.

2.4.2 Subjective biological motion

The ROI analysis showed that activity in two areas commonly associated with biological motion processing (pSTS and lingual gyrus) correlated with the extent to which a stimulus was judged to depict human motion. The Subjective-objective difference analysis supported and expanded upon the Subjective analysis in which variance associated with the objective modulator was partialled-out before the residual variance was correlated with the subjective modulator. The Subjective-objective difference analysis goes one step further and looks directly at the difference between the two conditions. It was demonstrated that pSTS represents the difference between subjective judgements and the objective sensory data.

Activity in posterior areas commonly associated with biological motion is typically discussed with reference to visual processing (Grossman and Blake, 2002; Giese and Poggio, 2003; Puce and Perrett, 2003). However, activity in biological motion processing areas has previously been found in the absence of visual input: for instance for imagined (Grossman and Blake, 2001; Deen and McCarthy, 2010) and auditory representations of biological motion (Bidet-Caulet et al., 2005). Additionally, a number of studies have demonstrated increased pSTS and/or lingual gyrus activity when participants view simple non-biological shapes that move with or without biological kinematics but that appear to move in an animate fashion (Castelli et al., 2000; Blakemore et al., 2003; Schultz et al., 2004, 2005; Santos et al., 2010). Santos and colleagues (2010) parametrically varied the amount of interaction between two circles and demonstrated that pSTS and lingual gyrus activity increased as a linear function of interaction. The current finding that pSTS activity correlates with the difference between subjective judgements and the objective sensory data brings together these studies. We speculate that in pSTS incoming sensory data is compared to a category exemplar (i.e. stored representation of 100% human motion). Hence pSTS plays an important role in judgement-based processing of biological stimuli.

Jastorff and Orban (2009) recently demonstrated that pSTS activity was modulated by the extent to which a stimulus depicted an intact PLD when participants were required to make same/different judgements, but not during passive viewing; they suggest a role for pSTS in behaviourally relevant analysis of action kinematics. Complementary to this finding, pSTS activity has been shown to vary as a function of the intention of an action (Pelphrey et al., 2003b, 2004; Saxe et al., 2004; Grèzes et al., 2004). For instance, Saxe and colleagues (2004) presented identical visual representations of an action in differing contexts; pSTS activity was found to vary with the inferred intention of the action.

Considering the pSTS as a comparator of exemplary action kinematics and the incoming sensory data broadly fits with the idea that pSTS is important for behaviourally relevant analyses of actions. An interesting question for further research concerns the function of the pSTS subjective-objective difference signal which may possibly play a role in categorical perceptual processing - minimising within-category and maximising between-category perceptual differences. Given that the difference signal would be greatest when the discrepancy between subjective and objective is largest it is also possible that this signal represents judgement uncertainty. The recent finding that pSTS activity is attention dependent - pSTS activity is high if a biological stimulus is attended and low if the stimulus is unattended but, nevertheless, present (Safford et al., 2010) – raises the question of whether the difference computation we suggest is an automatic or attention dependent process.

No significant correlation between BOLD response and subjective biological motion was observed in the fusiform gyrus ROI. Fusiform gyrus activity has been robustly reported in response to high-level stimuli such as faces and bodies (Kanwisher et al., 1997; Peelen and Downing, 2005). It is possible that PLDs activate these areas due to the form-from-motion they generate. It is likely that our stimuli did not activate fusiform gyrus because they consisted of a single dot and did not comprise a body or head.

2.4.3 Conclusion

The current study suggests that pSTS and lingual gyrus activity is associated with subjective, judgement-based, processing of biological stimuli. dmPFC activity is associated with the objective extent to which a stimulus represents biological motion.

2.4.3.1 What next?

The pSTS is reciprocally connected to the parietal MNS (Luppino et al., 1999), which in turn is reciprocally connected to the frontal MNS (Harries and Perrett, 1991; Seltzer and Pandya, 1994). Behavioural studies show that actions which are believed to be 'human' interfere more with on-going action execution than actions believed to be 'robotic' (Press et al., 2005; Stanley et al., 2007). A possible explanation for this effect is that animacy judgement related activity is fed-forward from pSTS to MNS areas, influencing the automatic motoric simulation of action kinematics. This idea presents an interesting avenue for future investigation. However, before such investigation can be conducted it must be established whether MNS activations do in-fact represent automatic motoric simulations of action kinematics. Chapter 3 investigates this question.

Chapter 3. Dynamic human motor activity when observing actions

Chapter 2 focused on posterior activations resulting from biological motion observation; suggesting that the pSTS plays a role in judging whether a motion stimulus represents human motion. Activity from the pSTS is fed-forward to the parietal MNS, which feeds into frontal MNS regions. Observing the actions of others activates many areas of our own motor system. It has been argued that these motor activations are evidence that we motorically simulate observed actions; a function that may support various abilities such as imitation and action understanding. Previous studies have demonstrated dynamic modulations in motor activity when we execute actions. Therefore, if we do motorically simulate observed actions, our motor systems should also be modulated dynamically during action observation. This Chapter directly tested this hypothesis. Using MEG, we recorded cortical activity while participants observed videoed actions performed by another person. Activity in the motor system was modulated dynamically during action observation providing evidence that MNS activations during action observation comprise motoric simulation at the level of action kinematics.

3.1 INTRODUCTION

Previous studies have demonstrated that observing the actions of others activates many areas of our own motor system. FMRI studies have demonstrated such activations in ventral and dorsal premotor cortices, inferior parietal lobule, and primary motor cortex (Rizzolatti and Craighero, 2004; Morin and Grèzes, 2008; Gazzola and Keysers, 2009; Kilner et al., 2009a; Rizzolatti and Sinigaglia, 2010). It has been argued that these motor activations are evidence that we motorically simulate observed actions - a function that may support various abilities such as imitation and action understanding (Hurley, 2008). In line with this, neuroimaging studies have demonstrated matching of effector categories (e.g. motor cortex is activated somatotopically during action observation (Buccino et al., 2001)) and behavioural studies have demonstrated matching of action categories (e.g. open actions are facilitated by observing open actions irrespective of effector (Leighton and Heyes, 2010)). Gangitano and colleagues (2001) employed single-pulse TMS to elevate motor system activity and recorded EMG activity from the first dorsal interosseus and right abductor pollicis brevis muscles whilst participants observed a hand open and grasp action sequence. Gangitano and colleagues (2001) found that participants' motor system activity was greater when they observed hand fully open compared to hand closed parts of the sequence,

presumably indicating that activity in participants' motor system was dynamically modulated as if they too were performing the observed action. Alaerts and colleagues (2010, 2011) replicated this experiment but with a force manipulation whereby the object that was grasped was either a light or heavy weight. Alaerts and colleagues demonstrated that muscle-specific facilitation followed the timecourse of the observed action and that motor excitability was considerably higher when observing heavy object compared with light object lifting. The results of previous studies therefore demonstrate dynamic modulation of mirror system activity when observing action sequences. In the current study we were interested in investigating whether motor system activity is modulated dynamically during action observation at the level of action kinematics. That is, if the action itself does not change (i.e. the action is always a finger point rather than a grasping action which features topographical changes in the action representation) but the kinematics of the movement varies (i.e. sometimes the finger point moves slowly, at other times the finger moves fast) can dynamic modulations of mirror system activity be observed?

The majority of studies that have investigated the functional role of activity in the MNS have employed fMRI. As a result we know a lot about which areas of the human brain are active when we observe an action, but very little about how this activity changes across time. MEG, which has temporal resolution superior to that of fMRI, provides a suitable technique to investigate activity changes over time. Previous studies that have employed MEG have demonstrated dynamic modulations in the power of oscillatory activity in the 15-30 Hz (*beta*) range during action execution (Kilner et al., 2000, 2003b). These effects originate in sensorimotor cortex, specifically primary motor cortex (e.g. Murthy and Fetz, 1992). For example, Kilner et al. (2000; 2003a) found that when participants moved a lever with their finger and thumb, *beta* oscillations were attenuated when they were at the midpoints of action compared with when they were at the endpoints.

MEG and EEG studies have demonstrated that sensorimotor oscillatory activity in both the *mu* and *beta* ranges is attenuated when observing actions (Cochin et al., 1998, 1999; Hari et al., 1998; Babiloni et al., 2002; Caetano et al., 2007; Kilner et al., 2009b). However, if motor activations during action observation reflect motoric simulation of the observed action it would be expected that sensorimotor *beta* oscillations are modulated dynamically during action observation. To address this question, the present study used MEG to measure *beta* oscillations while participants watched videos of sinusoidal arm movements.

Previous studies have suggested that observing actions with human form and motion activates motor

codes to a greater extent than observing actions with non-biological (e.g. robot) form and motion (Kilner et al., 2003a; Tai et al., 2004; Press et al., 2005). To investigate which features of an action drive the modulation of sensorimotor *beta* oscillations we employed a 2x2 factorial design in which sinusoidal arm movements varied in terms of form (human or point) and motion (human or constant velocity).

3.2 METHODS

3.2.1 Participants

Fourteen paid healthy participants took part in this study (four male, mean age 22.5 years, range 18 – 29 years). All were right-handed, had normal or corrected-to-normal vision, were naïve with respect to the purpose of the experiment, and gave informed consent. The experiment was performed with the approval of the ethics committee of University College London, and performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

3.2.2 Stimuli

Stimuli were generated by filming two models (one male and one female) executing vertical sinusoidal arm movements, at 250 frames per second. There were four such stimuli (male left arm, male right arm, female left arm, female right arm). A black box was superimposed over the model's head, and a white fixation cross was added to the centre of the videos. Videos started with a 1000 ms static of the first frame. The video then lasted for 5360 – 5480 ms, showing between 1.75 and 2.25 sinusoids of arm movement.

Offline the videos were edited to produce four different videos. These manipulations generated a 2x2 factorial design. The four videos were: (i) human BM (biological motion), created by selecting every 10^{th} frame from these videos so as to preserve the biological velocity profile generated by the actors; (ii) human CV, created by calculating the mean speed in the BM videos, according to the location of the index fingertip, and selecting frames such that the index fingertip moved at all times with this mean speed; (iii) point BM and (iv) point CV stimuli, created by substituting the index fingertip with a round beige point, and presenting this single point on a dark background. The total luminance of the point videos was matched to the total luminance of the human videos, and the luminance of the beige point was matched to the luminance of the index fingertip. Four videos in four conditions generated 16 videos. Example frames from the human and point video types are shown in Figure 3.

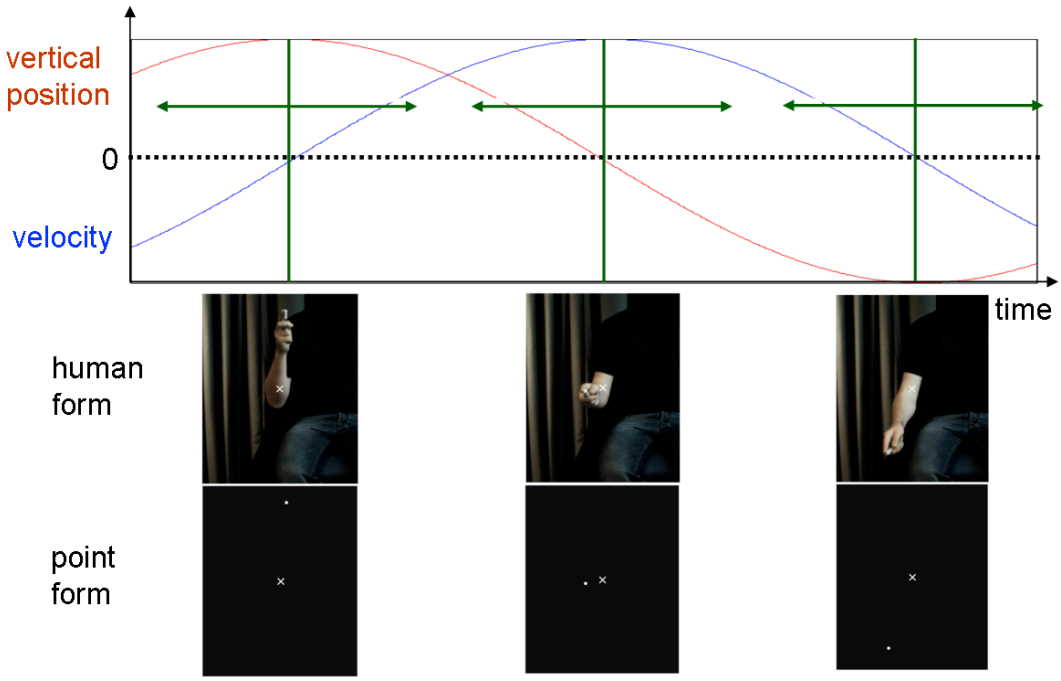

Figure 3. Analysis periods. The endpoints of the actions were found by taking the points of minimum velocity, and the midpoints were found by taking the points of maximum velocity. Two endpoints and two midpoints were found for each video type. A 600 ms time period was taken around these endpoints and midpoints (300 ms either side).

3.2.3 Procedure

Participants were tested individually in a dimly lit room. They were positioned in the scanner with the computer screen approximately 50 cm away from their face. They were given two response buttons, one to be held in their left hand and one to be held in their right hand. Videos were presented with a 2000 – 3000 ms (mean = 2500 ms) inter-trial interval. A fixation cross remained on the screen and participants were asked to maintain fixation throughout the experiment. An infra-red eyetracker (Tracksys Ltd., Nottingham) was used to ensure that participants maintained fixation on the cross.

To ensure that participants paid attention to the videos, on ~10 % of the videos a red or blue dot was superimposed on the index fingertip (human conditions) or point (point conditions) at 1480 ms or 5480 ms into the movement phase, with equal numbers of red and blue dots, and equal numbers of early and late presentations. The dot was superimposed for 1000ms. On the trials where a red or blue dot appeared, a question screen appeared at the end of the trial asking the participant whether they had seen a red or blue dot, and telling them whether they should press the left button for a blue dot and the right button for a red dot, or vice versa. Button assignments were not known in advance so that participants could not prepare a movement, and the number of left button presses for blue and red dots was equal. All response trials were excluded from analysis.

There were 272 trials (240 test trials and 32 response trials). The test trials consisted of 15 repetitions of each of the 16 videos. There were two response trials for each video type. These trials were presented in a different pseudo-randomised order for each participant; the only constraint being that a video would not be presented twice in a row. These trials were split into eight blocks of 34 trials, and participants were permitted to rest between blocks. Before testing commenced, participants completed 10 practice trials to ensure that they were able to maintain fixation on the cross and could perform the task.

We wished to define ROIs based on the conjunction of areas involved in action observation and execution. Therefore, at the end of the observation blocks, participants executed sinusoidal, up and down, actions with their left and right arm. Half of the participants executed actions with their left arm first and the other half executed actions with their right arm first. A board was inserted between their torso and arm such that they could not observe their arm actions. They were instructed to rest their elbow on the armrest, to ensure that their head did not move, and move their arm up and down taking approximately two seconds for one complete cycle. Participants were told to perform this action continuously whenever a green fixation cross appeared on the screen and to hold their arm still whenever a red cross appeared on the screen. This fixation cross appeared at the same location as that in the observation condition, and the timing of red and green crosses reflected the trial and inter-trial interval timing of the observation condition (green cross for 6450ms, and red cross for 2000 - 3000ms). Participants performed 20 trials (where one trial equaled a red cross followed by green cross) with each arm.

At the end of the experiment, participants observed a video from each of the four categories, six times. After each video had played, they were asked to rate a statement (Table 3) according to how much they agreed with it, on a scale of 0 to 25 (0 = least agreement, 25 = most agreement), to ascertain how human they perceived the movement to be.

Rated statements
The movement appeared purposeful and goal-directed
The image appeared to be moving by itself rather than driven by something else
The movement appeared to be active rather than passive
The movement appeared to be natural
The movement appeared to be human
The movement appeared to be computer generated

Table 3 The six statements rated by participants after the experiment.

3.2.4 MEG recording and data analysis

3.2.4.1 Recording and pre-processing

MEG was recorded using 275 3rd order axial gradometers with the Omega 275 CTF MEG system (VSMmedtech, Vancouver, Canada) at a sampling rate of 480 Hz. All MEG analyses were performed in SPM8 (Wellcome Trust Centre for Neuroimaging, London, UK, www.fil.ion.ucl.ac.uk/spm). The data were epoched relative to the onset of the video clip, bandpass filtered at 1 and 45 Hz, and then downsampled to 100 Hz.

3.2.4.2 Sensor space analysis

Wavelet decomposition

Quantification of the oscillatory activity was performed using a wavelet decomposition of the MEG signal. The wavelet decomposition was performed across a 1 – 45 Hz frequency range. The wavelet decomposition was performed for each trial, for each of the 275 sensors and for each participant. These time-frequency maps were averaged across trials of the same type (e.g. male left arm, human BM). The maps were subsequently log10 transformed to normalize, and averaged over 15 – 30 Hz, producing a single *beta* power timecourse for each sensor for each participant, for each trial type.

Analyses averaged over timerange

The timecourse was averaged from 500 ms to 4500 ms after the onset of the movement phase. This time window was chosen to capture *beta* modulations during a period of movement observation that did not contain possible confounds of event related fields associated with the onset or offset of the observed

movement. This time window was compared against a baseline at the start of each trial where no movement was observed, averaged from 500 ms before the static appeared to 500ms after the onset of the static. This analysis produced one value per sensor, per participant, for each trial type. Trials in the same condition (human BM, human CV, point BM, and point CV) were averaged. For each participant and for each condition, 2D sensor space maps of these data were calculated, and then smoothed using a Gaussian kernel (full width half maximum, FWHM, 20 mm, see Kilner and Friston (2010)). Analyses of *beta* power during action execution were performed in a similar way.

Analyses of dynamic effects

As the movements made by the different actors differed in the period of the sinusoidal movement, the data had to be aligned prior to further analysis so that modulations in the kinematics of the observed action were coincident for the different videos. Two endpoints and two midpoints were defined for each video type that occurred in the central part of the videos. The endpoints were defined as points of minimum absolute velocity and the midpoints were defined as the points of maximum absolute velocity. The velocity varied slightly according to the video observed, but the issue of importance is that it was always higher at midpoints than at endpoints. These time points were defined according to the BM videos and applied to both the BM and CV videos. Although the CV by definition does not have a maximum or minimum absolute velocity we cut the CV videos around the same points as the BM to control for a general effect of any modulations that might occur as a result of time during the movement. A 600 ms time period was taken around these endpoints and midpoints (300 ms either side, see Figure 3). For 'averaged over ROI' analyses, averages were computed for the 300 ms before the endpoints, the 300 ms after the endpoints, the 300 ms before the midpoints, and the 300 ms after the midpoints. This analysis produced four values per sensor, per participant, for each trial type. Trials in the same condition (human BM, human CV, point BM, and point CV) were averaged. For each participant and for each condition, 2D sensor space maps of these data were calculated, and then smoothed using a Gaussian kernel (full width half maximum, FWHM, 20 mm in space and 120 mm in time).

ROI

A spatial ROI was defined by calculating the conjunction of the areas with lower *beta* power in the observation conditions and the execution condition in the analysis averaged over time, relative to their baselines, at $t > 4.72$. This ROI was necessary because it is a pre-requisite of the MNS that it should be active during both action observation and action execution.

Contrasts of all images were taken to the second level with a design matrix including a participant

specific regressor to remove global differences in power between participants.

3.2.4.3 Source space analysis

A beamformer technique was implemented (Van Veen et al., 1997; Robinson and Vrba, 1999; Gross et al., 2001), based on areas with lower *beta* power in the observation conditions and the execution condition, relative to baseline. Given that the beamformer analysis required time windows of equal durations, the baseline period of 1000 ms was compared against a randomly chosen 1000 ms during observation and execution (1500 ms – 2500 ms after movement onset). Once the source had been estimated, a single timecourse for this derived source was calculated by weighted combination of the sensors contributing to it, across the whole timerange. The wavelet decomposition, analyses averaged over timerange, and dynamic analyses, were then conducted in the same way as the analyses performed in sensor space.

3.3 RESULTS

Unless otherwise stated, statistical tests were one-tailed and corrected for family-wise error rate (FWE). Initial non-dynamic analyses are corrected across all sensors, and all subsequent analyses are corrected across the ROI defined on the basis of the non-dynamic analyses.

3.3.1 Non-dynamic effects

Prior to proceeding with an analysis of any dynamic modulation of *beta* power during action observation, we performed a preliminary analysis to confirm that we could reproduce the previous finding that *beta* power over central sensors is attenuated during action observation. When averaged across the four conditions, *beta* power was significantly attenuated during action observation compared with baseline, over central sensors ('sensor space' analysis in Figure 3.2 A; peak voxel: $t(13) = 6.04$, $p < 0.05$). The key property of the action observation network is that it is similarly modulated during action observation and action execution. Therefore, it is important to show an overlap in the analysis for both action execution and observation. To this end we performed the same analysis for action execution. Relative to baseline, the *beta* power during action execution showed a similar pattern of attenuation in sensor space as did action observation (Figure 3.2 B; peak voxel: $t(13) = 6.74$, $p < 0.05$). A conjunction of the two contrasts for action observation and action execution showed significant overlap in sensor space of the location of *beta* power attenuation (Figure 3.2 C; peak voxel: $t(13) = 5.5$, $p < 0.05$), over central sensors. This is consistent with previous studies that have reported that the same motor areas are recruited during action observation and execution (Rizzolatti et al., 1996; Buccino et al., 2001; Grèzes and Decety, 2001; Gazzola and Keysers, 2009; Kilner et al., 2009a).

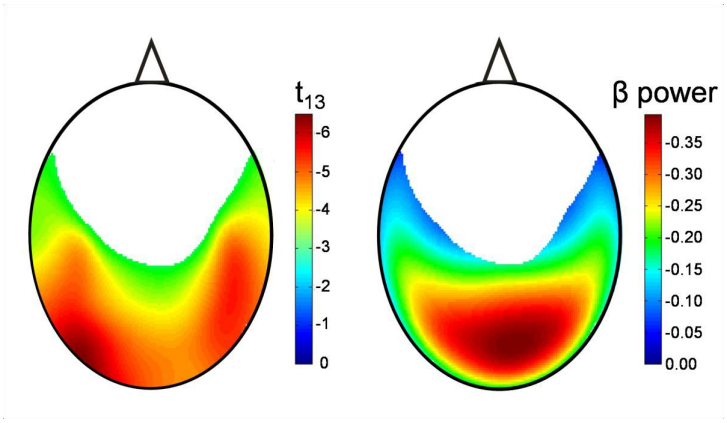

Figure 3.1. Human form > point form. T and contrast sensor space statistical parametric maps of the areas where the beta power when observing human form videos was lower than when observing point form videos, averaged over the timerange of the trial. The maps are thresholded at t > 3.01. Effects of Form were more posterior than the sensorimotor effects of interest in the present study.

Subsequent analysis of the *beta* power averaged across the period of action observation showed that in sensor space there was only a significant main effect of Form (whether a human or point stimulus was observed; Figure 3.1; peak voxel: $t(13) = 6.5$, $p = 0.001$). The main effect of Kinematics (whether the velocity profile was BM or CV) and the interaction between Form and Kinematics were not significant anywhere in sensor space (all $t < 2.7$ all $p > 0.3$). The significant main effect of Form showed a greater attenuation of *beta* power at posterior sensors when observing human relative to point form videos, and did not appear to overlap substantially with the pattern of *beta* attenuation found when both observing and executing action, relative to baseline. To test this we defined an ROI in sensor space based on the conjunction analysis of the sensor maps of *beta* attenuation during action observation and execution (Figure 3.2 C). Averaged across our ROI in sensor space, there were no significant main effects of Form ($F(1,13) = 3.0$, $p = 0.1$) or Kinematics ($F(1,13) = 1.8$, $p = 0.2$). Although there was no significant interaction between Form and Kinematics ($F(1,13) = 4.3$, $p = 0.06$) there was a trend towards an interaction in the expected direction whereby the beta power was more greatly suppressed for human relative to robot kinematics for human form actions compared to robot form actions. The significant main effect of Form seen in the sensor space analysis most likely reflects the vast difference in the visual appearance of the two sets of stimuli. As these modulations lie away from motor areas we will not consider them further here.

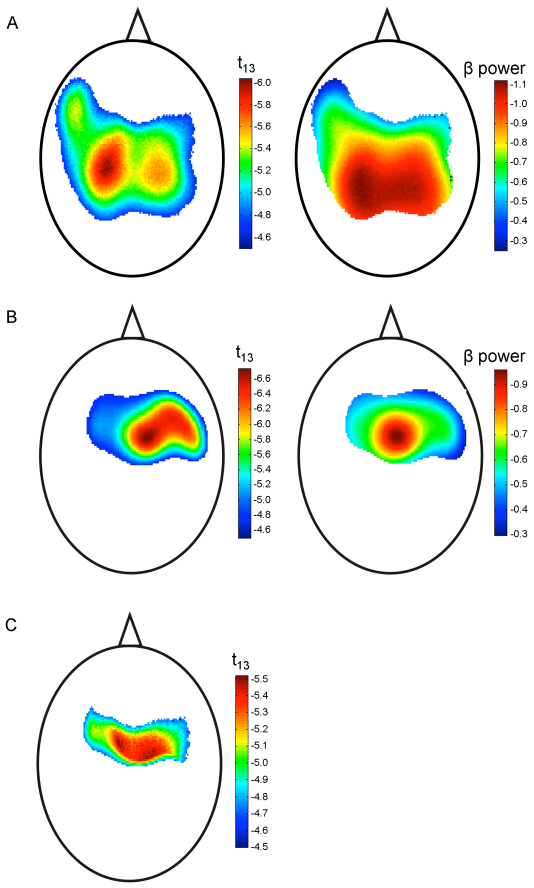

Figure 3.2. Non-dynamic effects of observation and execution. ***A*** T and contrast sensor space statistical parametric maps of areas where the *beta* power when observing action averaged over all four conditions (human BM, human CV, point BM, point CV) is lower than baseline, averaged over the timerange of the trial. T maps represent the t-statistic at each sensor, and contrast maps represent the mean difference in power. ***B*** T and contrast sensor space statistical parametric maps of areas where the *beta* power when executing action is lower than baseline, averaged over the timerange of the trial. ***C*** T sensor space statistical parametric map of areas where the *beta* power when observing action, and executing action, is lower than baseline, averaged over the timerange of the trial. All maps are thresholded at $t > 4.72$.

Dynamic effects of observation

All subsequent analysis in sensor space focused on dynamic modulations in power during action observation. To this end, two endpoints and two midpoints were defined for each trial type, as described above. This resulted in a 2x2x2 factorial design where the factors were Form (human or point), Kinematics (BM or CV) and Spatial Location (midpoint or endpoint). Conducting this repeated measures 2x2x2 ANOVA in sensor space and time, within the observation-execution conjunction mask (Figure 3.2 C), at a $p < 0.001$ uncorrected threshold, revealed an interaction between Kinematics and Spatial Location (peak voxel: $t(1,13) = 3.9$, $p = 0.001$ uncorrected, $p = 0.2$ FWE, two-tailed). The pattern of this effect in sensor space was consistent with activity in the sensorimotor cortex and occurred 240 ms before the midpoint or endpoint (Figure 3.3 A-C). This interaction was generated by an effect of

Spatial Location for BM videos ($t(13) = 3.1$, $p = 0.007$), such that there was lower *beta* power before the midpoint, relative to the endpoint, but no effect for CV videos ($t(13) = 1.3$, $p = 0.6$). Given that midpoint and endpoints were defined in terms of velocity (i.e. midpoints corresponded to points of maximum velocity and endpoints minimum velocity) this shows that the *beta* oscillations are modulated by the kinematics of the observed action. This modulation cannot simply be attributed to the phase of the observed action, namely whether it was a turning point or a straight movement, as there was no such modulation for the CV condition.

To further investigate this effect we conducted an analysis averaged over ROI. The sensor-time maps analyzed above were first averaged across the spatial ROI described previously (Figure 3.2 *C*) and subsequently averaged across two windows, one from -300-0 ms ('pre') and the second from 0-300ms ('post'). This now formed a 2x2x2x2 ANOVA where the factors were Form (human or ball), Kinematics (BM or CV), Spatial Location (midpoint or endpoint) and Time (pre or post). This analysis revealed a three-way interaction between Kinematics, Spatial Location and Time ($F(1,13) = 4.4$, $p = 0.05$). This effect did not interact with the Form of the stimulus ($F(1,13) < 1$). This interaction was generated by the presence of a Spatial Location x Time interaction for BM videos ($F(1,13) = 11.9$, $p < 0.005$) but no such interaction for CV videos ($F(1,13) = 0.2$, $p = 0.7$). For BM videos, there was an effect of Spatial Location in the 300 ms before the midpoint or endpoint ($F(1,13) = 5.3$, $p < 0.05$), such that there was lower *beta* power in the 300 ms before the midpoint relative to the endpoint, but not in the 300 ms after ($F(1,13) = 1.4$, $p = 0.3$, see Figure 3.3 D).

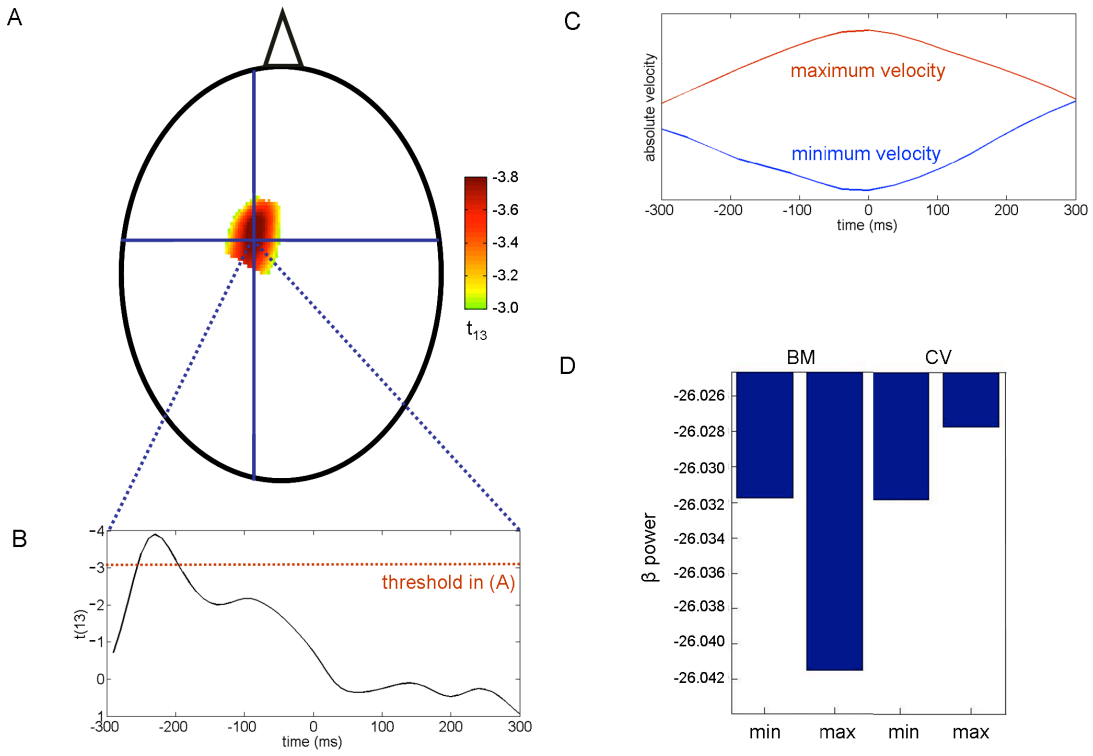

Figure 3.3. Dynamic effects of observation: sensor space analysis. ***A*** T sensor space statistical parametric map of the interaction between Spatial Location (endpoint versus midpoint) and Kinematics (BM versus CV), at 240 ms before the point of maximum or minimum velocity. The map is thresholded at t > 3.01, and is masked by the observation and execution conjunction mask in Fig. 2*C*. ***B*** The t values for the 600 ms time window (-300 ms to 300 ms) for the peak voxel for this interaction (marked by the crosshair in *A*). ***C*** The mean velocity across the 600 ms time window for the minimum and maximum velocity segments, averaged across all four videos. ***D*** The averaged *beta* power in the 300 ms before the endpoint (min) and the midpoint (max), for BM and CV videos.

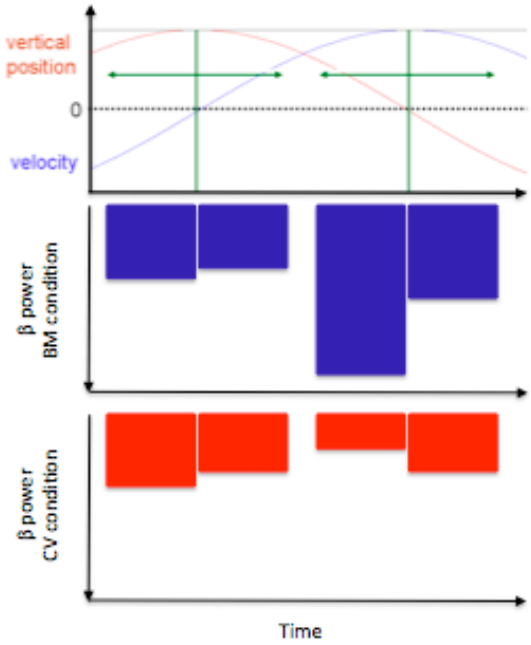

Figure 3.4. Illustration of beta power changes over time in relation to the changes in velocity and vertical position of the stimulus. Separate illustrations depict the changes in beta power modulation for observation of BM and CV stimuli.

Here we have demonstrated, both in a peak voxel analysis, and averaged over ROI, that: (i) *beta* power is modulated dynamically during action observation; (ii) the pattern of this dynamic modulation is dependent upon the kinematics of the observed action; and (iii), this pattern temporally predicts the dynamics that would be expected if executing the observed action. However, all of these effects were observed using a sensor space analysis. Although the spatial patterns are not inconsistent with generators in sensorimotor cortices we cannot be certain that the modulations observed reflect sensorimotor activity (Kilner and Friston, 2010). We have employed an axial gradiometer MEG, which means that one should not interpret the peaks in the *beta* power map as overlying the sources of activity (in fact, these peaks should lie away from the underlying source). To address whether modulations are found in sensorimotor cortex, we repeated the same analysis in source space.

Dynamic effects in source space

We performed two beamformer analyses; one revealing areas with lower *beta* power when observing action relative to baseline, and the other revealing areas with lower *beta* power when executing action. The conjunction of these two analyses revealed a source in the hand / arm area of sensorimotor cortex, with its peak at [-40.9, -29.0, 58.8], corresponding to the left postcentral gyrus (see Figure. 3.4. This is consistent with a previous MEG study that found stronger effects in the left hemisphere irrespective of

whether the observed action was a left or right arm movement; Kilner et al., (2009b)). This source analysis therefore also provides further evidence that action observation, like execution, activates sensorimotor cortex. The estimated timecourse of this source was used in all subsequent source analyses.

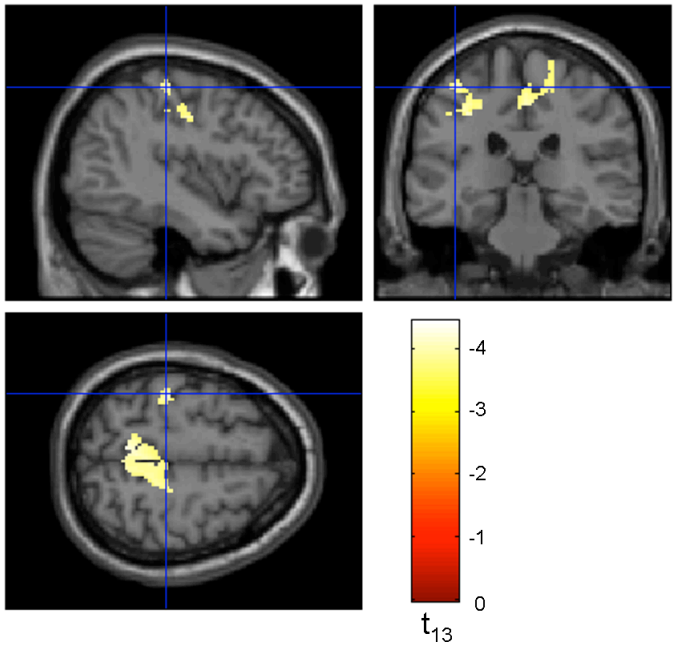

Figure 3.5. Sensorimotor source of activations. The conjunction of the sources identified as driving lower *beta* power both in action observation and execution conditions, relative to baseline, in Brodmann area 4, on the basis of a beamformer analysis, thresholded at $t > 3.63$. The source identified as corresponding to the hand / arm area in sensorimotor cortex, with its peak in the left postcentral gyrus (coordinates = [-40.9, -29.0, 58.8]), is marked with a crosshair.

Similarly to analyses in sensor space, there were no main effects of Form or Kinematics, and no interaction, when analyses were performed in source space at the left postcentral gyrus (all $F(1,13) < 1$, all $p > 0.45$).

The dynamic analysis replicated the sensor space findings. The analysis across the entire 600 ms time window revealed a two-way interaction between Kinematics and Spatial Location at 210 ms before the midpoint or endpoint ($t(1,13) = 2.8$, $p < 0.04$, see Fig. 5 *A*-*C*). This interaction was generated by the presence of an effect of Spatial Location for BM videos ($t(13) = 3.9$, $p = 0.001$), such that there was lower *beta* power before midpoints relative to endpoints, but not for CV videos ($t(13) = 0.2$, $p = 0.4$).

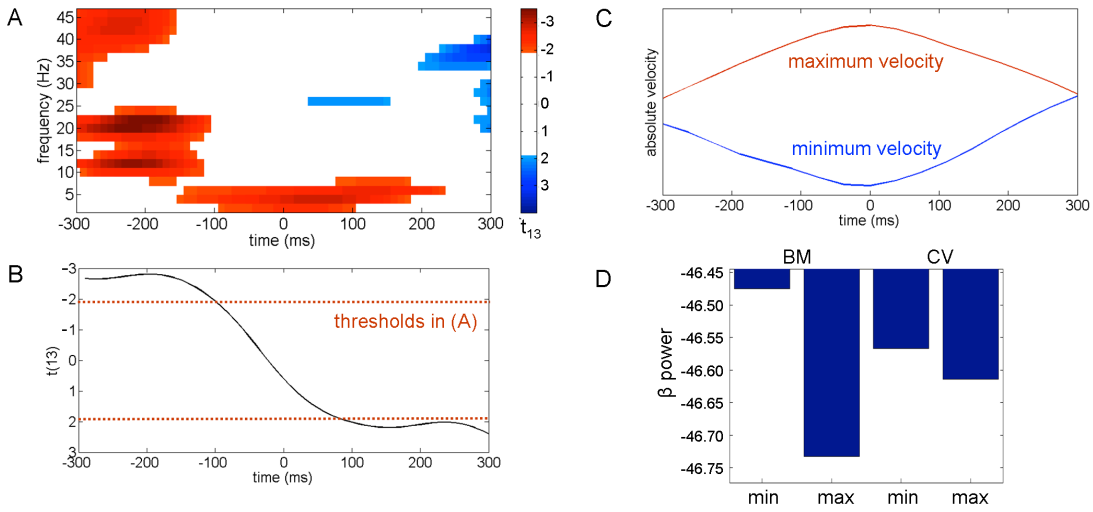

Figure 3.6. Dynamic effects of observation: source space analysis. ***A*** T statistical parametric map of the interaction between Spatial Location (endpoint versus midpoint) and Kinematics (BM versus CV), across time, for the 600 ms time window (-300 ms to 300 ms), and across frequency, for 1 - 45 Hz, at the left postcentral gyrus source. The map is thresholded at t > 1.96. ***B*** The t values for the power averaged across the *beta* band for the 600 ms time window (-300 ms to 300 ms) for this source. ***C*** The mean velocity across the 600 ms time window for the minimum and maximum velocity segments, averaged across all four videos. ***D*** The averaged *beta* power in the 300 ms before the endpoint (min) and the midpoint (max), for BM and CV videos.

The ROI analysis, averaged across the 'pre' and 'post' time windows, demonstrated the same effect, such that there was a three-way interaction between Kinematics, Spatial Location and Time ($F(1,13) = 18.6$, $p = 0.001$), which did not interact with Form ($F(1,13) < 1$). Again, this interaction was generated by the presence of a Spatial Location x Time interaction for BM videos ($F(1,13) = 22.4$, $p < 0.001$) but no such interaction for CV videos ($F(1,13) = 2.3$, $p = 0.2$). For BM videos, there was an effect of Spatial Location in the 300ms before the midpoint or endpoint ($F(1,13) = 16.5$, $p = 0.001$), such that there was lower *beta* power in the 300 ms before midpoints relative to endpoints, but not in the 300 ms after ($F(1,13) = 1.4$, $p = 0.3$, see Figure 3.5 *D*).

3.3.2 Behavioural data

The mean ratings of the statements (Table 3) (with the responses to question 6 inverted, such that a higher numerical response indicated that participants thought it was more human) were entered into an ANOVA, with factors form and kinematics. This ANOVA indicated a main effect of kinematics ($F(1,13) = 6.4$, $p < 0.03$), and a borderline effect of form ($F(1,13) = 4.5$, $p = 0.054$). There was no form x kinematics interaction ($F < 1$). Participants rated the human BM videos as most human (mean = 15.6, SEM = 1.1), the human CV (mean = 11.8, SEM = 1.4) and point BM (mean = 11.5, SEM = 1.6) videos as next most human, and the point CV videos as least human (mean = 8.8, SEM = 1.2).

3.4 DISCUSSION

In the present study we tested the hypothesis that activity in sensorimotor cortex is modulated dynamically during action observation in a similar way to that previously observed during action execution. Previous MEG research has demonstrated a dynamic modulation in power of sensorimotor *beta* oscillations during action execution over central sensors, with *beta* oscillations greater at the endpoints of an executed action than the midpoints (Kilner et al., 2000, 2003b). Furthermore, neuronal activity in the primary motor cortex of the macaque monkey is modulated dynamically by the kinematics of the executed action (Stark et al., 2007). In line with the hypothesis that sensorimotor activations during action observation reflect motoric simulation of that action we predicted dynamic modulation of *beta* oscillations during passive action observation. Results confirmed this prediction: oscillatory activity generated in the sensorimotor cortex in the *beta* range was modulated dynamically according to the phase of the observed action. These effects were found both in sensor and source space and support the hypothesis that sensorimotor activations during action observation reflect motoric simulation of the action.

To investigate which features of an action drive the modulation of sensorimotor *beta* oscillations we employed a 2x2 factorial design in which sinusoidal arm movements varied in terms of form (human or point) and motion (human or constant velocity). Dynamic modulation of motor activity was only found when participants observed actions in which the arm moved with human motion; not when it moved with CV. There are two possible explanations for this: firstly, the dynamic effects that we report are driven by differences in sensorimotor activation simply when observing accelerating and decelerating movements. Alternatively, in line with several previous studies, observing human action activates motor codes to a greater extent than observing non-biological motion (Kilner et al., 2003a; Tai et al., 2004; Press et al., 2005). Two previous fMRI studies (Dayan et al., 2007; Casile et al., 2010) support the latter interpretation. In both studies participants observed movements that obeyed the 2/3rds power law and movements with an inverted 2/3rds power law profile. Movements that obey the 2/3rds power law proceed slowly at curved relative to straight parts of motion (Lacquaniti et al., 1983); given that vertical sinusoidal arm movements follow a curved trajectory the movements employed in our biological videos would comply with the 2/3rds power law. Movements that obey an inverted 2/3rds power law move slowly at straight relative to curved parts of motion. Dayan and colleagues (2007) and Casile and colleagues (2010) demonstrated that motor system areas such as the dorsal premotor cortex are more active during observation of 2/3rds power law movements relative to inverted 2/3rds power law movements. Since these movement types are matched for acceleration and deceleration these results suggest that motor activations during action observation are not a result of the complexity of the velocity

profile and hence are likely specific to biological motion. The present study adds to this literature by indicating that observing human action activates motor cortical representations to a greater extent than non-biological movement, in a manner corresponding dynamically to that which would be expected for action execution. Further studies may investigate motor system responses to other familiar velocity profiles such as the gravitational profile that characterizes the velocity profile of a falling object.

Giese and Poggio (2003) suggest that form and kinematic of biological motion cues are processed in separate pathways that likely interact - possibly at the level of the pSTS. Here we report that within overlapping observation-execution areas, there was no influence of form (human or point) - only kinematics. A possible explanation is that there is little interaction between pathways before visual information feeds into motor areas (cf. Kilner et al., (2007a)). In line with this, in the macaque monkey Vangeneugden and colleagues (2009) found evidence of separate processing of form and kinematic information in the STS which is known to feed into motor structures (Keysers and Perrett, 2004). An alternative explanation is that, as suggested by Giese and Poggio (2003) form and motion pathways are integrated in visual areas such as pSTS but that the motion information is more highly weighted by the motor system.

Here we report activations from overlapping observation-execution areas. However, it may be noted that the source of these activations – sensorimotor cortex – is not typically considered part of the human MNS. There are two ways in which the present findings can be considered consistent with the hypothesis that the human MNS motorically simulates observed actions. First, it has been argued that, given the anatomical connection between premotor cortex and sensorimotor cortex (Matelli et al., 1986; Dum and Strick, 2002), sensorimotor cortex is activated postsynaptically during periods of action observation, and therefore that the attenuation of *beta* oscillations during action observation is likely to have resulted from MNS activation in premotor cortex (Rizzolatti and Craighero, 2004). Second, mirror neurons have recently been reported in primary motor cortex (Dushanova and Donoghue, 2010) and as a result there is an argument that sensorimotor cortex may now be considered an intrinsic part of the MNS.

An intriguing feature of our results is that *beta* power was lowest approximately 200-250 ms before a midpoint relative to an endpoint. In other words, the modulations in *beta* power across time did not coincide with the endpoints and midpoints of the observed action but preceded them. This finding differs from action execution findings which report that *beta* power is minimal during periods of maximum velocity and maximal during periods of zero velocity (Kilner et al., 2000; 2003a). In these

previous studies, the maximal changes in *beta* power occurred at, or slightly after, the endpoints and midpoints of the action. This finding that activity in M1 is modulated by the velocity of the executed action is supported by single cell studies demonstrating that M1neurons exhibit an increased firing rate when the monkey moves with a faster, rather than slower, velocity (Stark et al., 2007). Therefore, the modulations in *beta* power that we have reported here during action observation precede those that would be expected if one were executing the action. Although speculative, this pattern would fit with recent models of the MNS that have suggested that activity in these regions is predictive. These include models that are based on active inference (Kilner et al., 2007b, 2007c); models that employ forward modelling (Wolpert et al., 2003; Miall, 2003); models that explicitly claim a prospective prediction (Stadler et al., 2011), and those where activity reflects a learned sequence of visuomotor associations (Heyes, 2001, 2010), whereby observation of an action can activate visual and motor representations of the subsequent element in a learned sequence (Hollis, 1984; Bird and Heyes, 2005).

Despite the number of studies that have found greater motor activations when observing human action relative to non-biological motion, some studies have found no such biological specificity. For example, in an fMRI study, Gazzola et al. (2007) found that motor structures such as the IFG were activated equally when observing humans and industrial robots performing arm actions. In fact, if considering the analyses in the present study where we averaged cortical activations over the time period of action observation, we also found no evidence of biological specificity. The differences only emerged when analysing changes in cortical activation over time. Such *dynamic* analyses therefore appear to provide greater sensitivity for investigating specificity of the MNS, and hence could provide a useful tool for exploration of other questions concerning this system in the future.

3.4.1 Conclusion

The present study found evidence that observation of action elicits changes in sensorimotor activation across time, according to the phase of the movement that is being observed. These changes are in line with those that would be expected if one were executing the observed action, indicating that observing action is automatically activating motor programs required for its execution. These effects were driven by the kinematics of the observed actions: they were only present for human motion observation, not CV.

3.4.1.1 What next?

This Chapter concludes the section of this thesis that focuses on the typical brain. Chapter 2 suggested that the pSTS plays an important role in judging whether a motion stimulus represents human motion.

Chapter 3 demonstrated that motor system activations during action observation comprise automatic motoric simulations of action kinematics.

Previous studies have suggested atypical activation in both posterior areas, such as the pSTS (Herrington et al., 2007; Freitag et al., 2008), and MNS areas (Oberman et al., 2005; Dapretto et al., 2006) during action observation in ASC. These atypical activations have been suggested to relate to behavioral impairments in biological motion processing (Kaiser and Pelphrey, in press) and imitation (Williams et al., 2001). However evidence both supports and opposes biological motion processing and imitation impairments in ASC. With respect to biological motion processing, it is not known whether deficits are distinct from problems with global motion processing; and with respect to imitation, it is not known whether difficulties result from atypical modulation of imitation rather than atypical imitation per se. Chapters 4 to 7 draw on the findings described in Chapters 2 and 3 to investigate these questions about ASC.

Chapter 4. Unaffected Perceptual Thresholds for Biological and Non-Biological Form-from-motion Perception in Autism Spectrum Conditions

Previous studies have suggested atypical biological motion perception in ASC. However this literature is mixed and it is unclear whether deficits are specific to biological motion, or generalize to form-from-motion perception. To investigate whether biological motion processing deficits in ASC are distinct from global motion processing problems we compared psychophysical thresholds for both biological and non-biological form-from-motion perception in adults with ASC and controls. Participants viewed point-light displays depicting a walker (Biological Motion), a translating rectangle (Structured Object) or a translating unfamiliar shape (Unstructured Object). The figures were embedded in noise dots that moved similarly and the task was to determine direction of movement. The number of noise dots varied on each trial and perceptual thresholds were estimated adaptively. We found no evidence for an impairment in biological or non-biological object motion perception in individuals with ASC. Perceptual thresholds in the three conditions were almost identical between the ASC and control groups.

4.1 INTRODUCTION

A number of studies have explored whether individuals with ASC have compromised perception of biological motion; results are mixed. Four of these studies (Moore, et al. 1997; Hubert et al, 2007; Parron et al., 2008; Atkinson, 2009) required participants to watch PLDs depicting either a person or an object and to describe what they see. In these studies, which have included child (Moore et al., 1997), adolescent (Parron et al., 2008) and adult (Hubert et al., 2007; Atkinson, 2009) populations, individuals with ASC differed from controls in their ability to recognise emotions, but not in their ability to describe actions or subjective states (such as tired or bored). Thus, although these studies report impaired biological motion processing in individuals with ASC compared to controls, this impairment appears to be specific to emotion recognition from PLDs.

On the other hand, a number of studies have found impaired biological motion processing in tasks that do not require emotion processing. Studies conducted with children and adolescents tend to show that

biological motion processing is atypical in participants with ASC at this younger age. Klin and Jones (2008) reported an impairment in biological motion perception in an infant aged 15 months; a follow-up study suggested that toddlers with autism may not orient to PLDs of biological motion, but instead to non-social contingencies (Klin et al, 2009). A recent study by Annaz and colleagues (2011) replicated this finding using non-social PLDs (person walking) without an accompanying sound-track and thereby showed a lack of attention to biological motion that is not motivated by an aversion to social stimuli or attraction to points of audio-visual synchrony. Blake and colleagues asked participants whether sets of dots 'moved like a person'. They found that, compared with TD children, 8- to 10-year-old children with ASC were impaired at discriminating PLDs of human actions from phase-scrambled control stimuli (Blake et al., 2003). In a developmental extension of this, Annaz and colleagues (2010) showed that the performance, on a biological motion processing task, of children with ASC did not differ from that of TD children at 4 and 5 years. However, whereas TD children showed improvement from 5 to 12 years, children with ASC showed no improvement. Koldewyn and colleagues (2010) showed that adolescents with autism have decreased sensitivity to biological motion in a task that required them to determine the direction of walking of a PLD embedded in noise dots.

The adult literature is more mixed. Kaiser and colleagues (2010) report that, unlike control participants, individuals with ASC do not exhibit an enhanced sensitivity for human over non-biological motion. In contrast, Murphy and colleagues (2009) found no impairments in adults with ASC in either accuracy or RTs for direction detection of PLDs depicting a walking person, or a scrambled version of the same stimuli. Two imaging studies (Freitag et al., 2008; Herrington et al., 2007) scanned adults with ASC and Controls whilst they watched PLDs. Both studies found hypoactivation in areas typically associated with biological motion processing (such as the STS and area MT/V5) in the ASC participants compared to controls, but no behavioural differences between Groups.

There are also concerns regarding how specific any impairments in biological motion perception are, given that individuals with ASC can also perform poorly in other motion perception tasks. Studies have suggested the possibility that impairments observed in ASC might be explained by problems with integrating complex perceptual information (Bertone et al., 2003). For example a number of studies have reported that participants with ASC have higher Motion Coherence Thresholds (MCTs) than control participants (Spencer et al, 2000; Milne et al., 2002; Pellicano et al., 2005). It is therefore possible that individuals with ASC are less able than controls to pool motion signals across space (Bertone et al., 2003). However, it should be noted that there is debate in the global motion literature with some studies finding no difference between Control and ASC groups (Del Viva et al., 2006) and

others finding that only a subgroup of the ASC participants have motion coherence thresholds outside the normal range (Spencer and O'Brien, 2006; Tsermentseli et al., 2008; Milne et al., 2006: see Simmons et al. (2009) for an overview of this literature). Recently, Atkinson (2009) demonstrated a correlation between MCTs and emotion recognition from PLDs in adults with ASC (where high MCTs were associated with reduced accuracy in identifying emotions); Koldewyn et al. (2010) observed a similar finding in adolescents. Given that many studies reporting abnormal processing of biological motion in ASC (Blake et al. 2003; Klin et al., 2009) have employed PLDs, which require integrating the motion of multiple points across space, it is not clear that a deficit in perceiving biological motion from PLDs is distinct from the global motion processing deficit that has also been observed in ASC.

In the current study, we tested biological motion perception using PLDs depicting whole body movements. Biological motion not only has the dynamics of natural body movements, but also a meaningful, coherent, familiar and recognisable form. In order to tease apart these factors, as well as to assess non-biological structure-from-motion processing (see Hiris, 2007), we generated new point-light stimuli. There were three conditions: Biological Motion (BM), in which we used a point-light walker; Structured Object (SO), in which we used a translating point-light rectangle; and Unstructured Object (UO), in which we used translating set of dots comprising a meaningless, unfamiliar shape (see Figure 4). Thus BM featured biological motion and a recognizable, familiar shape; SO contained non-biological form-from-motion and a familiar shape; and UO contained non-biological form-from-motion and an unfamiliar shape. In each condition, the figures were embedded in similarly moving noise dots and the task was to determine direction of movement of the figure.

A variety of different measures of biological motion processing have been employed in existing studies, ranging from *d'* as an unbiased measure of sensitivity to biological motion (Blake et al. 2003), to verbal reports (Hubert et al., 2007). Here, we measured psychophysical thresholds. A Bayesian adaptive procedure was used to estimate perceptual thresholds in each condition. Thresholds corresponded to the number of noise dots that each participant could tolerate while performing direction discrimination at 75% accuracy. Hence a high threshold represents good performance on the task and a low threshold reflects relatively poor performance.

The pattern of thresholds, for individuals with ASC, across the three conditions of this task is indicative of specific perceptual difficulties:

1. Low thresholds, relative to those generated by control participants, in the BM but not SO or UO

conditions would be indicative of a specific difficulty with biological motion processing.

2. Low thresholds, relative to control participants, in the BM and SO conditions but not UO would be indicative of difficulties in processing familiar forms.

3. Low thresholds, relative to control participants, in the UO condition but not the BM and SO conditions would be indicative of preserved familiar form processing. This may compensate for any deficits in from-from-motion processing.

4. Low thresholds, relative to control participants, for all three conditions would be indicative of general difficulties in form-from-motion processing

5. Comparable thresholds for all three conditions would be indicative of typical biological and non-biological form-from- motion perception at this level of processing (i.e. determining the direction of motion).

4.2 METHODS

4.2.1 Participants

16 participants with ASC (13 males) and 20 control participants (13 males) took part (Table 1). ASC participants had a written diagnosis from a qualified clinician, which they received no more than 4 years before taking part in this experiment. ASC participants were also administered the ADOS (Lord et al., 1999). The groups were matched for age, gender and verbal (vIQ), performance (pIQ) and full scale IQ (fsIQ). For the majority of participants we acquired Autistic Quotient scores (Baron-Cohen, Wheelwright, Skinner, Martin and Clubley, 2001). Control and ASC participants produced significantly different Autistic Quotient scores (ASC mean±SD = 34.13±8.11 (N = 15); Control mean±SD = 14.6±5.47 (N = 15); $t(28) = -7.74$, $p < 0.001$). Ethical permission was granted from the University College London Ethics Committee and written informed consent was obtained according to Declaration of Helsinki.

	ASC	Control	Group Comparison
Total participants	16	20	
Gender (M:F)	13:3	13:7	p = 0.45 (Fisher's exact test)
Age in years	33.75 (12.70)	37.75 (11.35)	t(34) = 0.10, p = 0.33
Verbal IQ	114.00 (15.77)	114.84 (13.04) (N = 19)	t(33) = 0.17, p = 0.86
Performance IQ	107.19 (14.92)	108.63 (11.76) (N = 19)	t(33) = 0.32, p = 0.75
Full scale IQ	112.19 (16.25)	113.16 (12.35) (N = 19)	t(33) = 0.20, p = 0.84

Table 4 Participant details. Control and ASC group did not significantly differ in terms of gender, age, verbal IQ, performance IQ or full scale IQ. N denotes the number of participants for which data was available.

4.2.2 Stimuli

In all conditions, stimuli were PLDs composed of 12 white dots presented against a black background. Stimuli were presented on a CRT monitor at 1024 x 768 pixels resolution using Matlab (Mathworks, Natick, MA, USA) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). PLDs subtended approximately 4 x 8 degrees visual angle (127.95 x 255.9 pixels) when viewed from 55 cm.

In the BM condition, the stimulus was a point-light walker, created by videotaping an actor and encoding the joint positions in the digitized videos (Ahlström et al., 1997). In the SO condition, the stimulus was a recognisable, coherent shape (a rectangle) composed of point-lights. In the UO condition, the stimulus was an unfamiliar, less coherent shape, which was a single frame from the walker animation, inverted. Selected frames depicting all three types of stimuli are shown in Figure 4.

In the BM condition, the direction in which the point-light walker faced, right or left, was determined randomly on each trial. Like most studies on biological motion, the figure did not translate on the screen when 'walking' but moved as if on a treadmill. In the non-biological motion conditions (SO and UO), the shape translated at 0.5 pixels/frame either to the left or right on each trial, again randomly determined.

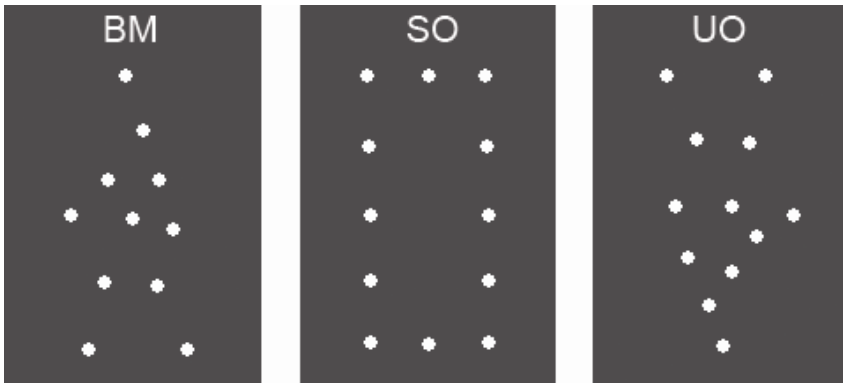

Figure 4. Selected frames depicting stimuli from the three conditions (BM, SO, and UO). Stimuli were point light animations composed of 12 white dots presented against a black background. In the Biological Motion (BM) condition, the stimulus was a point-light walker. In the Structured Object (SO) condition, the stimulus was a rectangle composed of point-lights. In the Unstructured Object (UO) condition, the stimulus was a single frame from the walker animation, inverted.

4.2.3 Procedure

Participants were seated 55 cm from the screen with their head comfortably stabilised using a chin rest. Each trial started with a fixation cross at the centre of the screen displayed for 750 ms, after which the visual stimuli were presented for 35 frames at 60 frames/s. On each trial, the initial position of the figure was spatially jittered randomly within a 2.2° radius (85.3 pixels) from the centre, in order to minimise the feasibility of a response strategy based purely on local motion information. Participants pressed one of two adjacent keys on the keyboard with their dominant hand to indicate the perceived direction of the movement (direction of walking for BM condition, direction of translation for the SO and UO conditions). If no response was given within 2000 ms from the end of the stimulus presentation, an incorrect response was registered.

Animations were presented with similarly moving 'noise dots' of the same shape, size and colour, a paradigm commonly used in the literature (e.g. Hiris, 2007; Peelen et al., 2006). To yield a psychometric measure of performance, the number of noise dots at which each participant performed at 75% accuracy was estimated using a Bayesian adaptive procedure, QUEST. In each block, a total of 60 such trials were administered and thresholds were estimated using the mean of the posterior probability density function (Watson and Pelli, 1983).

The size of the region populated by the animations plus the noise dots was approximately 6 x 12 degrees of visual angle (213.25 x 426.5 pixels). Noise dots moved similarly to the stimuli: In the BM condition, each noise dot had the same trajectory of one of the dots in the walker. In the SO and UO conditions, the

noise dots translated right or left at the same speed as the dots in the target shape. Twelve of the noise dots always translated in the direction opposite to that of the shape; since the shape was marked by 12 dots it was not possible to determine the direction of movement of the target simply from a summation of the overall movement direction in the display.

Testing sessions consisted of a practice block for each condition and three experimental blocks each of the BM, SO and UO conditions, administered in pseudo-random order across participants (e.g., First block: BM, UO, SO; Second block: UO, SO, BM; Third block: SO, BM, UO). In practice blocks, after being given instructions, participants completed 12 trials: the first 4 with no noise dots, the remaining each with a predetermined number of noise dots (5, 5, 10, 10, 25, 35, 50, 75). In the experimental blocks, there were 68 trials: the first 3 trials contained no noise dots, the next 5 trials contained a fixed number of noise dots (5, 5, 10, 30, 10), after which the QUEST procedure began with the first adaptive trial beginning at 16 noise dots. Participants could take breaks between blocks. There was also a 10 sec break after trial 45 in each block. Each experimental block lasted between 3-4 mins.

4.2.4 Data analysis

The estimated number of noise dots that each participant could tolerate while performing at 75% accuracy, henceforth Noise Threshold (NT), was measured in three blocks for each condition as described above. The averages of the three NT estimates were used as dependent measures in a mixed model repeated measures ANOVA with between subjects factor Group (ASC, Control) and within subjects factor Condition (BM, SO, UO). T-tests were used to examine differences between conditions. Pearson's correlations were conducted to investigate relationships between BM, SO and UO thresholds. A Chow test (Chow, 1960) was employed to examine whether the strength of these correlations differed significantly as a function of Group.

4.3 RESULTS

The ANOVA revealed a significant main effect of condition ($F(2,68) = 123.75$, $p < 0.001$; $\eta_p^2 = 0.78$). Whereas the average estimated NT was 25.72 (Control) and 25.29 (ASC) dots in the BM condition and 17.10 (Control) and 18.99 (ASC) dots in the UO condition, the SO condition was easier for both groups, with a mean NT of 70.42 (Control) and 70.10 (ASC) dots. All pairwise t-tests were significant (BM and SO: $t(35)= -10.82$, $p<0.0001$; SO and UO: $t(35)= 13.11$, $p<0.0001$; BM and UO: $t(35)=3.63$, $p<0.005$).

There was no main effect of group ($F(1,34) < 0.0001$; $p = 0.99$; $\eta_p^2 = 0.002$), nor was there a significant interaction between Condition and Group ($F(2,34) = 0.14$, $p = 0.87$). As shown in Figure 4.1, participants with ASC did not differ from Controls in any of the conditions (BM: $t(34) = 0.23$; $p = 0.82$; SO: $t(34) = 0.13$; $p = 0.90$; UO: $t(34) = -0.80$; $p = 0.43$). These effects remained insignificant when we repeated the ANOVA with covariates (IQ, age, AQ; all $p > 0.05$) [2].

Across all participants BM thresholds were correlated with SO thresholds ($r=0.43$; $p=0.01$), as were SO and UO thresholds ($r=0.59$; $p<0.001$). Within the control group BM and SO performance was correlated ($r=0.42$; $p=0.02$); but within the ASC group the correlation did not reach significance ($r=0.39$; $p=0.14$). Application of the Chow test (Chow, 1960) showed that the relationship between BM and SO thresholds was not significantly different between the groups $F(2, 31) = 0.13$, $p = 0.88$. The SO-UO correlation was still significant within the control and ASC groups separately, and was stronger in the latter ($r=-0.50$, $r=0.03$; $p=0.001$; $r=0.68$, $p=0.005$), although the group difference was not significant (Chow test: $F(2, 31) = 0.25$, $p=0.78$). BM thresholds did not correlate with age, (full scale) IQ, or ADOS scores (all $p > 0.05$) whereas SO and UO thresholds were significantly correlated with IQ ($r=0.520$; $p=0.002$ and $r=0.458$; $p=0.006$). SO and UO correlations with IQ were significant within the controls ($r=0.58$; $p= 0.009$, and $r=0.53$; $p=0.02$), but weaker and short of significance in the ASC group, possibly due to the smaller sample size ($r=0.46$; $p=0.08$ and $r=0.44$; $p=0.09$). The Chow test showed no significant differences between the groups on IQ-UO correlation ($F(2, 30) = 1.10$, $p = 0.35$) or IQ-SO correlation ($F(2, 30) = 0.31$, $p = 0.74$).

[2] Thresholds for the UO condition significantly deviated from the normal distribution for both the Control (Shapiro-Wilk $W(19) = 0.90$, $p < 0.05$) and ASC group (S-$W(19) = 0.84$, $p < 0.05$). To ensure the effects reported above were robust against violations of normality, data was log transformed and the 2 x 3 ANOVA rerun. The ANOVA conducted on the log transformed data showed a main effect of condition ($F(2,34) = 123.75$, $p < 0.001$) but no main effect of group nor interaction between Condition and Group (all $p > 0.05$). Thus, log transforming the data did not change the pattern of significance.

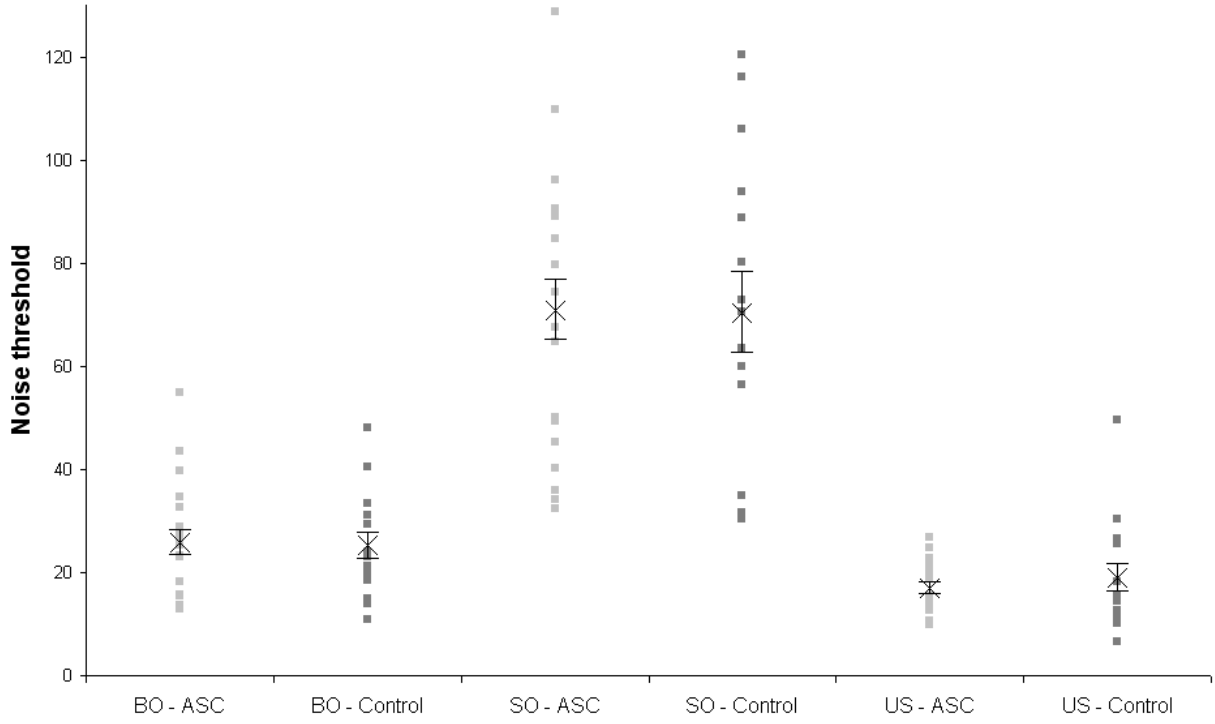

Figure 4.1. Noise thresholds. Dots represent data from individual participants, crosses show mean values ± standard error. There was a main effect of Condition but no main effect of Group and no Group by Condition interaction. Noise thresholds (NT) were higher in the Structured Object (SO) condition compared with the Biological Motion (BM) and Unstructured Object (UO) conditions, and higher in the BM condition compared with the UO condition. There was no difference between individuals with ASC and Controls.

4.4 DISCUSSION

In the present study, we examined psychophysical thresholds for the perception of biologically and non-biologically moving objects. Perceptual thresholds for motion detection from PLDs were measured in three conditions: Biological Motion (BM), in which we used a point-light walker; Structured Object (SO), in which we used a non-biologically moving, coherent, recognizable shape (a rectangle); and Unstructured Object (UO), in which we used a non-biologically moving, less coherent, unfamiliar shape (inverted single frame from BM condition). In all conditions the figure was embedded in noise dots that moved in the same way as the target dots and the task was to determine the direction of movement of the figure. A noise threshold was estimated in each condition adaptively (Watson and Pelli, 1983). Thresholds corresponded to the number of noise dots that each participant could tolerate while performing direction discrimination at 75% accuracy. Hence a high threshold represents good performance on the task and a low threshold reflects relatively poor performance. Results demonstrated

a significant main effect of condition, broadly consistent with findings on healthy adults by Hiris (2007). Thresholds were greatest in the SO condition and lowest in the UO condition. SO featured a familiar object that has strong visual form cues (straight lines and corners), which may assist in figure-ground segregation. UO on the other hand, had no familiar form. BM lay somewhere in between in difficulty, although the raw thresholds should not be directly compared between these conditions, as the form-from-motion is depicted quite differently for BM compared to the SO and UO conditions. While in all conditions the coherence between the local motion elements defines the perceived form, in SO and UO all local elements undergo the same movement, whereas in BM the local elements undergo correlated, but non-identical movements. Consistent with this, thresholds for SO and UO conditions were strongly correlated with each other.

Our main goal here was not to look at differences between these conditions per se, but to explore if individuals with ASC differed from controls. What we found was a clear lack of a difference between groups in the perception of biological and non-biological form-from-motion – adults with ASC performed very similarly to controls for all three conditions.

Is it possible that our paradigm was simply not powerful enough to detect any differences that may exist between the groups? A very similar paradigm has previously been employed with stroke patients wherein significant differences from controls were observed, despite the notoriously noisy nature of neuropsychological patient research (Saygin, 2007). The current paradigm has also been employed in a TMS experiment (van Kemenade et al., 2010) and in a single case study with a visual agnosic patient (Gilaie-Dotan et al., 2011). Both studies (van Kemenade et al., 2010; Gilaie-Dotan et al., 2011) found significant differences in performance with sample sizes smaller than here. Therefore the paradigm we used is sensitive enough to detect differences in performance between groups.

Our results for the BM condition are consistent with recent results from Murphy and colleagues (2009), where participants were presented with PLDs depicting a human walker, or a spatially scrambled version of the same stimulus. As in our study, the PLD was masked with noise dots and the task was to determine the direction of movement. Murphy et al. (2009) found no differences between ASC and control participants in accuracy and RTs in either the human walker or the scrambled walker condition. Similarly, we found no difference between ASC and control groups in direction discrimination thresholds, for PLDs depicting a walker, a non-biologically moving familiar object, or an inverted frame of a walker. Thus, we corroborate the findings of Murphy et al. (2009) and extend these results to non-

biological form-from-motion.

Our findings are interesting in the context of prior work that has indicated impaired global motion processing in ASC (Spencer et al., 2000; Milne et al., 2002; Spencer and O'Brien, 2006). Bertone et al. (2003) have suggested that such findings may be due to a deficiency in neuro-integrative mechanisms as manifest in impaired complex (second-order) motion processing and preserved simple (first-order) motion processing. Furthermore, Atkinson (2009) has demonstrated a correlation between MCTs and biological motion processing in adults with ASC, which was also observed in adolescents recently (Koldewyn et al., 2010). We designed our experiment such that optimal performance would require observers to integrate the motion of the signal dots in order to perceive a coherent moving form. A deficiency in global motion processing would therefore predict lower thresholds for the ASC group compared to the Control group in all conditions. One possibility is that participants were able to use local motion cues. Although direction discrimination cannot be determined with no motion integration, it is possible that observers judged the direction of motion using only a subset of dots (Thurman and Grossman, 2008). Even though the location of the stimuli was jittered from trial to trial, participants could have performed the task by identifying sub-parts of the figures (e.g., the arm of the walker, or the corner of the rectangle).

In addition, in form-from-motion perception, observers may also rely on form processing resources. A number of investigators have highlighted the role of form information in the perception of biological motion (Beintema et al., 2006; Lange et al., 2006), also supported by models of body movement perception and recent findings from neurophysiology (Giese and Poggio, 2003;Vangeneugden et al., 2009). Whether observers rely on a form-based template matching strategy (e.g. Beintema and Lappe, 2002; Lange et al., 2006) or on more dynamic representations (Cavanagh et al., 2001; Thurman and Grossman, 2008), we suggest that form-from-motion perception might rely on processes that are at least partially distinct from global motion processing. In support of this, Atkinson (2009) reported no significant relationship between MCTs and action recognition from PLDs. Indeed, one of the stimuli used in this study was very similar to our BM condition (a PLD of an actor walking on the spot). In light of Atkinson's data (2009), it is possible that emotion recognition from PLDs relies on global motion and form processing, whereas the recognition of the action depicted (or the detection of walking direction) may be achieved with a higher reliance on local motion cues and/or form cues. A recent study conflicts with this by demonstrating a correlation between MCTs and perception of a PL walker in adolescents with ASC (Koldewyn et al., 2010). However, Koldewyn and colleagues employed an atypical procedure for masking the PL walker wherein the same amount of noise dots were present on every trial; at easy

levels dot coherence was high, at more difficult levels dot coherence was low. This biological motion mask was identical to the stimulus employed to measure MCTs hence the probability of finding a correlation between conditions was inflated. In conclusion, body movement perception likely depends on a combination of different visual cues (kinematics, featural and configural motion and form cues), and the relative contributions of these cues may differ depending on the stimuli and on task requirements (Dittrich, 1993; Atkinson et al., 2007; Thirkettle et al., 2009; Loucks and Baldwin, 2009).

Existing studies of biological motion perception have required a number of different types of judgment to be made about the stimuli. The type of response required may be a source of variability in this field. Both our study and Murphy et al.'s used a walker direction task and found no difference between performance in ASC and in controls. In contrast, tasks requiring judgements about the presence of a human walker in a PLD (Blake et al., 2003) and perceived emotional state (Hubert et al., 2007; Parron et al., 2008) have found differences between control and ASC groups. One exception is the study by Koldewyn and collegaues (2010) where a significant deficit in a biological motion direction task was found in adolescents with ASC. However, as mentioned above, it is possible that atypical performance on this direction discrimination task was related to difficulties in processing the global motion mask in which the PL walker was embedded.

4.4.1 Conclusion

To summarise, we found intact perceptual thresholds for biological and non-biological form-from-motion perception in adults with ASC. Impairments in motion and form-from-motion perception in ASC are therefore only found for some stimuli and tasks. It is important to identify more specifically which processes are impacted in ASC before a link can be made between perceptual deficits and the higher-level clinical features of the disorder.

4.4.1.1 What next?

To investigate whether biological motion processing deficits in ASC are distinct from global motion processing difficulties this chapter has taken the approach of comparing thresholds for a biological motion condition with thresholds for a non-biological motion condition. Chapter 5 takes a different approach employing a novel biological motion processing paradigm which does not depend on intact global motion processing. Whereas good performance in the current Chapter required ignoring noise dots, good performance in **Chapter 5: Experiment 1** depends on sensitivity to perturbations to local biological motion (MJ) cues.

Chapter 5. Minimum-jerk biological motion processing in Autism Spectrum Conditions

Experiment 1: Reduced sensitivity to minimum-jerk biological motion in autism spectrum conditions

To investigate whether biological motion processing deficits in ASC are distinct from global motion processing problems. ***Chapter 4*** *investigated perceptual thresholds for direction discrimination from biological and non-biological form-from-motion stimuli embedded in noise dots. No differences were found between control and ASC groups. The current experiment takes a different approach in investigating this issue. Participants watched animations of a biological stimulus (a moving hand) or a non-biological stimulus (a falling tennis ball). The velocity profile of the movement was varied between 100% natural motion (minimum jerk (MJ) for the hand; gravitational (G) for the ball) and 100% constant velocity (CV). Participants were asked to judge which animation was 'less natural' in a two-interval forced choice paradigm and thresholds were estimated adaptively. Whereas good performance in* ***Chapter 4*** *required ignoring noise dots, good performance in the current experiment requires sensitivity to perturbations to characteristic human (MJ) motion. Crucially this judgement requires only local, not global, motion processing hence poor performance on this task cannot be a result of more general difficulties with global motion processing. There was a significant interaction between group and condition. Thresholds for the MJ condition were lower than the G condition for the Control group whereas there was no difference in thresholds of the two conditions for the ASC group. Furthermore, within the MJ condition participants with ASC performed significantly worse than control participants. Thus, unlike the controls, the ASC group did not show an increased sensitivity for perturbation to biological over non-biological velocity profiles.*

5.1 EXPERIMENT 1 INTRODUCTION

As previously discussed, a number of studies have reported difficulties with biological motion processing in ASC (Blake et al., 2003; Hubert et al., 2007; Parron et al., 2008; Kaiser et al., 2010a; Annaz et al., 2010, 2011). However, it is currently unclear whether these difficulties are distinct from problems with global motion processing. To address this issue, Chapter 4 compared thresholds for direction discrimination from biological and non-biological form-from-motion stimuli. No differences were found between control and ASC groups indicating typical biological and non-biological form-

from- motion perception at this level of processing (i.e. determining the direction of motion).

The current study employed a different technique to investigate the issue of whether biological motion processing deficits in ASC are distinct from global motion difficulties. A novel paradigm was designed to investigate whether a biological motion processing deficit is found in ASC when the stimuli do not require global motion integration and have no emotional content. Biological motion has a characteristic velocity profile that is mathematically described by the 'MJ model,' which is a cost function that minimises jerkiness over a specified movement trajectory (Flash and Hogan, 1985). We employed stimuli in which this 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% natural motion (MJ in the biological condition; gravitational in the non-biological condition), or 100% 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% natural motion and 15% 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 motion (MJ) condition and the non-biological (gravitational) condition.

Whereas good performance on the paradigm employed in **Chapter 4** required ignoring noise dots and determining the direction of signal dots, good performance in the current experiment required sensitivity to perturbations to characteristic human (MJ) motion.

5.2 METHODS

5.2.1 Participants

25 participants with ASC (18 males) and 23 control participants (18 males) took part. 16 participants (14 males) from the ASC group and 16 participants (12 males) from the Control group generated adequate data required for robust perceptual threshold estimation (see below). The groups were matched for age, gender and verbal, performance and full scale IQ, as measured by the Wechsler Abbreviated Scale of Intelligence (WASI) (see Table 5).

All participants had normal or corrected-to-normal vision and were screened for exclusion criteria (dyslexia, epilepsy, and any other neurological or psychiatric conditions) prior to taking part. All participants in the ASC group had a diagnosis of autism, Asperger's Syndrome (AS) or ASC from a GP or psychiatrist. The ADOS (Lord et al., 1999) was administered by a researcher trained and experienced in the use of this interview (see Table 5). We were unable to distinguish between participants with AS and autism, as we did not have information about early development of language and other skills in our participants. All participants gave informed consent to take part in the study, which was approved by the local ethics committee.

	ASC	**Control**	**Group comparison**
N	16	16	
Gender (M:F)	14:2	12:4	p = 0.65 (Fisher's exact test)
Age in years	34.1 (12.4)	33.3 (12.2)	$t_{(30)} = 1.72$; P = 0.86
Verbal IQ	117 (16.5)	118 (11.64; N=10)	$t_{(24)} = 0.43$; P = 0.87
Performance IQ	109 (12.9)	113 (11.55; N=10)	$t_{(24)} = 0.60$; P = 0.44
FS IQ	114.8 (15.56)	113 (15.06; N=10)	$t_{(30)} = 0.34$; P = 0.74
ADOS Total Score	7.06 (3.47)	NA	
ADOS RSI	5.06 (2.35)	NA	

Table 5 Participant details. Mean (±SD) scores for age, IQ and ADOS are provided. Note that IQ scores were available for only 10 out of 16 Control participants.

14 of the ASC participants and 10 of the Controls also took part in **Chapter 4**. There were no significant differences between the participants in this study and those who took part in **Chapter 4** in terms of age ($t(65) = -0.53$, $p = 0.60$) and full scale IQ ($t(63) = 0.48$, $p = 0.63$) and the two ASC groups did not differ in terms of ADOS total score ($t(29) = -0.40$, $p = 0.69$).

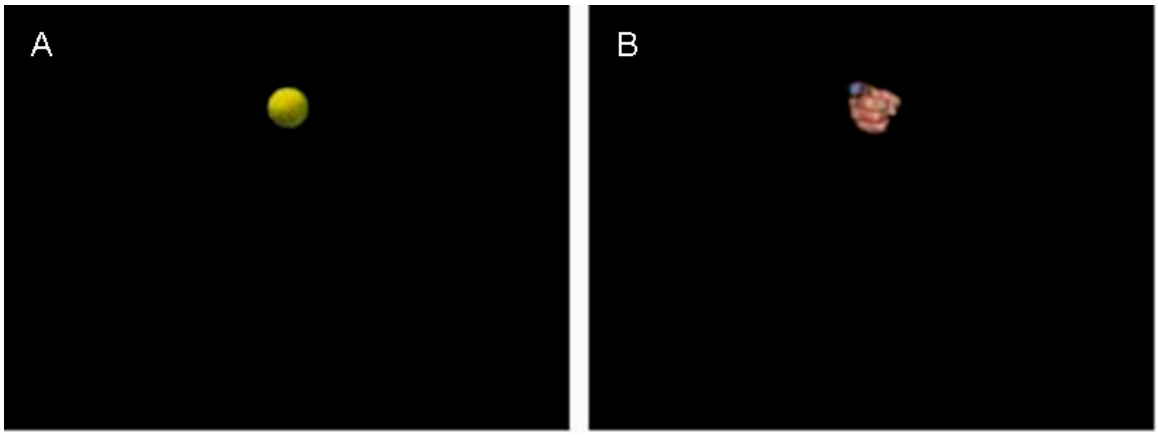

Figure 5. Stimuli. Participants watched pairs of animations that showed a biological stimulus (a hand) or a non- biological stimulus (a tennis ball) moving vertically across the screen. On each trial, the velocity profile of the movement was either 100% natural motion (MJ in the biological condition; gravitational in the non-biological condition), or 100% constant velocity or some linear combination of the two extremes. In each trial, participants were shown a 'reference' animation, which was always a combination of 85% natural motion and 15% 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 was less natural.

5.2.2 Design

Participants watched a series of visual stimuli constituting two conditions: biological (MJ) motion and non-biological (gravitational; G) motion.

5.2.2.1 Minimum jerk (MJ) condition

An image of a human hand (see Figure 5) was programmed to make a vertical sinusoidal movement of amplitude 110 mm and frequency 0.5 Hz. The velocity profile of the stimulus was generated by motion-morphing between two movement prototypes. The velocity profile of Prototype 1 was described by a constrained MJ model (Todorov and Jordan, 1998). The model assumes that if $\mathbf{r}(s) = [x(s), y(s), z(s)]$ is a 3D curve describing the path of the hand during a particular trial, where s is the distance along the path, and tangential speed is $\dot{s}(t)$ ($\dot{s}$ is a time derivative, $\mathbf{r}'$ is the derivative with respect to s, and boldface signifies vector quantities) the temporal profile of the movement will minimise the scalar function:

$$J = \int_0^T \left\| \frac{d^3}{dt^3} \mathbf{r}[s(t)] \right\|^2 dt$$

The velocity profile of Prototype 2 was described by a Constant Velocity (CV) vector.

5.2.2.2 Gravitational (G) condition

An image of a tennis ball (see Figure 5) was programmed to make a vertical downward movement of amplitude 215 mm and frequency 1 Hz. Thus, the tennis ball appeared from the top of the screen and finished off the bottom of the screen. As in the MJ condition, the velocity profile of the stimulus was generated by motion-morphing between two prototypes of movements. The velocity profile of Prototype 1 in this condition was described by the standard equation of motion:

$$h(t) = h_0 - 0.5\, gt^2$$

where h = height, h_0 = initial height, t = time and g = gravitational force [9.8m/s^2]. The velocity profile of Prototype 2 was described by a CV vector.

5.2.2.3 Motion-morphing

In both conditions, a series of new velocity profiles was created by linear combinations of the prototype velocity profiles using the following equation:

Motion morph = p_1 *(prototype 1) +* p_2 *(prototype 2)*

where the weights p_i determine the proportion of the morph described by the individual prototype. Therefore, in each condition, stimuli were either 100% Prototype 1 (MJ or G) or 100% Prototype 2 (CV), or some linear combination of the two in which p_i was determined by each participant's performance on the task.

5.2.3 Procedure

In each trial participants watched a target and a reference animation, for which order was counter-balanced across trials. The reference animation was always a combination of 85% natural motion and 15% CV, but for the target animation the ratio of CV to natural motion varied according to performance. The duration of each trial was 3.5 s. On each trial participants saw the hand stimulus move down the screen and back-up (2 s), pause for 1.5 s, then move down the screen and back-up again (2 s). The program then displayed the question "Less natural? Press 1 or 2" and waited for the participant's response. The procedure was the same for ball trials except that instead of moving down and up the screen the ball fell down twice. Prior to testing, each participant was read instructions by the

experimenter and performed at least 5 practice trials of each condition. Participants completed 6 blocks (3 of each condition) and there were 17 trials within each block. Block order was counter-balanced between participants, and participants were given breaks between blocks. The duration of the entire experiment was approx. 12 mins.

5.2.4 Threshold calculation

The psychophysical threshold was determined using a two-interval forced-choice adaptive staircase procedure. The velocity profile of the reference animation was the same throughout the experiment. The velocity profile of the target animation was initially a combination of 5% natural motion (MJ or G) and 95% CV. This ratio varied according to performance. Hence, at the start of the experiment the pair of animations (reference and target) was perceptually very different in terms of their velocity profile. The proportions of each prototype in the target morph were adjusted on a trial-by-trial basis using a weighted three-down, one-up, adaptive staircase technique. The three-down, one-up transformation targets the 79.4% correct point on the psychometric function. The probability of downward movement of the adaptive track must equal the probability of an upward movement; therefore if p is the probability of a positive response on a given trial, then $p \times p \times p$ must equal 0.5 hence the target probability is $3\sqrt{0.5} = 0.794$ (Kingdom and Prins, 2009). Three correct responses in a row incurred a 0.2 (large step-size) increase in the proportion of prototype 1 and one incorrect response led to a 0.2 decrease in the proportion of prototype 1. Therefore, the difference between the velocity profiles of the animations converged if the participant performed well and diverged if the participant's performance declined. After the first four reversals (defined as the point at which the animations stop converging and start to diverge or vice versa), step sizes changed to 0.025 to facilitate the calculation of a fine-grained threshold. The staircase procedure was terminated after 51 trials. If the number of reversals achieved within 51 trials was greater than 12 (the potential maximum was 15) the threshold was the mean of the last 8 small-step reversals values. If the number of reversals was less than 12 but greater than 3, the threshold was the mean of all available small-step reversals.

5.2.5 Data analysis

Threshold data were analysed using a 2x2 mixed-model repeated-measures ANOVA with between subjects factor Group (ASC vs Control) and within subjects factor Condition (MJ vs G), and Bonferroni-corrected t-tests were used to examine simple effect differences between conditions.

In addition, for the 14 ASC and 10 Control participants who took part in both the current experiment and **Chapter 4**, we conducted Pearson's correlations to examine the relationship between thresholds

acquired in the two studies.

5.3 RESULTS

Data were filtered such that only thresholds based on more than three small-step reversals were included in the analysis. For the ASC group (N=16), thresholds in the MJ condition were estimated from (mean) 5.19 (±2.61 SD) small-step reversals and from 4.69 (±1.92) small-step reversals in the G condition. For the Control group (N=16), thresholds were estimated from 5.88 (±1.59) reversals in the MJ condition and 5.56 (±1.86) in the G condition. There was no significant difference between groups in the number of reversals used for threshold calculation in either condition (MJ condition: $t(30) = -0.9$, $p = 0.38$; G condition $t(30) = -1.31$, $p = 0.2$). In addition, the number of reversals did not differ between conditions for each group (ASC: $t(15)=0.6$; $p = 0.56$; Control: $t(15)=0.42$; $p = 0.68$).

ANOVA revealed a significant main effect of condition ($F(1,30) = 4.56$, $p < 0.05$, $\eta_p^2 = 0.15$) and a significant interaction between condition and group ($F(1,30) = 4.37$, $p < 0.05$, $\eta_p^2 = 0.14$). There was no significant main effect of group ($F(1,30) = 0.17$, $p = 0.68$). The interaction was driven by a significant difference between the groups in the MJ condition (mean MJ thresholds for Control: 0.3 ± 0.02 (SEM); ASC: 0.40 ± 0.05; $t(30) = 2.197$, $p<0.05$) but not in the G condition (mean G thresholds for Control: 0.48 ± 0.05; ASC: 0.41 ± 0.05; $t(30) = -1$, $p = 0.32$). Thresholds in the MJ condition were significantly lower than in the G condition for the Control group ($t(15) = -3.127$, $p < 0.01$), whereas there was no significant difference between conditions for the ASC group ($t(15) = -0.03$, $p = 0.97$) [3]. See Figure 5.1.

[3] Gravitational thresholds for the ASC condition significantly deviated from the normal distribution (Shapiro-Wilk $W(16) = 0.822$, $p < 0.05$). To ensure the effects reported above were robust against violations of normality, data was log transformed and the 2 x 2 ANOVA rerun as above. The ANOVA conducted on the log transformed data showed a significant main effect of condition ($F(1,30) = 4.32$, $p < 0.05$) and a significant interaction between condition and group ($F(1,30) = 5.73$, $p < 0.05$). There was no significant main effect of group ($F(1,30) = 0.05$, $p = 0.83$). The interaction was driven by a significant difference between the groups in the MJ condition (log transformed mean MJ thresholds for Control: -0.55 ± 0.03; ASC: -0.43 ± 0.05; $t(30) = 2.097$, $p<0.05$) but not in the G condition (mean G thresholds for Control: -0.35 ± 0.04; ASC: -0.40 ± 0.06; $t(30) = -1.39$, $p = 0.175$). Thresholds in the MJ condition were significantly lower than in the G condition for the Control group ($t(15) = -3.321$, $p = 0.05$), whereas there was no significant difference between conditions for the ASC group ($t(15) = 0.213$, $p = 0.83$). Thus, log transforming the data did not change the pattern of significance.

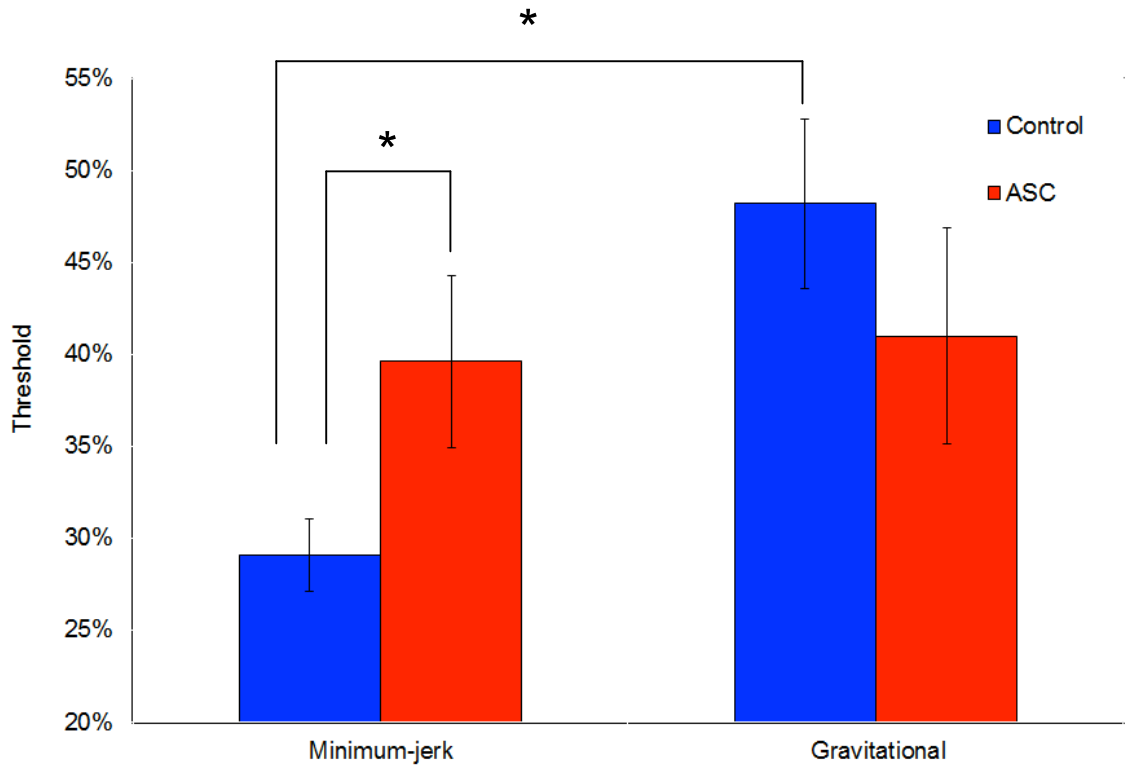

Figure 5.1. Interaction between group and condition. There was a significant interaction between group and condition driven by lower thresholds in the MJ condition than in the G condition for the Control group but not for the ASC group. Standard error bars are shown.

Thresholds in the MJ condition significantly correlated with score on the reciprocal social interaction subscale of the ADOS interview ($r = 0.53$, $p < 0.05$). There were no correlations with performance IQ, verbal IQ or full scale IQ (all $p > 0.05$).

Across all participants, and for the ASC and Control groups separately, thresholds for either biological or non-biological motion did not significantly correlate with BO, SO and UO thresholds reported in **Chapter 4** (all $p > 0.05$).

5.4 DISCUSSION

To our knowledge, this is the first study to have measured thresholds for detection of local motion perturbations to biological motion and non-biological motion. The thresholds reflect the amount of CV motion necessary to perturb a natural motion animation such that, if presented with the perturbed animation and a natural motion exemplar, the participant can no longer discriminate the less natural. Low thresholds, therefore, reflect high sensitivity to CV perturbations whereas high thresholds reflect low sensitivity to CV perturbations. The Control group exhibited mean thresholds for MJ motion of 30%, indicating that, on average, 70% of the velocity profile must be MJ for the target to be

discriminated as 'less natural' than the reference (which contained 85% MJ). In contrast, the mean non-biological (G) motion threshold (48%) was significantly lower for the Controls. Thus, on average, 52% of the velocity profile must be G for the target to be discriminated as 'less natural' than the reference (which contained 85% G). This suggests that the Control group was more sensitive to CV perturbations to the velocity profile of biological (MJ) motion than to perturbations to non-biological (G) motion. In the ASC group, mean thresholds were similar for both biological motion and non-biological motion (approx. 40% in both conditions). This indicates that, whilst the Control group was particularly sensitive to changes in the velocity profile of biological relative to non-biological motion, this increased relative sensitivity to biological motion was not found in the ASC group; individuals with ASC were significantly less sensitive to perturbations to biological motion than the control group.

The difference between the two groups' perceptual thresholds appears to be specific to biological motion since there was no difference between thresholds for non-biological motion. Since both groups obtained similar thresholds in the G condition, it is unlikely that the difference between groups in the MJ condition was due to differences in the interpretation of the task instructions, or attention.
The results obtained for the control group are in line with previous findings from Neal and Kilner (2010). Neal and Kilner videoed left and right hand reach-to-grasp actions, manipulated them (by flipping them along the vertical axis so that an action which appeared to be left-handed would move with right-hand kinematics and vice versa) and asked participants to determine whether the videos were manipulated or not. Participants were able to distinguish manipulated and un-manipulated videos demonstrating that typical control adults are sensitive to subtle perturbations to the kinematics of hand actions. The results of the current experiment agree with these findings and extend them to show a significant difference between control participants and those with ASC when it comes to detecting kinematic perturbations to hand actions.

The atypical biological motion processing found here is in line with previous findings of abnormal biological motion processing in children with ASC (Blake et al., 2003; Klin et al., 2009). However, the task used in the current study did not require global motion integration or processing of emotional content (Milne et al., 2002; Spencer and O'Brien, 2006; Bertone and Faubert, 2006; Hubert et al., 2007). Therefore, our data provide evidence for a biological motion processing deficit in ASC that cannot be explained by the need to integrate motion signals across space or the need to process the emotional content of the stimuli.

In contrast to the current results, **Chapter 4** reported no difference between control and ASC groups on

a different biological motion task. The lack of a correlation between thresholds in the current study and those from **Chapter 4** suggests that the two tasks tap into different mechanisms. The tasks differ in a number of ways. Firstly, good performance in **Chapter 4** required ignoring noise dots and identifying at least a sub-component (e.g. leg / arm) of the PL walker in order to determine the direction of motion. It has previously been argued that in noise-based biological motion tasks, processing of the biological stimulus is not all that is being measured and that segregation from the background noise dots could permit correct responding without an understanding of the PL stimulus (Beintema and Lappe, 2002). In contrast, good performance in the current experiment *depends* on processing the biological stimulus: the current paradigm required the detection of CV perturbations to characteristic human (MJ) motion. Another difference between the tasks is that the paradigm discussed in this Chapter depends on local motion processing and the static form of the stimulus carries no task relevant information. In contrast, the paradigm employed in Chapter 4 depends, at least to some extent, on form processing mechanisms. It is therefore possible that preserved form processing abilities in ASC provide a compensatory mechanism that can be employed for **Chapter 4** but not for the current study.

Another source of variability is the type of judgement required. **Chapter 4** required a simple perceptual judgement. In the current study, participants were asked to pick the 'less natural'; this task not only depends on accurate perceptual representation of biological motion but also on a robust stored representation of 'natural' human motion. Previous studies have reported difficulties in individuals with ASC when required to judge whether a PLD moves 'like a person' (Blake et al., 2003; Kaiser et al., 2010a; Annaz et al., 2010) - a task which requires a robust concept of how a person typically moves - and also in tasks which require the attribution of emotion hence requiring a representation of typical emotion related movements (Moore et al., 1997; Hubert et al., 2007; Parron et al., 2008; Atkinson 2009) but not for direction discrimination tasks (Murphy et al., 2009) which are unlikely to depend on stored representations of human motion. The separation between tasks that do and do not depend on stored representations reflects the distinction between objective and subjective processing of biological motion, discussed in **Chapter 2**: forming subjective judgements about motion stimuli was suggested to depend on a comparison between the objective sensory data and a stored representation of human motion. **Chapter 5: Experiment 2** investigates whether individuals with ASC exhibit poor sensitivity to perturbations to biological motion when the task does not depend on stored knowledge about 'natural' human motion.

Experiment 2: preserved perceptual discrimination for MJ biological motion in individuals with Autism Spectrum Condition

*In **Chapter 5: Experiment 1** participants were required to watch two animations of a hand making vertical sinusoidal movements across the screen and to 'pick the less natural'. Results indicated that, whilst control participants were particularly sensitive to changes in the velocity profile of biological relative to non-biological motion, this increased relative sensitivity to biological motion was not found in the ASC group. Thus, individuals with ASC were significantly less sensitive to perturbations to biological motion than the control group. In the current study, participants were required to watch two animations of a hand making sinusoidal movements across the screen and to judge if the animations moved in the 'same' way or in 'different' ways. Thus, the current study investigated whether individuals with ASC exhibit poor sensitivity to perturbations to biological motion when the task does not depend on stored knowledge about 'natural' human motion.*

5.5 EXPERIMENT 2 INTRODUCTION

In **Chapter 5: Experiment 1** participants were required to watch two animations of a hand executing vertical sinusoidal movements across the screen. One animation moved with typical human biological motion (MJ), the other animation moved with a velocity profile that is closer to robotic motion (MJ perturbed with CV motion); subjects were required to 'pick the less natural'. Thus, successful performance required perceiving that the two animations differ and knowing which animation is the 'less natural'. This task therefore required a stored representation of natural human motion. Whilst control participants were particularly sensitive to changes in the velocity profile of biological relative to non-biological motion, this increased relative sensitivity to biological motion was not found in the ASC group - individuals with ASC were significantly less sensitive to perturbations to biological motion than the control group. This result is in line with other studies that have reported atypical performance in ASC on tasks requiring a judgment about whether a PLD moves 'like a person' (Blake et al., 2003; Kaiser et al., 2010a; Annaz et al., 2010). In contrast, individuals with ASC do not exhibit atypical performance on biological motion tasks requiring simple perceptual judgements such as determining the direction of motion (Murphy et al., 2009; **Chapter 4**).

The current study aimed to investigate whether individuals with ASC exhibit poor sensitivity to perturbations to biological motion when the task does not require knowledge about 'natural' human motion. As in **Chapter 5: Experiment 1** participants were required to watch two animations of a hand

(hand form condition) or ball (ball form condition) executing vertical sinusoidal movements across the screen. Whereas **Chapter 5: Experiment 1** required participants to pick the 'less natural' animation, in the current study participants had to judge whether the movement of the animations was the 'same' or 'different'. Six 'difference levels' were covered ranging from 0% different (wherein the animations were identical) to 100% different (wherein the animations were maximally different: one was 100% natural motion (MJ or G) and the other was CV). Results were analysed with Signal detection Theory (SDT: Green and Swets, 1966) so as to acquire an index of sensitivity to the difference between the animations independent from any response bias (e.g. tendency to make 'same' judgements). For all participants we predicted that, as the difference between the animations increased (from 0% to 100%), sensitivity to this difference would also increase. We further hypothesised that, if the reduced ability to 'pick the less natural' for the MJ condition in **Chapter 5: Experiment 1**, is due to 'objective' perceptual difficulties in recognising that the two hand animations are different, individuals with ASC would exhibit a reduced sensitivity to the difference between the animations for the Hand but not Ball condition. That is, we predicted a significant interaction between group (ASC, control), difference level (0%, 20%, 40%, 60%, 80%, 100%) and Form condition (Hand, Ball) wherein individuals with ASC are less sensitivity to the difference between animations when the stimulus is a Hand but not when the stimulus is a Ball.

In **Chapter 5: Experiment 1** participants always saw a 'natural' reference animation and a motion-morph animation which comprised MJ motion perturbed with CV. Hence the results demonstrated a difficulty in ASC in detecting perturbations from 'natural' human motion. To investigate, in the current experiment, whether individuals with ASC also exhibit difficulties in detecting perturbations from CV motion we also manipulated the reference animation. In other words, another factor in our design was Reference Motion condition, which had two levels: 'Compare to 100%' and 'Compare to 0%'. For the Compare to 100% condition the reference animation moved with 100% natural motion (MJ for the Hand stimulus and G for the ball stimulus), the other animation was a motion-morph (100% natural motion, 100% CV or linear combinations of the two extremes). For the Compare to 0% condition both the Hand and Ball reference animations moved with CV and, again the other animation was a motion-morph. Hence, the 'Compare to 100%' condition was similar to **Chapter 5: Experiment 1** it indexed sensitivity to deviations from 100% MJ or G motion. The 'Compare to 0%' condition indexed sensitivity to a deviation from CV motion. If the ASC group exhibit poor sensitivity to the difference between the Hand, but not Ball, animations in both 'Compare to 100%' and 'Compare to 0%' conditions it may be concluded that these individuals exhibit motion processing difficulties for stimuli with biological form. However, if they exhibit difficulties specific to the Hand 'Compare to 100%' condition it may be

concluded that they have a specific difficulty in detecting deviations from characteristic human motion.

5.6 METHODS

5.6.1 Participants

20 participants with ASC (15 males) and 17 Control participants (14 males) took part. The groups were matched for age, gender and IQ, as measured by the Wechsler Abbreviated Scale of Intelligence (WASI) (see Table 5.1). All participants had normal or corrected-to-normal vision and were screened for exclusion criteria (dyslexia, epilepsy, and any other neurological or psychiatric conditions) prior to taking part. All participants in the ASC group had a diagnosis of autism, AS or ASC from a GP or psychiatrist. The ADOS (Lord et al., 1999) was administered by a researcher trained and experienced in the use of this interview (see Table 5.1). We were unable to distinguish between participants with AS and autism, as we did not have information about early development of language and other skills in our participants. All participants gave informed consent to take part in the study, which was approved by the local ethics committee. Participants comprised an entirely new sample with no overlap in participants between **Chapter 5 Experiment 1** and the current experiment.

	ASC	**Control**	**Group comparison**
N	20	17	
Gender(M:F)	15:5	14:3	p = 0.70 (Fisher's exact test)
Age in years	41.10 (2.71)	38.76(4.00)	t(35) = -0.50; p = 0.62
Verbal IQ	114.11 (3.33) N = 18	NA	
Performance IQ	108.83 (4.48) N = 18	NA	
Full scale IQ	112.94 (3.84) N = 18	118.24 (2.16)	t(33) = 1.18; p = 0.24

Table 5.1 Participant details. Mean (±SEM) scores for age, IQ and ADOS are provided. Note that only full scale IQ scores were available for Control participants. For two of the ASC participants no IQ score was available.

5.6.2 Design

A stimulus was programmed to make a vertical sinusoidal movement of amplitude 110 mm and frequency 0.5 Hz. On each trial two animations were presented: a reference (see below) and a motion-morph. The task was to decide if the animations moved in the "same" way or in "different" ways. The experiment followed a 2 (Form: Hand, Ball) x 2 (Motion reference: Compare to 0%, Compare to 100%) x 6 (Difference Level: 100%, 80%, 60%, 40%, 20%, 0%) design (Figure 5.2). For the Hand condition

the stimulus was an image of a human hand, for the Ball condition the stimulus was an image of a tennis ball. These images were identical to those employed in **Chapter 5: Experiment 1.**

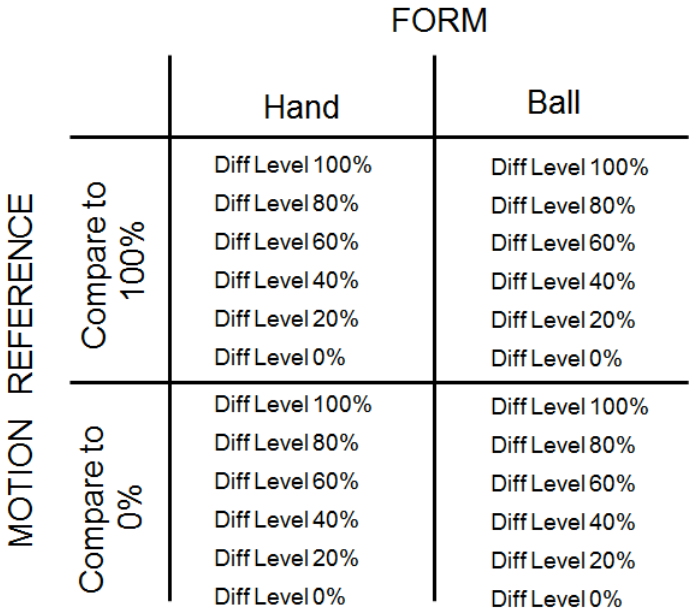

Figure 5.2. Design diagram. The experiment comprised a 2 (Form: Hand, Ball) x 2 (Motion reference: Compare to 0%, Compare to 100%) x 6 (Difference Level: 100%, 80%, 60%, 40%, 20%, 0%) design. There were 10 trials in each condition. Both groups (ASC and Control) completed identical experiments.

For the 'Compare to 100%' condition the reference Hand stimulus moved with 100% MJ as described by the constrained MJ model (Todorov and Jordan, 1998) employed in **Chapter 5: Experiment 1.** The model assumes that if $\mathbf{r}(s) = [x(s), y(s), z(s)]$ is a 3D curve describing the path of the hand during a particular trial, where s is the distance along the path, and tangential speed is $\dot{s}(t)$ ($\dot{s}$ is a time derivative, $\mathbf{r}'$ is the derivative with respect to s, and boldface signifies vector quantities) the temporal profile of the movement will minimise the scalar function:

$$J = \int_0^T \left\| \frac{d^3}{dt^3} \mathbf{r}[s(t)] \right\|^2 dt$$

For the 'Compare to 100%' condition the Ball stimulus moved with 100% G motion as described by the standard equation of motion employed in **Chapter 5: Experiment 1**:

$$\boldsymbol{h(t) = h_0 - 0.5\, gt^2}$$

where h = height, h_0 = initial height, t = time and g = gravitational force [9.8m/s^2].

For the 'Compare to 0%' condition both the Hand and Ball reference animations moved with CV. As in **Chapter 5: Experiment 1** the velocity profile of the motion-morph animation was generated by motion-morphing between *prototype 1* (MJ or G) and *prototype 2* (CV) using the following equation:

Motion morph = percentage1 (prototype 1) + percentage2 (prototype 2)

where the weights p_i determine the proportion of the morph described by the individual prototype. There were 6 motion-morph levels (Figure 5.3). The difference between the reference animation and the motion-morph animation ranged in 20% steps from 0% difference to 100% difference. This experiment employed a full-function design wherein the entire range of motion-morph stimuli was sampled. There were 10 exemplars at each of the 6 level for each Motion reference condition, for each Form condition. Participants watched 240 pairs of animations in total. For each participant separately all trials were pseudo-randomised, such that a trial from the same condition did not occur more than twice in a row. The duration of the entire experiment was approx. 20 minutes not including breaks.

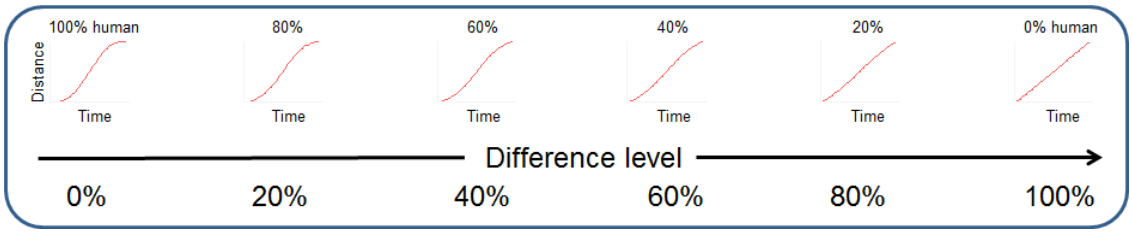

Figure 5.3. The 6 motion-morph levels comprising one condition. The difference between the reference animation and the motion-morph animation ranged in 20% steps from 0% difference to 100% difference.

5.6.3 Procedure

On each trial the participant watched a reference and a motion-morph animation, for which order was counter-balanced across trials. The task was to indicate, using a button press, if the animations moved in the "same" way or in "different" ways. Prior to testing, each participant was read instructions by the experimenter and performed a practice task on which they were required to make 5 correct consecutive responses before the experimental task began. After completion of the practice task participants completed the experiment in 3 blocks of 80 trials with rest breaks between blocks.

5.6.4 Data analysis

Performance was analysed using signal detection theory (SDT: Green and Swets, 1966) so as to index

sensitivity to the difference between the two animations (*d'*) independent of response bias (*C*). *d'* was calculated according to the following equation:

$$d' = z(FA) - z(H)$$

where z(FA) is the z score of the False Alarm rate (the proportion of "different" responses at the 0% Difference level) and z(H) is the z score of the Hit rate (proportion of "different" responses when Difference level > 0%). Z scores were calculated using the norminv excel function. Where FA or H = 0 the conventional adjustment of replacing the value with 1/2N was employed and where FA or H = 1 the conventional adjustment of replacing the value with 1- (1/2N) was employed. *d'* was calculated for each Difference level (20%, 40%, 60%, 80%, 100%) for the Hand/Compare to 100%, Hand/Compare to 0%, Ball/Compare to 100% and Ball/Compare to 0% conditions; hence for each participant 20 *d'* values were calculated. The 0% Difference level provides an estimate of FA; *d'* cannot be calculated for this level.

d' values were entered into a 2x2x2x5 mixed-model repeated-measured ANOVA with between subjects factor Group (ASC, Control) and within subjects factors Form condition (Hand, Ball), Motion reference condition (compare to 100%, compare to 0%) and Difference level (20%, 40%, 60%, 80%, 100%). Simple effects analyses were used to investigate significant interactions. P values are 2-tailed unless stated otherwise and Greenhouse Geisser correction is employed where Mauchley's test of sphericity is significant.

5.7 Results

The mixed model 2x2x2x5 ANOVA showed **no main effect of group or interaction between group and any of the other factors** (all $p > 0.05$). However, the ANOVA did show a **main effect of Motion reference condition** ($F(1, 35) = 5.63$, $p < 0.05$, $\eta_p^2 = 0.14$) driven by higher sensitivity in the compare to 100% condition (mean(SEM) = 0.85(0.12)) relative to the compare to 0% condition (0.65(0.11)). Also observed was a main effect of Difference level ($F(2.50, 87.61) = 64.49$, $p < 0.0001$, $\eta_p^2 = 0.65$: Greenhouse Geisser corrected; mean (SEM) 100% = 1.25(0.14), 80% = 1.08(0.13), 60% = 0.78(0.12), 40% = 0.51(0.10), 20% = 0.11(0.06)) whereby as the difference level decreased the sensitivity to that difference also decreased.

A significant interaction was observed between **Motion reference condition x Difference Level** (Table

5.2, $F(4, 140) = 6.43$, $p < 0.0001$, $\eta_p^2 = 0.16$). The Motion reference condition x Difference Level interaction was driven by a significant difference between the compare to 100% and compare to 0% conditions at the 40% ($F(1,35) = 14.88$, $p < 0.001$) and 60% ($F(1,35) = 7.98$, $p < 0.01$) difference levels but not at 20%, 80% and 100% (all $p > 0.15$; Figure 5.4).

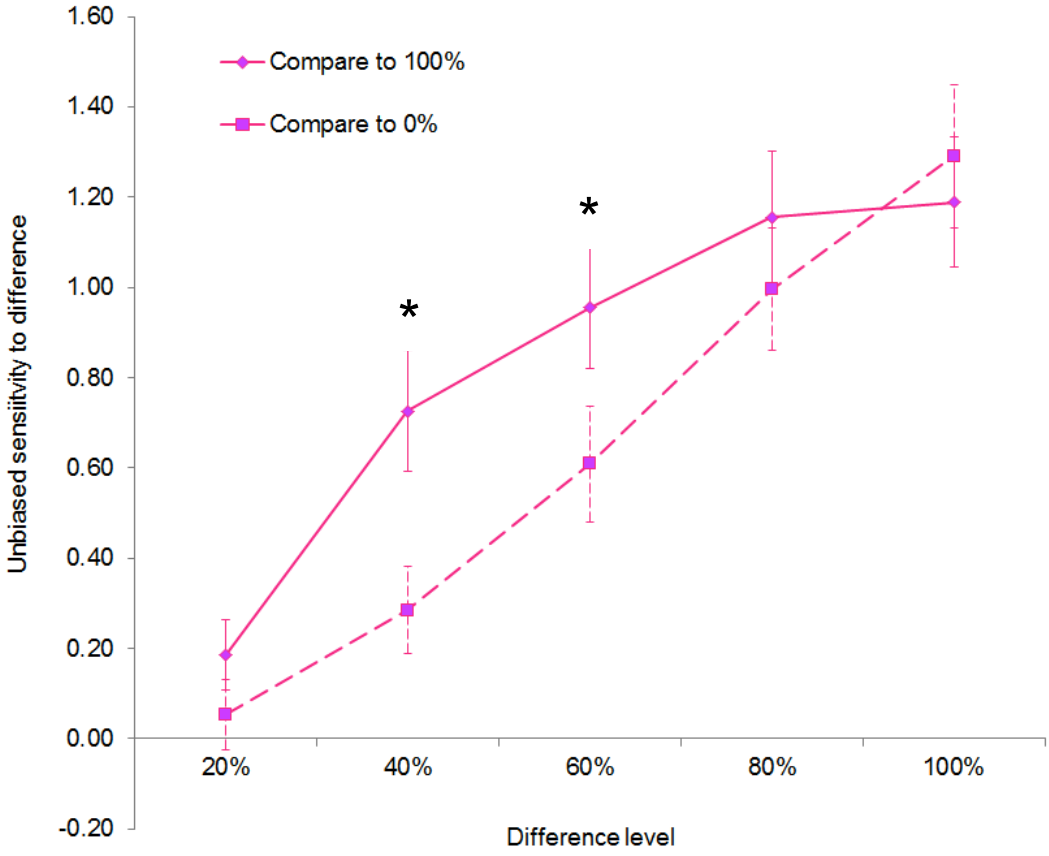

Figure 5.4. Significant interaction between Motion reference condition x Difference Level. * = $p < 0.05$

In addition there was a significant interaction between **Form condition x Motion reference condition x Difference level** ($F(4, 140) = 2.63$, $p < 0.05$, $\eta_p^2 = 0.07$). This interaction was driven by a significant difference between compare to 100% and compare to 0% conditions for the Hand Form condition at the 40% ($F(1,35) = 11.16$, $p < 0.01$) and 60% ($F(1,35) = 20.60$, $p < 0.001$) levels only (all others $p > 0.05$) but for the Ball Form condition at the 20% ($F(1,35) = 6.70$, $p < 0.05$) and 40% ($F(1,35) = 5.75$, $p < 0.05$) levels only (all others $p > 0.05$; Figure 5.55).

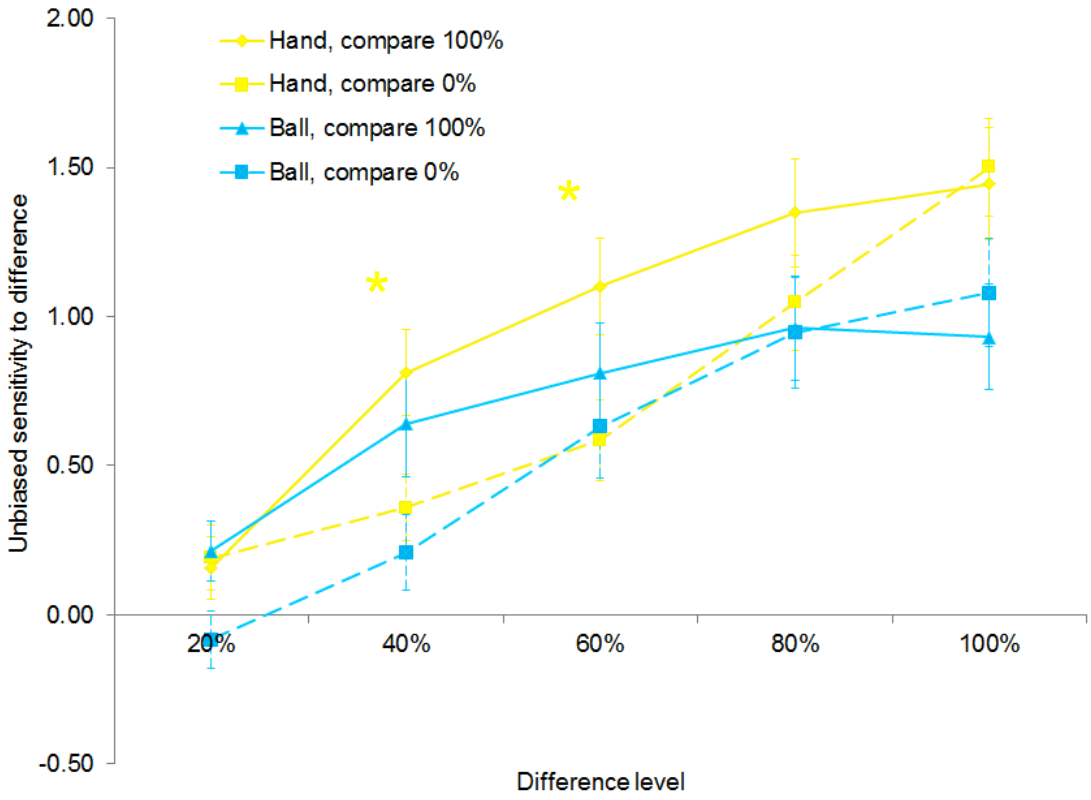

Figure 5.5. Significant interaction between Form condition x Motion reference condition x Difference level. * = $p < 0.05$

The **Form condition x Difference Level** interaction was marginally significant ($F(2.97, 104.00) = 2.61$, $p = 0.056$, $\eta_p^2 = 0.07$: Greenhouse Geisser corrected; see Table 5.2 for mean and SEM values). This marginally significant interaction was driven by a significant difference between Hand and Ball conditions at the 100% difference level only ($F(1,35) = 10.00$, $p < 0.01$); all others $p > 0.05$) [4].

[4] *d'* scores for the ASC group for the hand/Compare to 0%, 40% difference level condition significantly deviated from the normal distribution (Shapiro-Wilk $W(20) = 0.77$, $p < 0.01$). To ensure the effects reported above were robust against violations of normality, an outlying value was removed from the dataset and the 2 x 2 ANOVA rerun as above. This ANOVA showed a main effect of Motion reference condition ($F(1, 34) = 6.29$, $p < 0.05$), a main effect of Difference level ($F(2.51, 85.23) = 63.78$, $p < 0.0001$: Greenhouse-Geisser corrected), a significant interaction between Form condition x Difference Level ($F(3.03, 102.96) = 2.96$, $p < 0.05$: Greenhouse-Geisser corrected) and a significant interaction between Motion reference condition x Difference Level ($F(4, 136) = 5.83.43$, $p < 0.0001$). However, the interaction between Form condition x Motion reference condition x Difference level was only marginally significant ($F(4, 136) = 2.32$, $p = 0.06$). As above there was neither a main effect of Group nor an interaction between Group and any other factor.

Condition	Reference	Difference level	Mean	SEM
Hand	compare to 100%	100%	1.45	0.19
		80%	1.35	0.18
		60%	1.11	0.16
		40%	0.81	0.15
		20%	0.14	0.10
	compare to 0%	100%	1.50	0.17
		80%	1.05	0.16
		60%	0.57	0.14
		40%	0.36	0.11
		20%	0.18	0.11
Ball	compare to 100%	100%	0.94	0.18
		80%	0.98	0.17
		60%	0.82	0.17
		40%	0.64	0.18
		20%	0.21	0.10
	compare to 0%	100%	1.10	0.18
		80%	0.95	0.19
		60%	0.64	0.18
		40%	0.22	0.13
		20%	-0.08	0.10

Table 5.2 Mean and Standard Error of the Mean (SEM) values organised by Form condition (Hand, Ball), Motion reference condition (compare to 100%, compare to 0%) and Difference level (100%, 80%, 60%, 40%, 20%).

5.8 DISCUSSION

The current study aimed to investigate whether individuals with ASC exhibit poor sensitivity to perturbations to biological motion when the task does not require knowledge about 'natural' human motion. As in **Chapter 5: Experiment 1** participants were required to watch two animations of a hand or a ball executing vertical sinusoidal movements across the screen. Whereas in **Chapter 5: Experiment 1** participants were required to pick the 'less natural' animation, in the current study participants had to judge whether the movement of the animations was the 'same' or 'different'. If the reduced ability to 'pick the less natural' for the hand/MJ condition in **Chapter 5: Experiment 1**, was due to difficulties in perceiving that the two hand animations were different, individuals with ASC would be predicted to exhibit a reduced sensitivity to the difference between the animations in the current experiment. We did not find this to be the case: our results showed no main effect of Group or

interaction between Group and Form Condition, Motion Reference Condition or Difference Level. We therefore conclude that individuals with ASC do not differ from control participants on this biological motion processing task, which did not require knowledge about 'natural' human motion.

5.8.1 Implications for biological motion processing in ASC

In **Chapter 5: Experiment 1** we found that individuals with ASC exhibited a reduced sensitivity, relative to control participants, to perturbations to biological motion. However, on the current task our ASC and control groups were equally sensitive to perturbations to biological motion. An obvious difference between the two experiments is the judgements participants are asked to make. In **Chapter 5: Experiment 1** participants were required to watch two animations and 'pick the less natural'. This task not only requires participants to be able to perceive that the two animations are different but also to have a concept (or stored representation) of 'natural' human motion. A likely strategy is that participants compare each of the animations to their stored representation and pick the closest to be the 'natural' animation. The current experiment required participants to judge if the two animations were the 'same' or 'different'; no concept of natural human motion was required. The results of these studies therefore lead to a novel testable hypothesis: individuals with ASC have atypical stored representations of 'natural' human motion.

The paradigms employed in **Chapter 5: Experiment 1** and the current study differed in ways other than task. One difference was that whereas **Chapter 5: Experiment 1** employed an adaptive staircase design the current study employed a full-function design. The two designs have different advantages. Adaptive staircase methods sparsely sample stimulus levels at which participant performance is good (e.g. 100% different) and densely sample levels at which participant performance is poor (e.g. 20% different), thus making this a good method for estimating individual thresholds (i.e. the point at which a participant can no longer see the difference between two animations (Kingdom and Prins, 2009)). Full-function methods sample all stimulus levels equally. Therefore whilst this is an inferior method for estimating individual thresholds it provides estimates of participant performance at all stimulus levels and thus can be useful for comparing the patterns of sensitivity between groups. Although these methods have their relative advantages and disadvantages it is unlikely that these explain the discrepancy in the findings from **Chapter 5: Experiment 1** and the current study. For example, it is unlikely that the use of an adaptive staircase method in **Chapter 5: Experiment 1** resulted in an inflated difference between the ASC and control group in the Hand/MJ condition as this inflated difference should have also been evident in the Ball/G condition. A similar argument can be made with respect to analysis technique: whereas the current experiment employed SDT to acquire an unbiased measure of sensitivity (*d'*),

Chapter 5: Experiment 1 compared perceptual thresholds. If the use of perceptual thresholds as opposed to *d'* resulted in the apparent reduced sensitivity to biological motion in the ASC group in **Chapter 5: Experiment 1,** this should also have been evident for the Ball condition.

5.8.2 General implications

As expected, we found that as Difference level increased, participants became increasingly accurate in their "different" judgements: correctly classifying pairs as "different" and making few erroneous responses. Interestingly we found that participants were more sensitive to the difference for the 'compare to 100%' relative to the 'compare to 0%' condition. That is participants were better at detecting perturbations to 100% MJ or G compared to detecting perturbations to CV motion. This result may reflect familiarity: relatively few objects move at CV on earth, increased relative experience with MJ and G may lead to a relative enhanced sensitivity to perturbations to these motion types. It was further demonstrated that the difference in sensitivity between 'compare to 100%' and 'compare to 0%' conditions differed depending on Difference level (Figure 5.4). At the extremes (20% and 80% and 100% difference levels) sensitivity did not differ as a function of detecting perturbations to MJ/G versus CV. However at the 40% and 60% difference levels participants were more sensitive to perturbations to 100% MJ or G motion compared to perturbations to CV. This pattern of data is in line with the categorical processing literature, which suggests that within-category differences are minimised and between-category differences maximised. For instance, it could be that when the two animations are at, or close to, 100% MJ or G they can both be classed a 'human' or 'gravitational' motion, thus within category differences are minimised and sensitivity to the difference between the animations is low. It is possible that when one animation is 100% MJ or G and the other is 60%MJ:40%CV they fall into different classes, with the former being classed as 'human' or 'gravitational', and the latter being considered an 'atypical' motion type. Since between-category differences are maximised, this would result in an elevated sensitivity to the difference. This effect would not be seen for the compare to 0% condition if participants do not have a category for 'constant velocity' motion.

A 3-way interaction between Form condition, Motion reference condition and Difference level shows that the pattern of data described above was exhibited for the Hand condition but not the Ball condition (Figure 5.5). A possible interpretation is that participants exhibit categorical processing for the Hand stimulus but not for the Ball stimulus.

5.8.3 Conclusion

Participants with and without ASC watched two animations of a hand or a ball make vertical sinusoidal

movements across the screen and judged whether the animations moved in the 'same' way or in 'different' ways. Results showed no main effect of Group or interaction involving Group. We therefore conclude that individuals with ASC do not differ from control participants on this biological motion processing task which did not require knowledge about 'natural' human motion. This finding contrasts with **Chapter 5: Experiment 1,** which employed a biological motion task that did depend on stored knowledge of 'natural' human motion. The results of these two studies therefore lead to a novel hypothesis which should be investigated in future studies: individuals with ASC have an atypical stored representation of 'natural' human motion.

5.8.3.1 What next?

Chapter 5: Experiment 1 demonstrated reduced sensitivity to perturbations to biological motion in ASC. **Chapter 5: Experiment 2** suggested that this is not due to atypical 'objective' processing of biological motion (i.e. perceiving whether two animations are the 'same' or 'different') and may be due to atypical stored representations of 'natural' human motion. Irrespective of the mechanism that underpins this deficit, reduced sensitivity to biological motion could result in atypical effects of motion perception on action execution. Chapter 6 investigates the effects of both motion (biological motion or CV) and form (human or robot) on the Interference Effect in ASC.

Chapter 6. Atypical interference effect of action observation in autism spectrum conditions

Observing incongruent actions interferes with ongoing action execution. This interference effect has previously been found to be larger for actions with biological form and motion than for actions with non-biological form and motion (Kilner et al., 2003a, 2007a; Tai et al., 2004; Press et al., 2005). Chapter 5 demonstrated a reduced sensitivity to CV perturbations to MJ biological motion in ASC. In addition, a reduced influence of human form on visuomotor priming has previously been reported in ASC (Pierno et al., 2008). The current study used virtual reality to investigate the biological specificity of interference effects of action observation in ASC. A group of high-functioning adults with ASC and age- and IQ-matched healthy controls performed horizontal sinusoidal arm movements whilst observing horizontal and vertical movements conducted by a virtual reality agent with either human or robot form, which moved with either biological motion or at CV. In another condition, participants made the same arm movements while observing a real human. 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 to congruent movements. Control participants exhibited a significant interference effect during the observation of real human and virtual human agent incongruent movements but no interference effect for the observation of virtual robot agent movements, this pattern of interference effect was not found for the ASC group. Indeed, the ASC group showed no significant difference in the way they responded to either of the human form conditions and the way the control group responded to the robot condition. The current study is the first demonstration of atypical interference effects in ASC.

6.1 INTRODUCTION

Observing an incongruent action made by another human interferes with ongoing action execution (Bouquet et al., 2007; Chaminade et al., 2005; Gowen et al., 2008; Kilner et al., 2003a, 2007a; Oztop, et al., 2005; Stanley et al., 2007). 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 arm movements are more variable in the direction of the observed incongruent movement than when observing a congruent movement (Gowen et al., 2008; Kilner et al., 2007; Kilner et al., 2003). Action observation can therefore be said to 'interfere' with action execution. The Interference Effect, defined as variance in the plane orthogonal to the participant's movement (the error plane) for incongruent minus congruent movement observation, is greater when the observed action is made by a real human than when it is made by a robot (Kilner et al. 2003). Kilner, Hamilton and Blakemore (2007) demonstrated that videos in which arm movements made by a human actor had been manipulated such that the finger-tip moved at a constant velocity (CV) resulted in a reduced Interference Effect compared to videos in which the finger-tip moved with typical biological motion (MJ velocity profile). Therefore, the Interference Effect appears to be greater for observed stimuli that look and move like humans than for stimuli that look or move like robots.

The current study was designed to investigate the Interference Effect in ASC, a developmental disorder characterised by impairments in social interaction, language and communication (American Psychiatric Association, 1994). There is accumulating evidence of a dysfunctional action observation system (Gallese, 2006; Gallese and Goldman, 1998; Williams et al., 2001) and atypical biological motion perception in ASC. While adults with ASC perform like control participants in making simple judgments such as direction of walking from biological motion point-light display stimuli (Murphy et al., 2009; Saygin et al., 2010), they demonstrate impairments in more complex judgments such as emotion recognition (Atkinson, 2009; Hubert et al., 2007). In **Chapter 5: Experiment 1** of this thesis participants observed animations of human hand images that made sinusoidal movements with either MJ biological motion, constant velocity or linear combinations of these two extremes. Participants were required to pick the less natural animation from two exemplars. Relative to control participants, adults with ASC required a greater difference between the two animations in order to distinguish the less natural stimulus, suggesting that individuals with ASC exhibit a reduced sensitivity to the difference between biological and non-biological motion.

Previous studies have found evidence for Interference Effects in individuals with ASC. Gowen and

colleagues (2008) required participants to execute sinusoidal arm movements whilst observing congruent and incongruent movements depicted by either a real human, a two-dimensional animation of a dot that moved with biological motion or a dot animation that moved at CV. They found that high-functioning adults with ASC did not differ from control participants in the magnitude of the Interference Effect resulting from observation of real human, biological dot or non-biological dot movement. Interference Effects can also be measured in terms of RT. For instance, Brass, Bekkering and Prinz (2001) instructed participants to perform a tapping or lifting finger movement in response to a photograph depicting either a tapping or a lifting finger movement. Finger movement RTs were greater when the photograph depicted the incongruent finger movement. Individuals with ASC also exhibit this kind of RT Interference Effect (Bird et al., 2007; Press et al., 2010; Spengler et al., 2010a).

Based on the premise that children with ASC avoid human contact but are responsive to machines, therapists and teachers are increasingly using robots (Costa et al., 2010) and virtual reality (for review see Wang and Reid, 2011) to teach social skills to children with ASC. An observational study by Robins, Dautenhahn and Dubowski (2006) reported that children with ASC are more likely to exhibit social behaviours, such as watching, approaching and touching, when presented with a robot that has robotic rather than human appearance, and when presented with a human wearing a robot costume rather than typical human clothing. Another study required participants to observe either a human or a robotic arm performing a reach-to-grasp action towards a spherical object and then to perform the same action (Pierno et al., 2008). Pierno and colleagues found that, whereas control children (10-13 years) exhibited facilitation – as revealed by faster movement duration – following human but not robot observation, children with ASC exhibited facilitation after robot but not human observation. Although this research has been restricted to children, it suggests that individuals with ASC may differ from controls in their reactions to human and robot form.

Previous studies of the Interference Effect in ASC have not investigated separable influences of actor form and actor motion. Furthermore, studies of the influence of actor motion on the Interference Effect have been restricted to 2D stimuli. The aim of the current study was to investigate the effect of actor form (human or robot) and actor motion (biological motion or constant velocity) on the Interference Effect in high functioning adults with ASC, by using three-dimensional virtual reality stimuli. Participants were instructed to execute horizontal sinusoidal arm movements while observing movement stimuli in a virtual reality environment. To investigate the biological specificity of the Interference Effect, participants observed either congruent (horizontal) or incongruent (vertical) movements conducted by a virtual reality agent that had either human or robot form, the finger-tip of which moved

with either biological motion or at constant velocity (CV). In another condition, participants observed congruent or incongruent arm movements conducted by a human model. We predicted that, whereas control participants would exhibit a greater Interference Effect for stimuli with human as opposed to robot form, individuals with ASC would not exhibit this same pattern.

6.2 METHODS

6.2.1 Participants

15 control participants were recruited from the UCL subject pool. 14 participants with ASC were recruited from the ICN Autism database. The groups were matched for age (control mean (SD) = 37.60(15.06); ASC = 41.07(14.22); $t(27) = -0.64$, $p = 0.53$), gender (control M:F =13:2 , ASC M:F = 11:3) and full scale IQ (control mean (SD) = 118.93(8.92); ASC = 114.36(13.33); $t(27) = 1.09$, $p = 0.28$), as measured by the Wechsler Abbreviated Scale of Intelligence (WASI).

All participants had normal or corrected-to-normal vision and were screened for exclusion criteria (dyslexia, epilepsy, and any other neurological or psychiatric conditions) prior to taking part. All participants in the ASC group had a diagnosis of Autism, AS or Autism Spectrum Disorder (ASD) from an independent clinician (Table 6.1). The ADOS (Lord et al., 1999) was administered by a researcher trained and experienced in the use of this interview. All participants gave informed consent to take part in the study, which was approved by the local ethics committee and performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

6.2.2 Design and stimuli

To compare the influence of both form and motion on executed action in individuals with ASC and controls, we used a 2 (Actor Form: virtual human agent, virtual robot agent) x 2 (Actor Motion: biological motion (BM), constant velocity (CV)) x 2 (Congruency between participant and actor movement: congruent, incongruent) design for the virtual reality conditions. See Figure 6.

To compare the influence of observed form on executed action, we used a separate 3 (Actor Form: virtual human agent, virtual robot agent, real human) x 2 (Congruency: congruent, incongruent) design. See Figure 6.

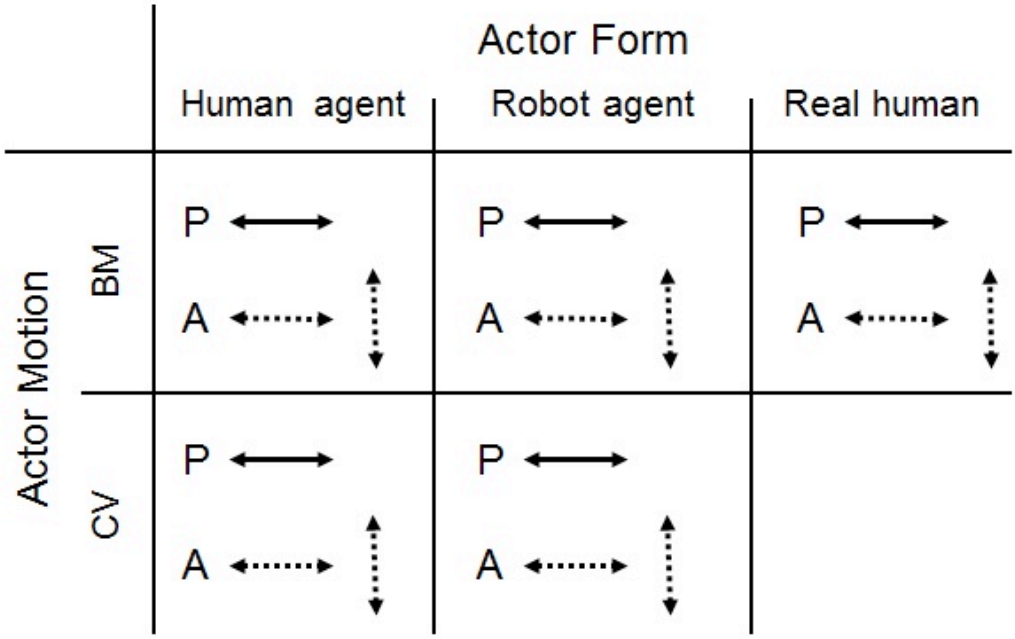

Figure 6. Experimental design. Three different actor forms were employed: human agent, robot agent and real human. For the agent conditions two motion types were employed: biological motion (BM) and constant velocity (CV). For 50% of trials in every condition the direction of the movement was congruent with the participant's movement, for 50% of trials the direction was incongruent. In total there were 10 experimental conditions. P, participant. A, actor.

6.2.2.1 Actor Form

There were three different types of actor form: real human, virtual human agent and virtual robot agent. The 'real human' was a Caucasian male, aged 31. The virtual human agent (Figure 6.1**A**) was represented as a Caucasian male aged around 30 years with similar appearance to the real human. The same skeleton was employed for the robot but all limb segments were replaced with grey cylinders (Figure 6.1**B**). To remove any distracting influence of eye cues the virtual human agent had covered eyes, the virtual robot agent did not feature eyes and the real human had closed eyes. Actors were positioned in the virtual reality theatre such that they appeared to stand 2 m in front of the participant. For each trial only one actor was visible.

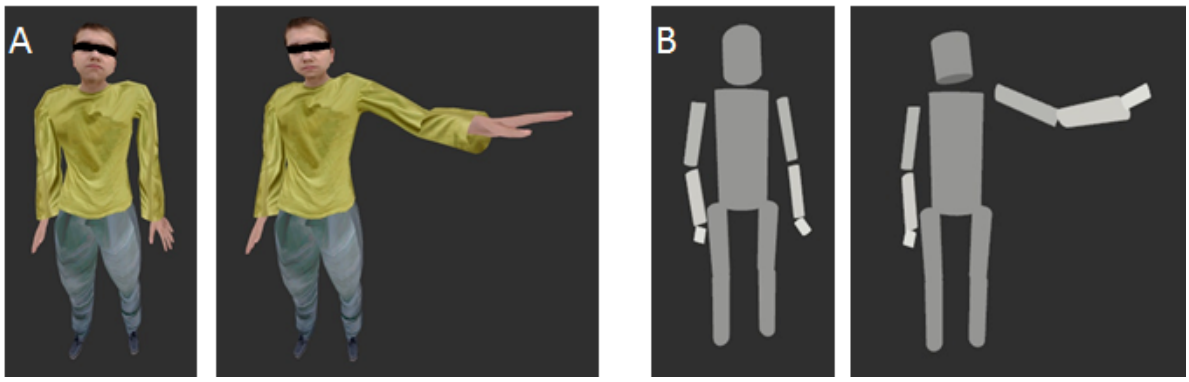

Figure 6.1. Actor form. **A.** The virtual human agent was represented as a Caucasian male aged around 30 years with similar appearance to the real human. **B.** The virtual robot agent was created by replacing the limb segments of the human agent with grey cylinders.

6.2.2.2 Actor Motion

There were two types of actor motion: biological motion (for the real human and virtual agent conditions) and constant velocity (for the virtual agent conditions only).

Biological motion (BM)

The velocity profile of both congruent and incongruent arm movements for the virtual reality human and robot stimuli was created by motion tracking the 'real human' actor while he performed sinusoidal vertical and horizontal right arm movements at a rate of 1Hz. These arm movements were used to animate the right arm of the human and virtual robot agents.

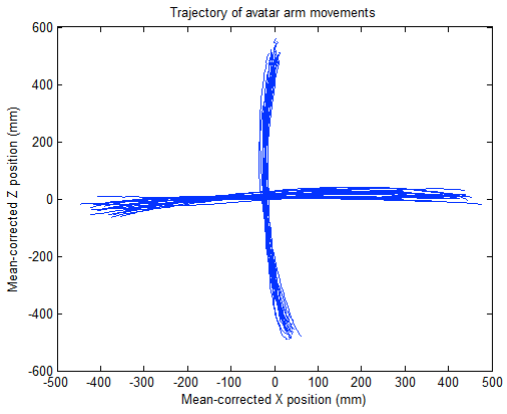

Figure 6.2. Arm movement trajectories for vertical and horizontal virtual agent movements. Both biological and constant velocity movements followed the same trajectories.

Constant velocity (CV)

CV movements were created by re-sampling the motion-tracked human movement at irregular intervals determined by a linear model. This resulted in sinusoidal movements that preserved the average distance

covered (horizontal movements = 807.76mm; vertical = 977.45mm), average duration (horizontal = 0.84secs, vertical 0.86secs), average speed (horizontal = 961.62mm/sec; vertical = 1136.57mm/sec) and trajectory (Figure 6.2) of the biological motion movements. The CV movements differed from the BM movements in that the finger tip of the virtual actor moved across space at a constant velocity rather than following the bell-shaped velocity profile that is characteristic of MJ biological motion (Figure 6.3: Abend et al., 1982; Flash and Hogan, 1985).

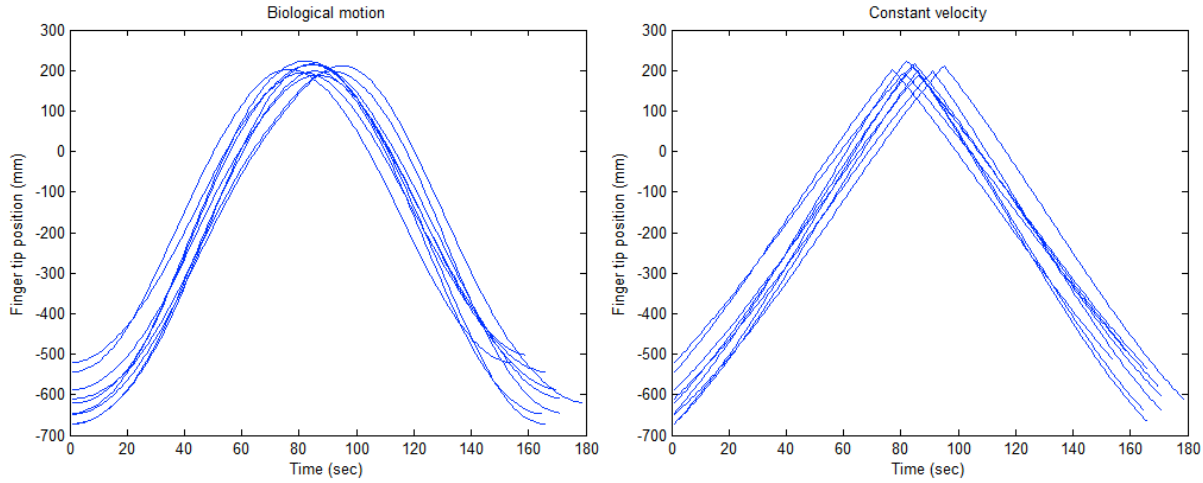

Figure 6.3. Biological and constant velocity movements. Biological motion and constant velocity movements were matched in terms of average distance covered, average duration, average speed and trajectory but differed in that, for biological movements, the finger-tip followed a bell-shaped velocity profile, whereas for CV movements the finger-tip moved at a constant velocity.

6.2.3 Display

The experiment took place in a (cave-hybrid) immersive virtual reality theatre (Cruz-Neira et al., 1992). This consists of 3 vertical walls and a floor which make up a continuous projection surface, and onto which 3D computer graphic imagery is projected. The participant wears stereo shutter glasses to enable 3D viewing, as well as a small head-tracking device which allows the projected imagery to be perspective correct for the participant at all times.

6.2.4 Data recording

Data were recorded using a Vicon motion tracking system (http://www.vicon.com/). Markers that were reflective in infrared were placed in the following positions: finger, wrist, elbow and shoulder of the participant's right arm. The position of each of these sensors was monitored by six infrared cameras at 100 Hz in x, y and z coordinates.

6.2.5 Procedure

Participants stood in the virtual reality theatre and made horizontal sinusoidal movements with their right arm. These arm movements were cued by a sequence of three high-pitched and three low-pitched tones. Participants were instructed to synchronise their movements so that they were at the far right when they heard the high-pitched tone and on the far left when they heard the low-pitched tone. This ensured that participants moved in phase with the actor. Whilst performing the horizontal arm movements, participants watched the virtual human agent, the virtual robot agent, the real human or a blank screen. For each trial the participant viewed 6 movements accompanied by a tone and 10 movements without a tone. There were 10 experimental conditions and one baseline condition (see Figure 6) with 5 trials for each condition. Participants conducted 5 real human trials at the start and 5 at the end of the experiment. Within the real human condition, congruent and incongruent trials were randomly interleaved. All other trials were blocked according to the form of the actor. In each block participants saw both congruent and incongruent, BM and CV trials. Block order was pseudorandomised such that no participant saw two or more identical blocks in a row; block order was counterbalanced between participants. Prior to recording, the experimenter read standardised instructions and demonstrated the required arm movement. Participants were given one practice trial.

Participants were given breaks after the first five real human trials, one-third and two-thirds of the way through the virtual agent trials and before the last five real human trials. The entire experiment took one hour including set-up and breaks.

6.2.6 Data-analysis

Data analysis was based on that employed by Kilner and colleagues (2003a, 2007a). Data from each participant's finger marker were reconstructed, using Vicon software, in x, y and z dimensions. 10 cycles from the middle of each trial were analysed allowing for the participant's arm movement to align with the visual stimulus and the tone pacemaker. Data were segmented into movements from right to left and left to right (Figure 6.4 for example single trial data).

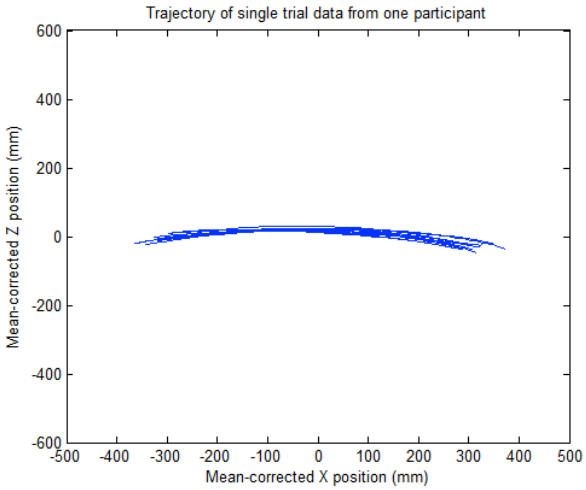

Figure 6.4. Example arm movement trajectory. Single trial from an individual participant drawn at random.

6.2.6.1 Interference Effect

For each segmented movement the variance in the movement in the vertical plane was calculated. Outlying movements in which the variance was greater than or less than 1.96 standard deviations away from the mean (p(chance) < 0.05) were excluded (Table 6). The mean variance was calculated across all trials for each condition. For each participant, for each condition, an 'Interference Effect' (an index of the extent to which the observed movement affects the executed movement) was calculated as variance in executed movement produced whilst the participant observed a vertical (incongruent) arm movement minus the variance produced whilst the participant observed a horizontal (congruent) arm movement. Data from 3 participants (2 ASC and 1 control) were excluded because of technical difficulties during data collection, which resulted in error (vertical) plane variance scores greater than 1.96 SD away from the mean (p(chance) < 0.05). Data from a further 4 participants (2 ASC and 2 control) were excluded from the final analysis on the basis that the recorded Interference Effect was greater than (1 ASC and 1 control) or less than 1.96 SD (1 ASC and 1 control) away from the group mean. Data from 10 participants with ASC and 12 control participants were included in the final analysis; these groups did not significantly differ in terms of age ($t(20) = -0.08$, $p = 0.94$) or full scale IQ ($t(20) = 0.17$, $p = 0.87$; Table 6.1).

Form	Congruency	Motion	Control		ASC	
			Mean	SD	Mean	SD
Human agent	Incongruent	Biological	40.20	7.26	36.9	8.5
Human agent	Incongruent	CV	39.60	10.06	36.3	12.3
Human agent	Congruent	Biological	41.00	7.47	39.1	7.8
Human agent	Congruent	CV	40.80	9.14	39.7	8.7
Robot agent	Incongruent	Biological	42.27	6.20	38.5	9.6
Robot agent	Incongruent	CV	40.40	8.97	39.2	9.6
Robot agent	Congruent	Biological	40.07	8.90	40.7	8.2
Robot agent	Congruent	CV	38.87	9.69	36.5	10.8
Real human	Incongruent	Biological	36.60	13.69	43.4	5.5
Real human	Congruent	Biological	40.40	8.37	43.9	5.3

Table 6 Included trials by condition and group. There was no systematic relationship between the number of trials included in the analysis and the condition or participant group.

Two separate ANOVAs were conducted to examine the effects of the conditions and of group membership on error plane variance.

The first was a mixed model 2x2x2x2 ANOVA with factors Group (ASC, control); Actor Form (virtual human agent, virtual robot agent), Actor Motion (BM, CV) and movement Congruency (congruent, incongruent), and was performed on data from the virtual reality conditions.

The second ANOVA investigated only BM movements and followed a 2x3x2 design with factors Group (ASC, control), Actor Form (virtual human agent, virtual robot agent, real human) and Congruency (congruent, incongruent).

Conducting these ANOVA models with number of included trials (mean variance – 1.96*SD > variance < mean variance + 1.96*SD) as dependent variable showed no main effects of, or interactions between, any of the factors (all $p > 0.05$). Hence, there was no systematic relationship between the number of included trials and group membership or experimental condition.

	ASC	Control	Group comparison
Gender (male: female)	8:2	10:2	p = 1 (Fisher's exact test)
Age (mean(SD))	40.5(14.74)	40(15.79)	t(20) = -0.08, p = 0.94
Full-scale IQ (mean(SD))	116.60(15.08)	117.50(9.48)	t(20) = 0.17, p = 0.87
Performance IQ (mean(SD))	110.30(20.20)	na	
Verbal IQ (mean(SD))	116.00(11.79)	na	
ADOS total (mean(SD))	10.30(3.43)	na	
ADOS communication (mean(SD))	3.60(1.07)	na	
ADOS reciprocal social interaction (mean(SD))	6.70(2.54)	na	

Table 6.1 Participant details. The ASC and control groups were matched in terms of gender, age and full-scale IQ.

6.3 RESULTS

6.3.1 Interference Effect generated by human and virtual robot agents

A mixed model 2x2x2x2 ANOVA with factors Group (ASC, control); Actor Form (virtual human agent, virtual robot agent), Actor Motion (BM, CV) and movement Congruency (congruent, incongruent) showed a significant interaction between **Group x Actor Form x Congruency** ($F(1,20) = 5.05$, $p < 0.05$, $\eta_p^2 = 0.20$). This interaction was also significant if age and (full scale) IQ were included as covariates ($F(1,18) = 4.83$, $p < 0.05$, $\eta_p^2 = 0.20$). Simple effects analyses, with age and IQ as covariates, demonstrated that, whereas the control group produced significantly more error plane variance when observing incongruent (adjusted mean(SEM) = 423.14(98.42)) compared to congruent (342.21(77.50); $F(1,18) = 5.12$, $p < 0.05$) movements conducted by the virtual human agent, individuals with ASC did not (incongruent adjusted mean(SEM) = 335.03(107.84), congruent = 370.25(84.90); $F(1,18) = 0.80$, $p = 0.38$). Neither groups demonstrated a difference in error plane variance generated whilst observing incongruent and congruent movements performed by the virtual robot agent (all $F(1,18) < 1$, $p > 0.3$). These results demonstrate that, for the control group, virtual human agent but not virtual robot agent movements produced a significant Interference Effect, whereas neither human nor virtual robot agent movements produced a significant Interference Effect for the ASC group (Figure 6.5).

To further investigate the Group x Actor form x Congruency interaction, the Interference Effect (error plane variance for incongruent trials minus error plane variance for congruent trials) was calculated for virtual human agent BM, virtual human agent CV, virtual robot agent BM and virtual robot agent CV.

The Interference Effect data were entered into a 2x2x2 ANOVA with factors Actor Form, Actor Motion and Group and with age and IQ as covariates. The ANOVA demonstrated a significant interaction between Group x Actor form ($F(1,18) = 4.83$, $p < 0.05$). Simple effects analyses demonstrated that compared to the control group the ASC group demonstrated significantly smaller Interference Effects when observing the virtual human agent (ASC adjusted mean(SEM) = -35.22(39.18), control = 80.93(35.76), $F(1,18) = 4.79$, $p < 0.05$) but not when observing the virtual robot agent (ASC = 30.76(32.36), control = -3.51(29.53), $F(1,18) = 0.61$, $p = 0.45$). Furthermore, whereas the control group exhibited a significantly greater Interference Effect for virtual human agent compared to virtual robot agent observation ($F(1.18) = 3.36$, $p < 0.05$ (1-tailed)), individuals with ASC showed no difference between the two actor forms ($F(1.17) = 1.71$, $p = 0.21$).

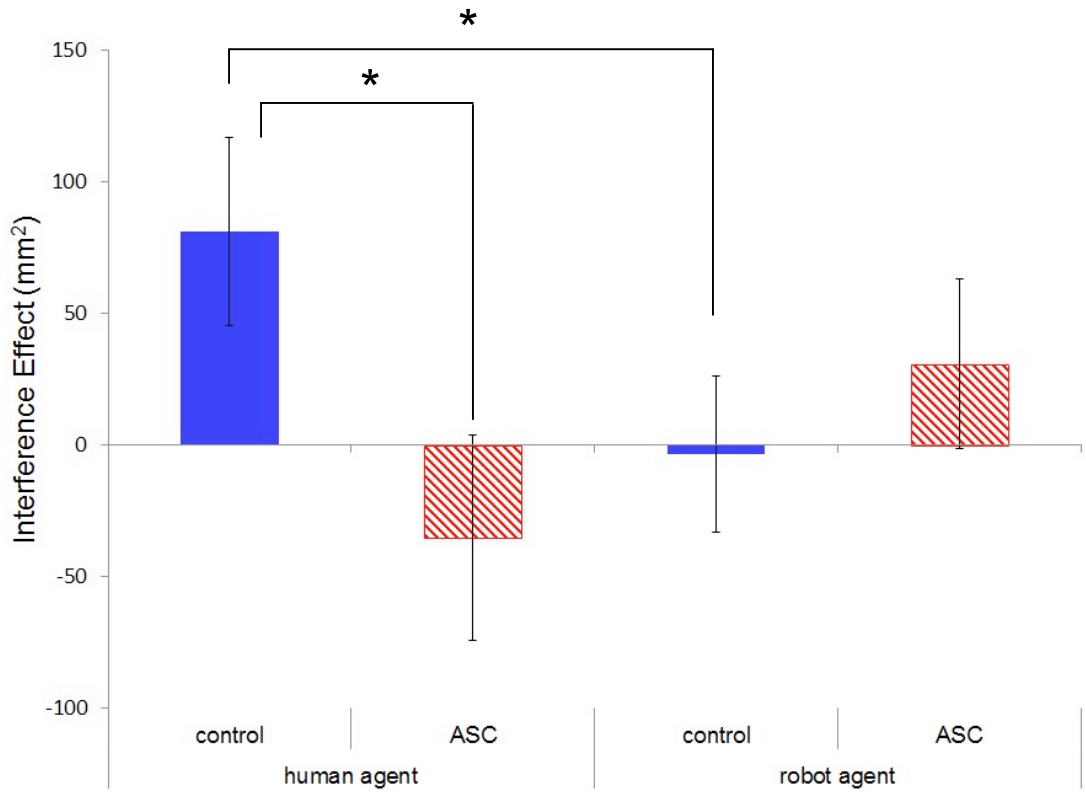

Figure 6.5. Adjusted mean (+/-SEM) Interference Effect (incongruent minus congruent variance) is displayed. The control group exhibited a significant Interference Effect in the human agent biological motion (BM) and human agent CV conditions but not in the robot agent BM or CV conditions. In contrast individuals with ASC did not exhibit a significant Interference Effect for any condition. * = $p<0.05$

The 2x2x2x2 ANOVA also showed a significant **Actor Motion x Group interaction** ($F(1,20) = 6.82$, $p < 0.05$, $\eta_p^2 = 0.25$), which was also significant if age and IQ were included as covariates ($F(1,18) = 6.78$, $p < 0.05$, $\eta_p^2 = 0.21$). Simple effects analyses with age and IQ as covariates demonstrated that, regardless of congruency, the control group produced more error plane variance when observing BM (adjusted mean(SEM) = 408.47(95.90)) compared to CV motion (377.15(91.20)) and this difference was

marginally significant ($F(1,18) = 4.07$, $p = 0.06$). In contrast, for the ASC group, there was no significant difference ($F(1,18) = 2.85$, $p = 0.11$) between error plane variance produced when observing BM (339.56(105.07)) compared to CV (368.27(99.92)) motion.

This analysis revealed no other main effects or interactions (all $p > 0.05$). Note that the lack of a main effect of group demonstrates that, across conditions, both groups demonstrated comparable levels of error plane variance whilst performing horizontal arm movements[5].

6.3.2 Interference Effect generated by biological motion

The mixed model 2 (Group: ASC, control) x 3 (Actor form: virtual human agent, virtual robot agent, real human) x 2 (Congruency: congruent, incongruent) ANOVA (excluding CV conditions) revealed a trend toward an interaction between **Actor form, Group and Congruency** ($F(2,40) = 2.80$, $p = 0.07$, $\eta_p^2 = 0.12$). However, this interaction was not significant, there were no other main effects or interactions (Figure 6.6). The interaction between Actor form, Group and Congruency reached significance when age and full-scale IQ were included as covariates ($F(2,36) = 3.21$, $p = 0.05$, $\eta_p^2 = 0.15$). Since incongruent movements were expected to generate greater error plane variance than congruent movements, we conducted 1-tailed simple effects analyses with age and IQ as covariates. These demonstrated that the control group produced significantly more error plane variance when observing incongruent (adjusted mean(SEM) =415.22(96.16)) compared to congruent (350.03(77.57); $F(1,18) = 3.27$, $p < 0.05$) movements conducted by the virtual human agent, and more variance when observing incongruent (491.04(122.41)) compared to congruent (416.25(122.41)) real human movements, although this trend did not reach significance ($F(1,18) = 2.53$, $p = 0.06$). In contrast, the

[5] Variance scores significantly deviated from the normal distribution (Shapiro-Wilk $W < 0.05$). To ensure the effects reported above were robust against violations of normality, data was log transformed and the 2x2x2x2 ANOVA rerun (as above with factors Group (ASC, control); Actor Form (virtual human agent, virtual robot agent), Actor Motion (BM, CV) and movement Congruency (congruent, incongruent) and age and IQ as covariates). This reanalysis also showed a significant interaction between **Group x Actor Form x Congruency** ($F(1,18) = 4.92$, $p < 0.05$). In addition there was a marginally significant **Group x Actor form x Actor Motion** interaction ($F(1,18) = 4.38$, $p = 0.051$). Differing from the above results, there was no significant **Actor Motion x Group interaction** ($F(1,18) = 2.35$, $p = 0.14$). Simple effects analyses showed that the **Group x Actor form x Actor Motion interaction,** which was not found in the above analysis, was driven by greater variability in movements when observing CV versus MJ movements conducted by the robot agent (adjusted log transformed mean BM (SEM) = 2.41 (0.11), CV = 2.47 (0.10); $F(1,18) = 6.02$, $p < 0.05$) but not human agent (BM = 2.47(0.10), CV = 2.47 (0.10); $F(1,18) = 0.01$, $p = 0.93$) for the ASC group but not for the control group (Robot agent BM (2.46 (0.10)) versus CV (2.43 (0.09) $F(1,18) = 2.17$, $p = 0.16$); Human agent BM (2.43(0.09)) versus CV (2.43(0.09); $F(1,18) = 0.05$, $p = 0.82$).

difference between the incongruent (411.73(105.84)) and congruent (456.90(123.54)) conditions for virtual robot agent movements was non-significant ($F(1,18) = 0.68$, $p > 0.05$).

For the ASC group the difference between incongruent and congruent conditions was non-significant for virtual human agent movements (incongruent = 331.13(105.35)), congruent = 358.36(84.99); $F(1,18) = 0.47$ $p > 0.05$) and virtual robot agent movements (incongruent = 339.13(115.95), congruent = 329.62(135.34); $F(1,18) = 0.25$, $p > 0.05$). Individuals with ASC demonstrated a trend in the opposite direction (variance for congruent movements greater than variance for incongruent movements) for real human observation (incongruent = 292.25(140.80), congruent = 355.01(134.11); $F(1,18) = 1.48$, $p = 0.06$)[6].

To further investigate the Group x Actor form x Congruency interaction the Interference Effect was calculated for virtual human agent BM, virtual robot agent BM and real human. The Interference Effect figures were entered into a 3x2 ANOVA with factors actor form and group and with age and IQ as covariates. The ANOVA demonstrated a significant interaction between **Group x Actor form** ($F(2,36) = 3.22$, $p = 0.05$, $\eta_p^2 = 0.15$). Simple effects analyses demonstrated that, compared to the control group, the ASC group exhibited a reduced Interference Effect of real human actions and this difference was marginally significant ($F(1.18) = 3.88$, $p = 0.065$). No other simple effects analyses were significant (all $p > 0.06$).

There were no significant correlations between Interference Effect scores and ADOS total score or scores on the ADOS reciprocal social interaction or communication subscales (all $p > 0.05$).

[6] To ensure these effects were robust against violations of normality data was log transformed and the 2x3x2 ANOVA analysis rerun. This reanalysis also showed a significant interaction between Group x Actor form ($F(2,34) = 3.18$, $p = 0.05$, $\eta_p^2 = 0.15$).

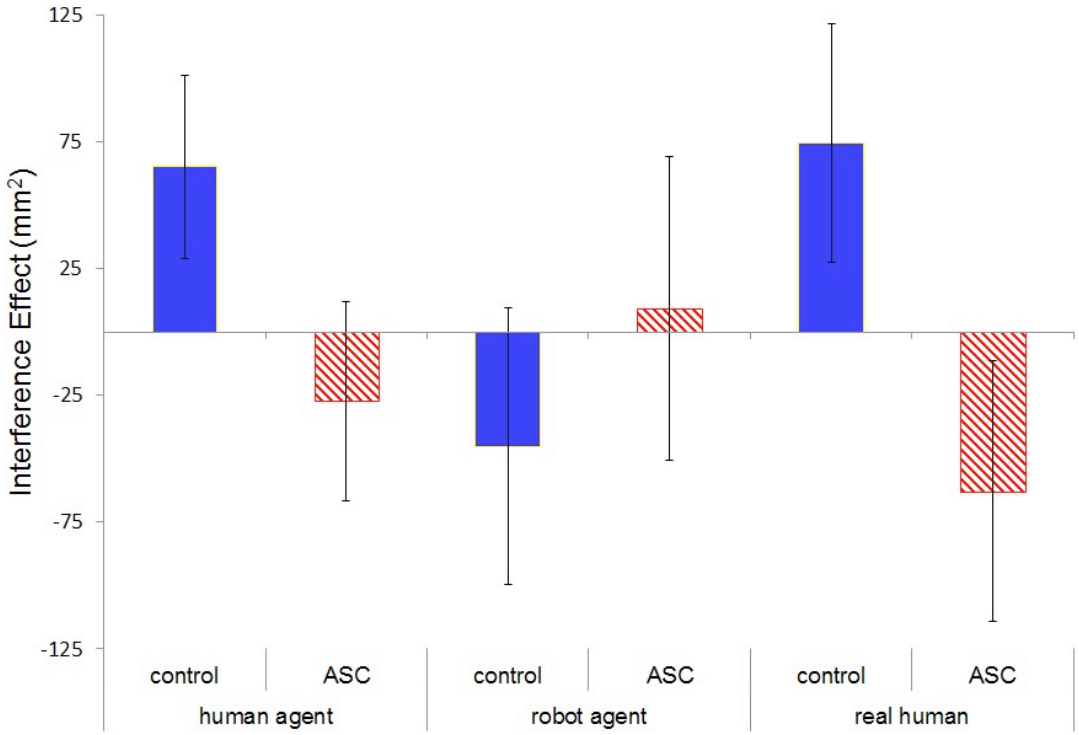

Figure 6.6. Adjusted mean (+/-SEM) Interference Effect (incongruent minus congruent variance) is displayed. The control group exhibit a significant Interference Effect when observing human agent biological motion (BM) movements and a marginally significant Effect for real human movements but no Interference Effect for robot agent BM movements. The ASC group did not exhibit a significant Interference Effect for human agent, robot agent or real human movements.

6.4 DISCUSSION

Individuals with ASC and control participants executed horizontal sinusoidal arm movements whilst observing congruent (horizontal) and incongruent (vertical) movements conducted by a 3D virtual reality agent with either human or robot form, which moved with either biological motion (BM) or at a constant velocity (CV). Participants also executed the same arm movements whilst observing a real human making congruent or incongruent arm movements. Finger-tip position was recorded and average variability in the error (vertical) plane was the dependent variable. Results from control participants replicated the previously reported effect of actor form (Kilner et al., 2003): control participants exhibited a significant Interference Effect for observation of the virtual human agent and the real human but not for the virtual robot agent. In contrast, individuals with ASC did not exhibit a significant Interference Effect for either the virtual human agent, real human or virtual robot agent. There was no effect of actor motion (BM vs CV) on the Interference Effect for either group. This is the first demonstration that, whereas control adults exhibit a greater Interference Effect in response to human form compared to robot form actors, individuals with ASC do not show this Interference Effect.

6.4.1 Interference effect in healthy controls

Previous Interference Effect studies have not investigated separable effects of form and motion using 3D stimuli. To enable the manipulation of actor form (human versus robot) and actor motion (BM versus CV) whilst keeping all other factors constant, the current study used 3D virtual agents. As expected, we found that control participants exhibit a greater Interference Effect in response to human form compared to robot form actors. The lack of a difference in the Interference Effect between BM and CV conditions for the control group was unexpected as it goes against previous findings of greater Interference Effects for BM compared to CV movements (Kilner et al., 2007a). Furthermore, this finding contrasts with the results reported in **Chapter 3** which showed that movements with BM but not CV kinematics are automatically motorically simulated. However, as Kilner and colleagues (2007a) suggest, this effect may depend on experience and prior expectations of how a stimulus should move. Although Kilner and colleagues (2007a) found a significant difference in the magnitude of the Interference Effect mediated by a human video stimulus that moved with MJ BM compared to CV, they found no difference between MJ and CV ball stimuli. The authors argue that, whereas participants were unlikely to have previously seen videos of humans moving with CV, through exposure to computer animations, participants may be equally familiar with CV and MJ ball movements. It might therefore be equally possible to simulate the movement of the MJ and CV ball and both may create an Interference Effect. This explanation is of relevance to the current study. Both **Chapter 3** and the study by Kilner and colleagues (2007a) reported differences between BM and CV movements using video stimuli. In contrast the current study employed computer-animated virtual agents. Our participants may have had previous sensorimotor experience with (for example) computer game virtual agents moving with biological motion or CV, such previously acquired sensorimotor experience could result in an Interference Effect for CV movements conducted by virtual agents.

6.4.2 Interference effect in ASC

The current study was the first to investigate the modulation of the Interference Effect according to human and robot actor form and BM and CV in ASC. As with control participants, in our ASC group there was no modulation of the Interference Effect according to motion. However, whereas control adults exhibited a greater Interference Effect in response to human form compared to robot form, individuals with ASC did not exhibit this modulatory effect of form.

6.4.2.1 Modulation of Interference Effect according to motion

Although no modulation of the Interference Effect by motion type (BM vs CV) was observed for either

the control or ASC group, the current experiment demonstrated a marginally significant effect on movement variance by observed motion regardless of action congruency. In line with previous work (Bouquet et al., 2007; Gowen et al., 2008) the BM condition, compared to the CV condition, resulted in more variable arm movements for control participants. In contrast, there was no effect of motion type for individuals with ASC. Similarly, Gowen and colleagues (2008) reported that, regardless of congruency, control participants made more variable movements when observing a dot that moved with BM compared to a dot moving with CV; individuals with ASC did not exhibit this pattern. For the current experiment such a finding is surprising since, unlike the stimuli employed by Gowen and colleagues (2008), our BM and CV movements followed identical trajectories and differed only in velocity profile. In **Chapter 5: Experiment 1** participants were required to differentiate an animation that moved with MJ BM and the same animation degraded by CV perturbations. Relative to control participants, adults with ASC required a greater CV perturbation in order to successfully differentiate the two animations. This reduced sensitivity to the difference between BM and CV may relate to the absence of an effect of motion type on arm movement variance that we observe for individuals with ASC in the current study.

6.4.2.2 Modulation of Interference Effect according to form

Whereas control adults exhibited a greater Interference Effect in response to human form compared to robot form, individuals with ASC did not exhibit this modulatory effect of human form. This result is in line with Pierno and colleagues' (2008) finding that visuomotor priming was greater for control children relative to children with ASC following observation of human actions. However, Pierno and colleagues (2008) also demonstrated that visuomotor priming was greater for children with ASC following observation of robot actions. Based on these data one may expect a greater Interference Effect for robot action for the ASC group relative to the control group. However, we found no evidence of a greater Interference Effect for robot action for the ASC group. Interestingly, the results from the current study demonstrated that the ASC group showed no significant difference in the way they responded to either of the human form conditions and the way the control group responded to the robot condition (Figure 6.6). Thus, this suggests that the way the ASC group responded to human actions is similar to the way control participants responded to robotic actions. Differences in the predictability and repeatability of the movement stimuli could explain the discrepancy between the current findings and those of Pierno and colleagues (2008). The reach-to-grasp actions performed by Pierno and colleagues' (2008) robotic actor followed smooth humanlike motion but the duration, average velocity and time to grip aperture were identical in every trial, making the robot movement more predictable than the human movements.

We found an interaction between group and actor form, which was driven by a higher Interference Effect from observing human compared with robot actions in the control group but not in the ASC group. It should be noted that there were no main effects of group in either of our analyses (Figure 6.5, Figure 6.6), suggesting that across the various conditions individuals with ASC and controls exhibited comparable levels of error plane variance. Coupled with the lack of a difference between the groups in the number of trials that had to be discarded from the analysis (Table 6), this suggests that our participants with ASC understood the task instructions and performed the task in a similar way to control participants.

The lack of significant Interference Effects for individuals with ASC contrasts with previous studies (Bird et al., 2007; Gowen et al., 2008; Press et al., 2010). It is possible that the discrepancy between the current and previous studies is a result of the different action preparation affordances of the paradigms employed. In previous Interference Effect paradigms (Bird et al., 2007; Gowen et al., 2008; Press et al., 2010) participants were instructed to make one of two pre-specified actions upon presentation of a cue. In this situation the action not currently executed might be prepared for its imminent execution, and so the motor representation of the incongruent action will be active. Hence, a weak cortical motor response to action observation may be sufficient for motor activity to reach the motor execution threshold and be expressed as a typical Interference Effect. In contrast, in the current paradigm the participant was only ever instructed to execute one action type; therefore, action preparation for the incongruent action is unlikely.

The current results can be interpreted in a number of ways. Firstly, the lack of an Interference Effect in ASC is in line with the broken MNS hypothesis of ASC (Bernier et al., 2007; Dapretto et al., 2006; Oberman et al., 2005; Théoret et al., 2005; Williams et al., 2006). As demonstrated in **Chapter 3** MNS activations during the observation of non-goal directed actions comprise automatic motoric simulations. It is this automatic motor simulation that is thought to interfere with action control (Blakemore and Frith, 2005). Following this logic, it maybe that the atypical Interference Effects here observed are a consequence of atypical MNS function in ASC. However, as discussed in the introduction to this thesis, it is important to consider non-imitation related components of a task when evaluating imitation (or Interference Effect) impairments. Correspondingly, an alternatively explanation for the lack of Interference Effect is that the social modulation of imitation is atypical in ASC. That is, human form acts as a 'pro-social prime' for typical individuals but not for individuals with ASC. Such pro-social priming could result in elevated imitation levels (Leighton et al., 2010; Cook and Bird, 2011) for the control group alone. **Chapter 7** investigates whether the social modulation of imitation is atypical in

ASC.

6.4.3 Conclusion

This Chapter demonstrated that observing incongruent arm movements generated by actors with human form (virtual human agent, real human) results in an Interference Effect in ongoing executed actions in control participants. This effect was not seen for control participants when they observed incongruent movements conducted by a virtual agent with robot form. In contrast, individuals with ASC differed from controls in that they showed no Interference Effect when observing incongruent human or robot movements.

6.4.3.1 What next

A possible explanation, for the results presented in this Chapter, is that the social modulation of imitation is atypical in ASC hence the human form acts as a 'pro-social prime', elevating imitation levels for typical individuals but not for individuals with ASC. **Chapter 7** investigates whether the social modulation of imitation is indeed atypical in adults with ASC.

Chapter 7. Atypical Social Modulation of Imitation in Autism Spectrum Conditions

Chapter 6 *demonstrated atypical imitation (as indexed by the Interference Effect) in ASC: unlike control participants, individuals with ASC showed no Interference Effect when observing incongruent human or robot movements. A possible explanation is that human form acts as a 'pro-social prime', elevating imitation levels in typical individuals but not for individuals with ASC.* ***Chapter 7*** *investigates whether the social modulation of imitation is indeed atypical in adults with ASC. We subliminally primed individuals with ASC and age- and IQ-matched controls with either a pro- or non- social attitude. Following priming, an automatic imitation paradigm was used to acquire an index of imitation. Whereas imitation levels were higher for pro-socially primed relative to non-socially primed control participants, there was no difference between pro- and non- socially primed individuals with ASC. We conclude that adults with ASC demonstrate atypical social modulation of imitation. This finding may explain difficulties with imitation revealed by paradigms such as that employed in* ***Chapter 7****. Furthermore, given the importance of imitation in social interaction, we speculate that difficulties with the modulation of imitation may contribute to the social problems characteristic of ASC.*

7.1 INTRODUCTION

Imitation is intricately linked with social interaction. Being imitated increases rapport (Chartrand and Bargh, 1999), altruistic behavior (van Baaren et al., 2004) and trust (Bailenson and Yee, 2005). Furthermore, individuals imitate more when in possession of a positive social attitude (Lakin and Chartrand, 2003; Leighton, Bird, Orsini, and Heyes, 2010). For example, subliminal pro-social, compared to non-social, priming results in significantly higher levels of imitation (Cook and Bird, 2011; Leighton et al., 2010). Thus, imitation is bi-directionally associated with good social interaction and is therefore a key component in building social relationships with others. Crucially, successful social interaction relies on appropriate modulation of the degree of imitation according to the demands of the social situation (Lakin and Chartrand, 2003).

ASC are characterised by impairments in social interaction, language, and communication (American Psychiatric Association, 1994). A number of studies have demonstrated reduced imitation and Mirror Neuron System (MNS) activity in individuals with ASC compared to control participants (Williams, Whiten, and Singh, 2004). The MNS is a network of brain areas active when an individual both executes

and observes an action (Catmur et al., 2008; Iacoboni et al., 1999) and has been argued to comprise the neural mechanism that underpins imitation (Catmur, Walsh, and Heyes, 2007; Heiser, Iacoboni, Maeda, Marcus, and Mazziotta, 2003; Iacoboni et al., 1999). It has been hypothesised that a 'broken MNS' and corresponding imitation impairment is a core feature of ASC (Williams, Whiten, Suddendorf, and Perrett, 2001). However, experimental evidence both supports (Avikainen et al., 2003; Dapretto et al., 2006; McIntosh et al., 2006; Oberman et al., 2005) and opposes (Bird et al., 2007; Dinstein et al., 2010; Gowen et al., 2008; Hamilton et al., 2007; Leighton et al., 2008; Press et al., 2010; Spengler et al., 2010a) the presence of an imitation impairment in ASC. Furthermore, clinical observations of high levels of echolalia (automatic repetition of speech patterns) and echopraxia (automatic imitation of observed actions) in individuals with ASC (Rutter, 1974; Russell, 1997; Williams et al., 2004) are incompatible with an imitation deficit in ASC, and instead suggest problems with inhibition of imitation.

In response to the inconsistent literature it has been suggested that, rather than an imitation deficit *per se*, individuals with ASC may have difficulties with appropriately modulating levels of imitation (Hamilton, 2008; Spengler et al., 2010a; Kana et al., 2011). Although this hypothesis has not previously been tested, it is consistent with studies of individuals with ASC that report hypoactivity in parts of the brain thought to be involved in the modulation of imitation (Castelli, Happé, Frith, and Frith, 2000; Spengler et al., 2010a). Given the importance of appropriate levels of imitation for positive social interaction (Lakin and Chartrand, 2003) this hypothesis may go some way towards explaining difficulties with social interaction in individuals with ASC.

The present study used a behavioural measure of imitation, as opposed to a measure of MNS activity, to directly test the hypothesis that the social modulation of imitation is atypical in individuals with ASC. High-functioning adults with ASC and age and IQ-matched controls first completed a previously-validated (Bargh and Chartrand, 2000; Leighton et al., 2010; Cook and Bird, 2011) technique to unconsciously prime either a pro-social, or non-social attitude. Participants were asked to 'unscramble' re-arranged sentences, a proportion of which were related to either pro-social attitudes ("she is my friend") or non-social attitudes ("he is often alone"). Following this subliminal priming, participants completed an automatic imitation task. We predicted that, as in previous studies (Cook and Bird, 2011; Leighton et al., 2010), pro-socially primed control participants would show increased levels of imitation relative to non-socially primed control participants. In line with the impaired modulation of imitation in ASC hypothesis, we predicted no significant difference in levels of imitation for pro-socially and non-socially primed ASC groups.

7.2 METHODS

7.2.1 Participants

19 adults (mean 40.9 years) with ASC and 22 age- and IQ-matched control individuals participated in this experiment (see Table 7 for further details). All participants had normal or corrected-to-normal vision and were screened for exclusion criteria (dyslexia, epilepsy, and any other neurological or psychiatric conditions) prior to taking part. Participants with ASC had a written diagnosis from an independent clinician, which they received no more than 5 years before taking part in this experiment, and all participants (save one for whom data was not available) scored above threshold for Autism Spectrum Disorder on the ADOS (Lord et al., 1989). We were unable to distinguish between participants with AS and Autism, as we did not have information about early development of language in our participants. Participants were randomly assigned to either the Pro- or Non-social Prime Group. ANOVAs demonstrated no main effect of, or interaction between, Prime Group and Diagnostic Group on age or full scale IQ (all ps > 0.1). The two ASC groups did not differ with respect to ADOS score (non-social mean (SEM) = 10.00(1.00), pro-social mean (SEM) = 9.88(1.01), $t(16) = 0.08$, $p = 0.93$), age (non-social mean (SEM) = 41.30(3.84), pro-social mean (SEM) = 40.56 (4.50), $t(17) = 0.13$, $p = 0.90$), full scale IQ (non-social mean (SEM) = 114.44(4.99), pro-social mean (SEM) = 111.44(6.11), $t(16) = 0.38$, $p = 0.70$), verbal IQ (non-social mean (SEM) = 116.22(3.33), pro-social mean (SEM) = 112.00(5.92), $t(16) = 0.62$, $p = 0.54$) or performance IQ (non-social mean (SEM) = 108.89(6.57), pro-social mean (SEM) = 108.78(6.48), $t(16) = 0.12$, $p = 0.99$). Informed consent was obtained from all participants. The study was approved by the local ethics committee, and performed in accordance with the 1964 Declaration of Helsinki.

	Non-social		**Pro-social**	
	ASC	Control	ASC	Control
Participants per group	10	11	9	11
Mean age (SEM)	41.30 (3.84)	35.27 (5.29)	40.56 (4.50)	34.55 (4.72)
Mean full scale IQ (SEM)	114.44 (4.99) (N = 9)	119.43 (4.11) (N = 7)	111.44 (6.11)	117.44 (7.73) (N = 10)
Mean ADOS total (SEM)	10.0 (1.00)	n/a	9.88 (1.01) (N = 9)	n/a

Table 7 Participant information. Age, full scale IQ, and ADOS scores. Note that the ADOS total cut-off value for a diagnosis of ASC is 7. N denotes the number of available data sets.

7.2.2 Priming Task

Participants were asked to select, in order, 4 words from 5 displayed on a computer screen to make a grammatically correct sentence (adapted from Leighton et al., 2010). 24 out of 36 total trials contained a word semantically related to the target attitude (pro-social or non-social; 0). 12 of the sentences were neutral (e.g. "the car was small"). This corresponds to a 2/3 saturation level, which has previously been shown to be effective for priming target attitudes without provoking conscious awareness of this target attitude (R. Van Baaren, personal communication). Priming words were generated in a pilot session by an independent group of participants. Although not identical they overlapped with those employed by Leighton et al. (2010).

Words were arranged vertically down the screen and presented in Arial, font size 24. The colour of the words (red, green, black or blue) varied randomly over trials in order to suggest to the participant that the aim of the task was to investigate the effect of colour on word processing and hence distract from the priming nature of the task. Priming task duration was approximately 15 mins.

Pro-social				
		Sentence		*Distracter*
she	is	a	friend	over
he	is	very	talkative	purchased
he	likes	being	sociable	battery
Jack	is	now	married	weekend
often	she	is	outgoing	travel
the	beach	is	crowded	onion
Tom	is	normally	cooperative	adjacent
James	was	naturally	agreeable	geography
she	loves	her	family	tendency
Clare	is	very	friendly	apple
he	thinks	about	others	surfed
Jill	enjoys	group	work	scarf
the	curtains	were	pink	team
apples	are	english	fruits	chatty
printers	use	ink	cartridges	gathering
the	flag	was	multicoloured	together
the	sky	is	blue	unity
the	moon	was	full	sharing
cars	can	be	silver	joined
bananas	grow	in	Jamaica	interactions
the	water	flowed	fast	society
cotton	wool	is	soft	meeting
Champagne	is	very	expensive	community
cacti	grow	in	deserts	popularity
Non-social				
she	is	a	rebel	over
he	is	very	selfish	purchased
he	likes	being	alone	battery
Jack	is	now	single	weekend

often	she	is	withdrawn	travel
the	beach	is	secluded	onion
Tom	is	normally	uncooperative	adjacent
James	was	naturally	disagreeable	geography
she	loves	her	independence	tendency
Clare	is	very	private	apple
he	thinks	about	himself	surfed
Jill	enjoys	independent	work	scarf
the	curtains	were	pink	individual
apples	are	english	fruits	think
printers	use	ink	cartridges	solitary
the	flag	was	multicoloured	solo
the	sky	is	blue	detached
the	moon	was	full	lone
cars	can	be	silver	separate
bananas	grow	in	Jamaica	one
the	water	flowed	fast	isolated
cotton	wool	is	soft	personal
Champagne	is	very	expensive	self
cacti	grow	in	deserts	unpopular
		Neutral		
the	pans	are	dirty	pillow
it	snowed	on	Tuesday	puzzle
the	road	was	icy	wooden
the	bread	was	dry	phase
Italy	is	in	Europe	hill
the	blanket	was	woollen	tree
the	balcony	was	high	radio
trains	are	often	dirty	test
the	zoo	was	small	cars
the	fire	spread	quickly	bench
the	circus	came	here	open
the	car	went	fast	spoon

Table 7.1 Pro-social, non-social and neutral sentences and distracter words employed in the Priming Task. Words semantically related to the target attitude are highlighted in grey.

7.2.3 Automatic Imitation Task

The Automatic Imitation Task was based on that used by Iacoboni and colleagues (1999) and Brass, Bekkering, Wohlschläger and Prinz (2000) (see also Cook and Bird, 2011). Videos (6° visual angle vertically x 9° horizontally, 3000ms duration) of a human hand were presented in vertical orientation on a computer screen at a distance of approximately 57cm. The participant rested their hand in a horizontal orientation on the computer keyboard, with their index finger holding down the 'V' key and their middle finger holding down the 'B' key. The orthogonality of the stimulus and participant hands allow automatic imitation to be isolated from spatial compatibility. The participant was required to lift and replace their index or middle finger upon the appearance of a 1 or a 2, respectively. 50% of trials comprised a five-frame video clip of a concurrent lifting action that was either compatible (e.g. the participant was required to make an index finger response and observed an index finger action) or incompatible (the participant was required to make an index finger response and observed a middle-

finger action) with the required movement (Figure 7). Imitation was calculated as the difference in RT on congruent and incongruent trials. 50% of trials comprised a three-frame 'baseline' video clip in which the fingers remained static and either the compatible or incompatible finger acquired a green mask; enabling acquisition of baseline RTs for index and middle finger movements independent of imitation. 120 trials were presented in pseudo-random order. There were no breaks during the task, the duration of which was approximately 15 minutes.

7.2.3.1 Automatic imitation videos

Videos comprised five frames (Figure 7**a**). The first was a photograph of a hand at rest against a blue worktop. This frame was displayed for a variable interval with range 800-2400 ms and acted as a warning signal. The second frame was a photograph of the index or middle finger 1/3rd of the way through a lifting action and a number 1 or 2. The third was a photograph of the same finger 2/3 of the way through a lifting action. These frames were displayed for 34 ms. The fourth frame was a photograph of the finger in the fully lifted position, which was displayed for 500 ms. These display durations ensured the appearance of a short video clip of a finger being lifted with the concurrent appearance of a number. The fifth frame was a blank screen. This frame remained on screen until the duration of the trial had reached 3000 ms and until the participant had returned both fingers to the letters V and B on the keyboard.

7.2.3.2 Baseline videos

Baseline videos comprised three frames (Figure 7**b**). The first was a photograph of a hand at rest, displayed for a variable interval with range 800-2400ms. For the second frame the finger in the photograph was coloured green and a number 1 or 2 was added to the image. This frame was displayed for 568 ms. The third frame was a blank screen the same blue as the background in frames 1 and 2. This frame remained on screen until the duration of the trial had reached 3000 ms and until the participant had returned both fingers to the response keys, hence both Automatic Imitation and Control Trial types were of the same duration.

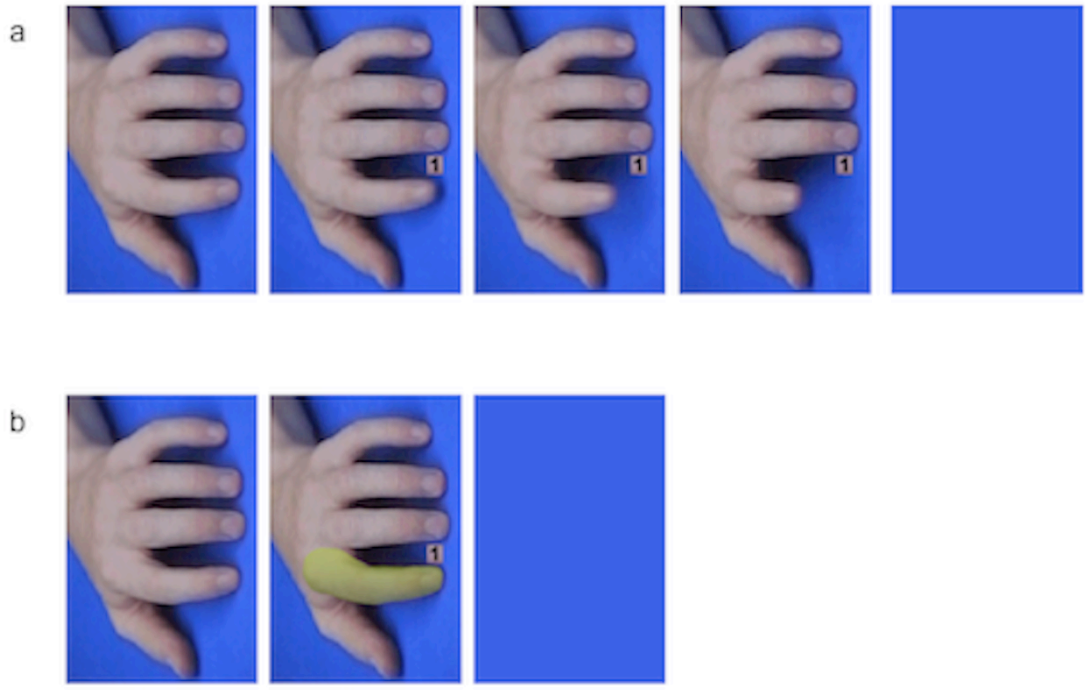

Figure 7. Video stimuli. *a.* The five-frame video clip. Frame one was displayed for a variable interval (range: 800–2400ms). Frames two and three were displayed for 34ms each and frame four for 500ms. These display durations ensured the appearance of a short video clip. The fifth frame (a blank screen) remained on screen until the duration of the trial had reached 3000ms and the participant had returned both fingers to the letters V and B on the keyboard. *b.* The three frames of a 'baseline' trial. Frame one was displayed for a variable interval. Frame two was displayed for 568ms and the final frame was displayed until the duration of the trial had reached 3000ms and the participant had returned both fingers to the letters V and B.

7.2.4 Testing Procedure:

Participants were informed that they would be asked to take part in two separate experiments, one on the effect of colour on word processing and the other on responses to numbers. Prior to testing all participants were read standardized instructions and completed 5 example trials of the Scrambled Sentence Priming task. Participants were shown an example of each trial type from the Automatic Imitation Task. All participants were also presented with a written version of the instructions. For both the pro- and non-social priming tasks, participants were told that they would see five words on the screen and that they should use four out of the five words to make a grammatically-correct sentence. The subjects were instructed to select the words by clicking on each one with the computer mouse. They were told that once they had clicked on the fourth and final word in their created sentence, a new screen would appear with five different words. For the Imitation and Effector Priming Control tasks participants were told to place the index finger of their right hand on the letter 'V' on the computer keyboard and the middle finger of their right hand on the letter 'B' on the keyboard. Participants were

told to lift their index finger if a number 1 appeared on the screen and lift their middle finger if a number 2 appeared on the screen. Before the Imitation and Effector Priming Control tasks commenced participants conducted a training session. The training program required participants to make 5 correct consecutive responses in order for them to continue onto the experimental version of the task. The probability of making 5 correct consecutive responses by chance is < 0.05, therefore the training task ensured that participants could perform the task before data collection began.

Following the computer tasks, participants were asked to complete a debriefing questionnaire designed to ascertain whether participants had guessed the purpose of the experiment (see Leighton et al. 2010 and Cook and Bird, 2011). This questionnaire included the following questions: "What do you think the purpose of this experiment was? What do you think this experiment was trying to study? Did you think that any of the tasks were related in any way? If yes, in what way? Did anything you did on one task affect anything you did in another task? If yes, then how did it affect you? When you were arranging the words, did you notice anything unusual about the words? Did you notice a pattern or theme to the words? Did you have a particular goal or strategy when arranging the words?"

7.2.5 Data analysis:

7.2.5.1 Priming Task

For all participants all of the sentences produced in the Priming task were scored. A grammatically incorrect sentence yielded an error score of 1. Error scores for all 32 sentences were then summed to give an error score across all sentences.

7.2.5.2 Automatic Imitation Task

For the Imitation and Effector Priming Control tasks error-trials in which the participant lifted the incorrect finger were removed from the analysis. RTs were filtered such that those less than 150 ms were excluded under the assumption that they were expectancy errors and those longer that 2000 ms were excluded under the assumption that they reflected a lapse in attention. Reported p-values are two-tailed unless otherwise stated.

7.3 RESULTS

7.3.1 Priming Task

Errors were infrequent on the Priming Task (mean error rate was l0%). To test whether either Diagnostic or Prime Group significantly affected the number of errors we employed a 2x2 ANOVA with between-subjects factors Diagnostic Group and Prime Group. There was no main effect of

Diagnostic Group or Prime Group and no interaction (all $F(1,37) < 1$, all $p > 0.40$; see 0 for mean and SEM values).

7.3.2 Automatic Imitation Task

Paired-samples t-tests demonstrated that all four groups exhibited significant imitation, i.e. RTs on Compatible trials were significantly faster than on Incompatible trials (all ps < 0.01, see 0). A 2x2 ANOVA on the magnitude of Automatic Imitation shown on this task (RT on Incompatible Trials minus RT on Compatible Trials, see Figure 7.1) showed an interaction between Diagnostic- (ASC, Control) and Prime Group (Non-social, Pro-social), $F(1,37) = 2.92$, $p = 0.048$ (1-tailed), $\eta_p^2 = 0.07$). Simple effects analyses demonstrated that the effect of social priming was clearly shown in the Control Group: participants who were unconsciously primed with a pro-social attitude imitated more (mean (SEM) = 82.51ms (22.20)) than those primed with a non-social attitude (35.42ms (10.18); $F(1,37)= 5.87$, $p = 0.02$ $\eta_p^2 = 0.14$). However, the ASC Group showed no such social modulation of their automatic imitative behaviour: the degree of imitation shown by the pro-socially primed participants with ASC (34.83ms (8.76)) was not different from that shown by the non-socially primed participants with ASC (36.61ms (8.01); $F(1,37) = 0.007$, $p = 0.93$, $\eta_p^2 = 0.00$). In addition, simple effects analysis showed that the degree of imitation shown by the Control Pro-Social Group was significantly greater than that shown by the ASC Pro-social Group ($F(1,37) = 5.42$, $p = 0.03$, $\eta_p^2 = 0.13$). In contrast, the Control and ASC Non-social Groups did not differ ($F(1,37) = 0.004$, $p = 0.95$, $\eta_p^2 = 0.00$)[7].

There was no significant correlation between ADOS total score and automatic imitation values (all $P > 0.05$).

[7] Shapiro-Wilk test showed that the distribution of automatic imitation scores for the Control Group deviated from the normal distribution ($W(22) = 0.78$, $p < 0.001$) . The Shapiro-Wilk test was not significant for the ASC Group ($W(19) = 0.95$, $p = 0.47$). To ensure the effects reported above were robust against violations of normality, data was square root transformed and the ANOVA rerun. This reanalysis also showed a significant interaction between Prime- and Diagnostic Group ($F(1,37) = 2.82$, $p = 0.05$) hence the square root transformation did not change the pattern of significance.

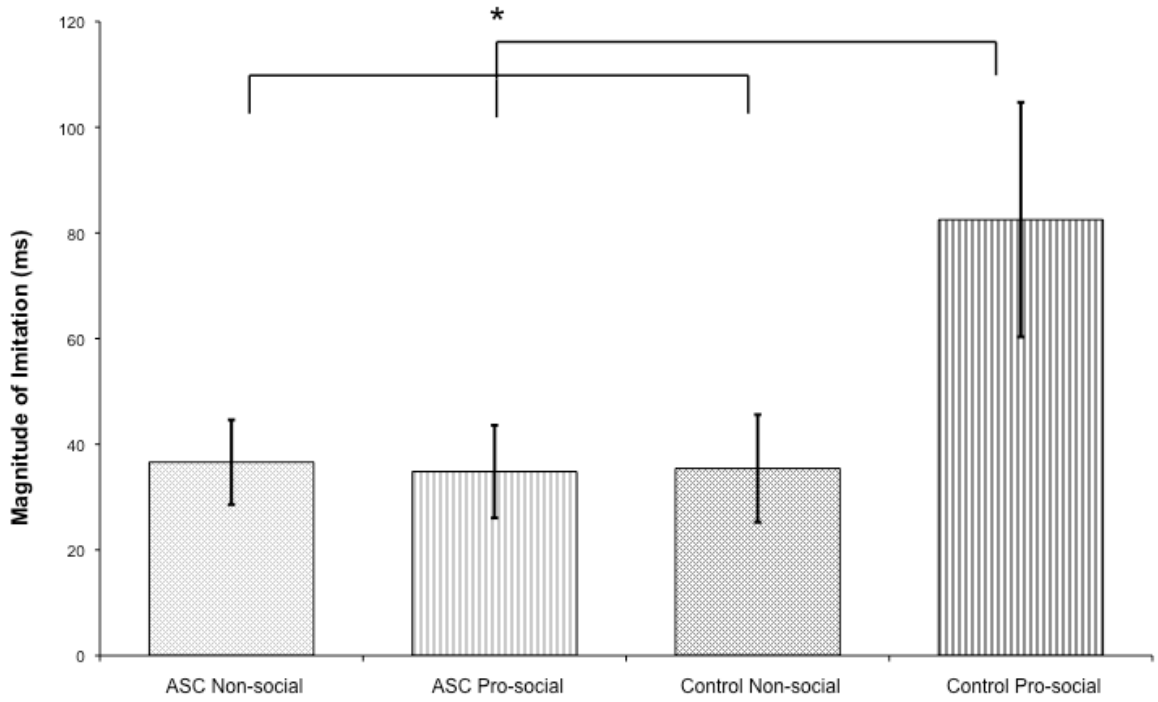

Figure 7.1. Pro-socially primed participants in the Control Group imitated more than non-socially primed participants. Participants with ASC showed no such social modulation of imitation: the degree of imitation shown by the ASC Pro-social Group did not differ from that shown by the ASC Non-social Group. Furthermore the Control Pro-Social Group showed significantly greater imitation than the ASC Pro-social Group. In contrast, the Control and ASC Non-social Groups did not differ. * indicates $p < 0.05$.

Previous research has shown that the magnitude of imitation is modulated by mean RT (Press, Bird, Flach, and Heyes, 2005). A 2x2 ANOVA on baseline trial RT (mean RT across all baseline trials - i.e. trials in which the finger remained static and acquired a green mask) showed no significant effects of Prime Group, Diagnostic Group nor interaction (all ps > 0.1, see 0). A 2x2 ANOVA on incongruent (e.g. participant lifted index finder and middle finger acquired green mask) minus congruent (e.g. participant lifted index finder and index finger acquired green mask) baseline trial RTs showed no significant effects of Prime Group, Diagnostic Group nor interaction (all ps > 0.1). Therefore we are confident that the interaction between Prime Group and Diagnostic Group on the magnitude of imitation is not a product of mean RT differences.

	Non-social		**Pro-social**	
	ASC	Control	ASC	Control
Mean priming task errors (SEM)	5.20 (2.90)	3.64 (1.16)	2.70 (1.05)	2.91 (0.93)
Mean incompatible RT (SEM)	568.03 (38.48)	511.19 (28.83)	523.09 (30.85)	591.92 (43.30)
Mean compatible RT (SEM)	531.43 (35.88)	475.77 (22.64)	488.26 (29.39)	509.41 (30.57)
Mean incompatible baseline RT (SEM)	592.68 (43.88)	541.58 (31.67)	529.77 (29.56)	582.21 (38.77)
Mean compatible baseli RT (SEM)	535.37 (29.16)	495.97 (21.59)	526.40 (31.81)	534.80 (35.53)

Table 7.2 Priming task errors and compatible and incompatible RT (ms) data for the imitation task and the baseline trials.

7.3.3 Debriefing questionnaire

Examination of the debriefing questionnaire data indicated that no participant correctly guessed the purpose of either the Priming or Automatic Imitation task. Furthermore, no participant correctly identified a link between the studies or a theme among the words presented in the Priming task. Therefore, we can conclude that no participant was aware of the type of priming they had received or that the purpose of the study was to examine imitation and its relationship with social attitudes.

7.4 DISCUSSION

In agreement with previous studies (Cook and Bird, 2011; Leighton et al., 2010) we found that control participants primed with words promoting pro-social attitudes (e.g. *friend, crowded, team, talkative*) showed significantly higher levels of imitation than control participants primed with words promoting non-social attitudes (e.g. *himself, solo, one, private*). There was no significant difference between imitation levels shown by individuals with ASC primed with pro-social words compared with those primed with non-social words. These results comprise the first experimental evidence of atypical social modulation of imitation in individuals with ASC. The ability to appropriately modulate levels of imitation to suit the social situation is important in social interactions (Lakin and Chartrand, 2003) hence we speculate that difficulties with the modulation of imitation may contribute to the social problems characteristic of ASC. In addition, this finding suggests that future studies of imitation and MNS function in ASC should consider the extent to which the task includes cues that may act as unconscious social primes. Efforts should be made to either eliminate these cues (and therefore investigate un-

modulated MNS function), or include social cues as a factor in the experimental design.

Although no previous studies have directly tested the hypothesis that social modulation of imitation is atypical in ASC, Oberman and colleagues (2008) investigated MNS activity whilst participants observed hand actions conducted by a familiar (self or parent) and unfamiliar (stranger) other. Oberman and colleagues (2008) measured mu wave suppression as an indirect measure of MNS activity. They demonstrated that children with ASC showed significantly less mu wave suppression compared to typically-developing children whilst observing actions performed by the unfamiliar actor. However, when observing actions performed by the familiar actor there was no difference between the groups. If familiarity is considered a social prime these results may be interpreted as evidence of social modulation of the MNS in ASC and therefore incompatible with the results of the present experiment. However, different stimuli were used in familiar and unfamiliar conditions in the study by Oberman and colleagues. Therefore, rather than being a product of social modulation, the results may be a consequence of stimulus-specific characteristics. For example, observation of familiar and unfamiliar actors may prompt differing levels of attention or motivation. In the present study identical automatic imitation paradigms were employed for both pro-social and non-social groups and therefore there were no differences in stimulus characteristics that might constitute different bottom-up signals for attentional engagement or motivation.

Although there is no bottom-up role for attention in our results, it is possible that attention may play a 'top-down' role in our observed effect: pro-social priming may increase imitation by enhancing attention to biological stimuli. However, as we have previously argued (Cook and Bird, 2011), there is little evidence to support this hypothesis in the context of this paradigm. For both the pro-social and non-social groups, the imitation paradigm *required* attention to the same part of the screen as the movement stimuli (i.e. the cue to move was presented equidistant from the index and middle fingers of the video hand); any trials in which participants did not attend were detected by checking for incorrect responses, and for abnormally long or short RTs, and these trials were excluded from the analysis. Furthermore, using this same paradigm we have previously reported evidence (Cook and Bird, 2011) that the distribution of RTs does not fit with a model of social priming affecting attentional process (where pro-social and non-social groups should differ even for the fastest responses). Rather, the distribution of RTs fits a model of social priming affecting an inhibitory process (where pro-social and non-social groups need not necessarily differ for the fastest responses but should differ for the slowest responses). Therefore, it is likely that, rather than attentional mechanisms, social priming affects the inhibition of imitative responses; that is the pro-social group, compared to the non-social group are less

likely to inhibit automatic imitative responses.

Why might the effect of social priming on the inhibition of imitative responses differ between control participants and those with ASC? A recent set of studies suggests that the control of imitation relies on social cognitive processes for distinguishing one's own actions from the actions of another individual (Brass et al., 2003, 2005; Spengler et al., 2010c). These social cognitive processes and imitation-inhibition both elicit activity in mPFC and TPJ: key nodes in the social brain network (Brothers, 1990; Frith, 2007; Frith and Frith, 2010). Spengler, Bird and Brass (2010) recently showed that, in individuals with ASC, low levels of mPFC and TPJ activity during a mentalising task were associated with poor imitation-inhibition. Although the neural correlates of pro-social priming have not been elucidated and it is not clear that imitation-enhancement and imitation-inhibition depend on overlapping brain areas, the work of Spengler and Brass suggests a testable hypothesis for future investigation: compared to control participants, individuals with ASC have a reduced social brain response to pro-social primes and hence exhibit atypical modulation of imitation. This hypothesis bears similarities with the 'social relevance hypothesis' proposed by Oberman and colleagues (2008) which suggests that, compared to typically-developing individuals, those with ASC require stimuli with greater social relevance in order to elicit comparable levels of MNS activity.

It is also possible that atypical modulation of imitation following pro-social priming is an instance of a more general failure of top-down modulation in individuals with ASC (Frith, 2003). Studies of functional connectivity using magnetic resonance imaging report both greater and lesser connectivity between frontal and posterior areas in individuals with ASC compared to control participants. Bird, Catmur, Silani, Frith and Frith (2006) reported a reduced top-down influence of attention on face processing. Similarly, Kana, Keller, Cherkassky, Minshew and Just (2009) demonstrated underconnectivity between frontal and posterior regions during a mentalising task. More recently, greater task-independent connectivity between PFC and MNS regions has been reported in individuals with ASC compared to controls (Shih et al., 2010). Accordingly, atypical functional connectivity between brain areas that underpin the modulation of imitation (e.g. PFC) and those that underpin imitation itself (e.g. MNS) may be responsible for the impaired social modulation of imitation evidenced in the present study.

7.4.1 Conclusion

This Chapter presented evidence that control participants primed with words promoting pro-social attitudes show significantly higher levels of imitation than control participants primed with words

promoting non-social attitudes and that this effect of between pro- and non-social priming is absent in ASC. These results comprise the first demonstration of atypical social modulation of imitation in individuals with ASC. The ability to appropriately modulate levels of imitation to suit the social situation is important in social interactions hence this finding may help to explain some of the social problems characteristic of ASC.

Chapter 8. General Discussion

Imitation and action perception are important in social interactions. This thesis aimed to address questions about the neural mechanisms that underpin these functions in the typical brain and to investigate atypical imitation and action perception in adults with ASC.

8.1 THE NEURAL MECHANISMS OF ACTION PERCEPTION IN THE TYPICAL BRAIN

8.1.1 Findings from Chapters 2 and 3

Chapter 2 investigated the outstanding question of whether activity in posterior brain areas commonly associated with biological motion processing is correlated with the extent to which a stimulus objectively depicts, or is subjectively judged to depict, human motion. A novel fMRI paradigm was employed in which the amount of objective biological motion in the stimuli (percentage human motion) was manipulated and the subjective perception of biological motion (percentage of 'human' judgements) was measured. Data demonstrated the novel finding that pSTS activity correlates with the difference between subjective judgements and the objective sensory data. It was speculated that, in forming judgements about motion stimuli, incoming sensory motion data is compared to a stored representation of human motion in the pSTS. **Chapter 2** therefore postulated an important role for pSTS in judging whether stimuli represent human motion.

As can be seen from **Chapter 1**: Figure 1.2 previous studies have implicated the pSTS in the visual representation of biological motion and in judgement formation - in particular animacy judgment formation. The finding presented in **Chapter 2,** that activity in pSTS is correlated with the difference between subjective judgements and the objective sensory data, may explain why activity in this area has been reported in both biological motion perception tasks and in tasks that do not feature biological motion but require animacy judgements. Caution should therefore be exercised when interpreting pSTS activity as representing visual processing of biological motion since animacy judgement formation may also play a part.

Chapter 2 also reported that activity in dmPFC correlated with an objective measure of biological motion but not with participants' subjective judgements about biological motion or with the difference between subjective judgements and the objective measure. In short, dmPFC activity was greater when the stimulus moved with biological motion relative to when the stimulus moved with biological motion

perturbed with CV. Although three previous studies have found activity at similar coordinates during observation of biological motion (coordinates for Chapter 2 [-6 35 43]; Grèzes et al., 2001 [-6 42 40]; Pelphrey et al., 2005 [4 30 39]; Ptito et al., 2003 [4 63 14]) none of these we were able to demonstrate that activity in dmPFC correlates with the objective extent to which the stimulus depicted biological motion. **Chapter 2** reports, for the first time, that activity in dmPFC correlated with the degree to which a single dot moved with a velocity profile characteristic of human motion.

The area of dmPFC discussed in Chapter 2 has previously been found to be active in response to external agency attribution, and the control of imitation (Spengler et al., 2009, 2010b, 2010a) (Brass et al., 2009; Spengler et al., 2010c). In particular a recent set of studies by Wang and Hamilton have shown that typical adults exhibit greater automatic imitation of hand actions following direct gaze relative to indirect gaze and that this effect of eye-gaze on automatic imitation is mediated by a cluster of activity in dmPFC close to our cluster (Wang et al., 2011a, 2011b: their coordinates [6 44 34], our coordinates from Chapter 2 [-6 35 43]). Given that this area is active for both agency attribution, imitation inhibition and the modulation of imitation by eye-contact it was suggested, in Chapter 2, that this region may play an important role in the processing of behaviourally relevant information about biological stimuli.

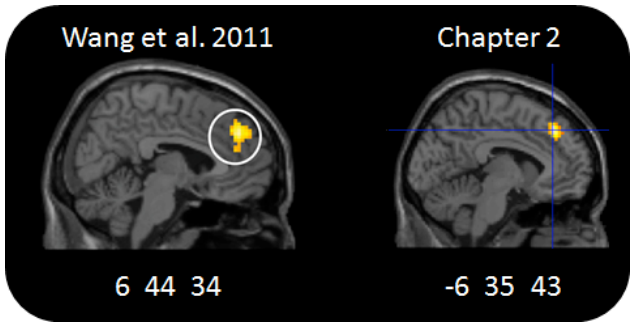

Figure 8. Right: Activity from the interaction between automatic imitation and eye-gaze direction from Wang et al., 2011b. Left: Activity from the dmPFC cluster reported in Chapter 2. MNI coordinates also reported.

In addition to posterior regions such as the pSTS, action observation has previously been found to activate anterior regions including MNS areas (Saygin et al., 2004; Saygin, 2007). It has been argued that motor activations during action observation are evidence that we motorically simulate observed actions - a function that may support various abilities such as imitation and action understanding (Hurley, 2008). In line with this, neuroimaging studies have demonstrated matching of effector categories (e.g. motor cortex is activated somatotopically during action observation (Buccino et al., 2001)) and behavioural studies have demonstrated matching of action categories (e.g. open actions are

facilitated by observing open actions irrespective of effector (Leighton and Heyes, 2010)). However, no previous study has demonstrated motoric simulation at the level of action kinematics. Previous studies have shown that *beta* power over sensorimotor cortex is more greatly attenuated during the midpoints relative to the endpoints of action execution (2000, 2003b). Chapter 3 reported that *beta* power over sensorimotor cortex is more greatly attenuated during the midpoints relative to the endpoints of passive action observation. This demonstrates that activity in the MNS comprises a motoric simulation of the kinematics of observed actions. This finding is a key piece of evidence in a wider argument that the MNS automatically simulates action and therefore may be implicated in action understanding and imitation of action kinematics.

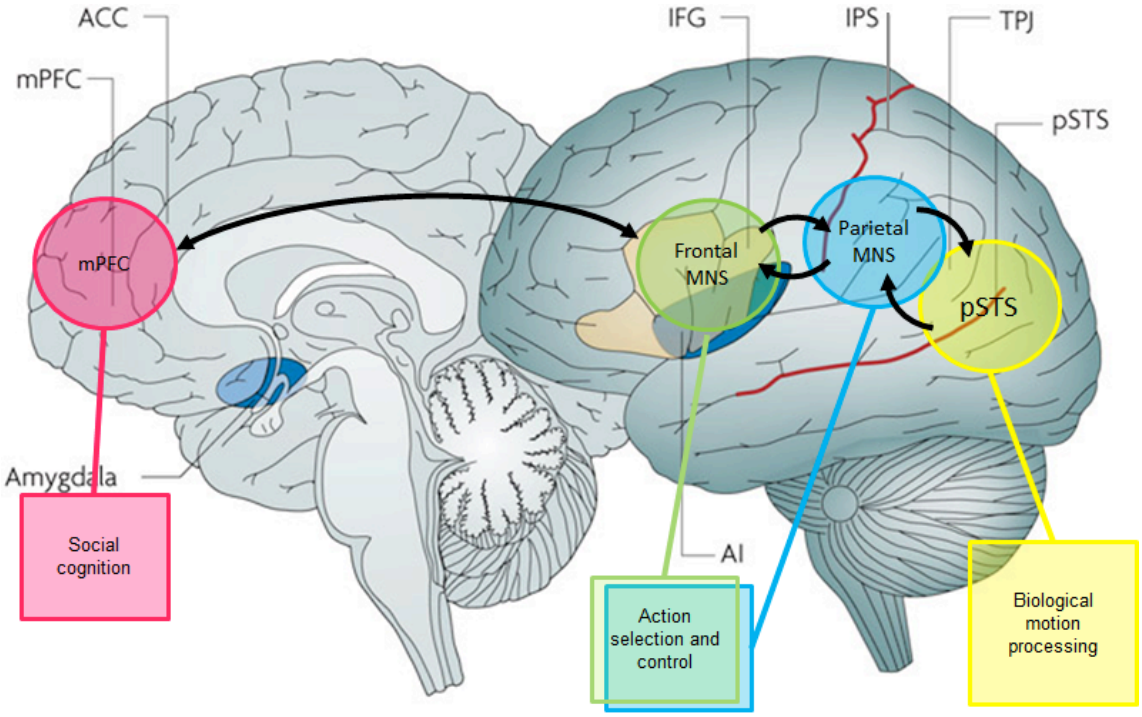

Figure 8.1. Simple model of action observation and execution based on previous literature

8.1.2 Theoretical implications

This thesis started with a simple model of the neural mechanisms that underpin action observation and execution. The model considered biological motion perception as a sensory input to the MNS and control processes as a modulatory influence on output from the MNS (Figure 8.1). The work in this thesis suggests that a number of significant modifications can be made to this model; the updated model is illustrated in Figure 8.2.

Chapter 2 suggests that 'biological motion perception' can be subdivided into subjective and objective components. Processing of subjective biological motion refers to forming judgments, such as animacy judgements, about biological motion stimuli. **Chapter 2** suggested that pSTS plays an important role in this function. Previous studies have associated pSTS activity with high level representations of actions (Grossman et al., 2010); in these studies 'animacy' is matched between conditions and pSTS activity has been shown to differentiate action types (e.g. kicking and walking). Correspondingly, the updated model (Figure 8.2) postulates that pSTS activity is associated with animacy judgments and high level representation of actions.

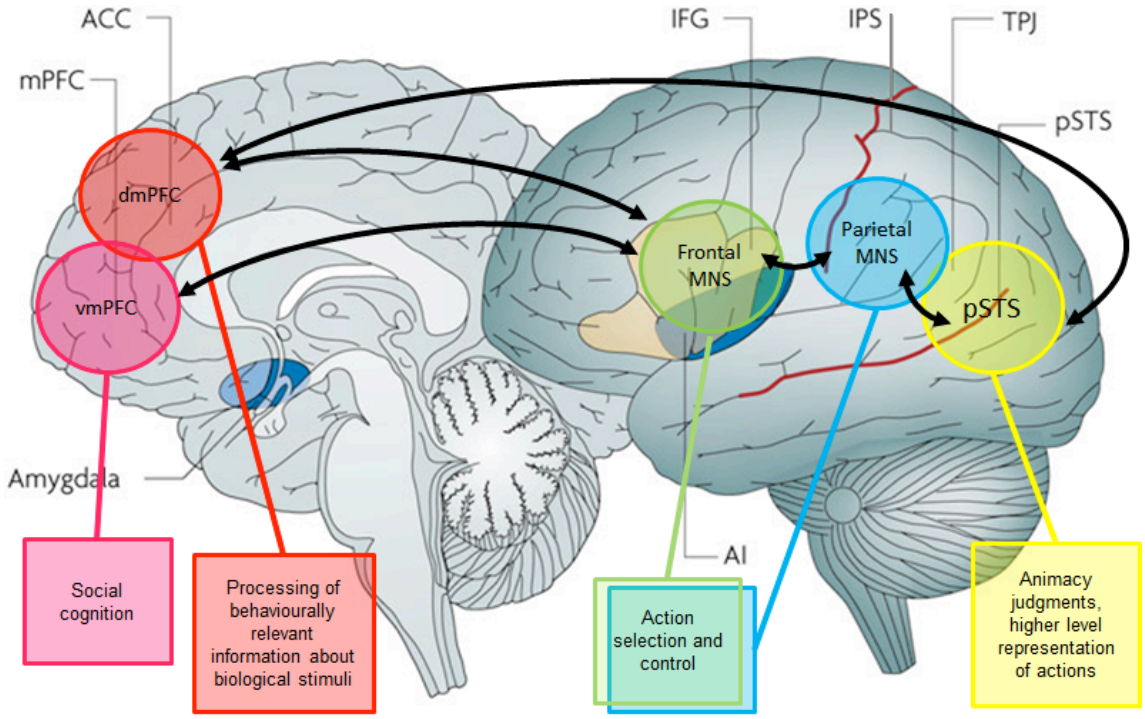

Figure 8.2. Neural model of action perception and imitation based on work reported in this thesis.

In our subdivision of biological motion perception, objective processing of biological motion refers to responding to the objective sensory data. **Chapter 2** suggested that this process is associated with dmPFC activity. This region is also implicated in agency attribution (Sperduti et al., 2011) and in the control of imitation, including the modulation of imitation by direct eye-gaze (Wang et al., 2011b). On this basis, the updated model distinguishes dmPFC from vmPFC and postulates that dmPFC activity is associated with the analysis of behaviourally relevant information about biological stimuli. Interactions between pSTS and dmPFC – based on known anatomical connections (Leichnetz and Astruc, 1976; Carmichael and Price, 1995; Bachevalier et al., 1997) - are also included in the updated model.

Completing the circuit are connections from dmPFC to the MNS (Carmichael and Price, 1995; Luppino et al., 1999; Gong et al., 2009). Such connections between dmPFC (and also vmPFC) and MNS regions have been suggested to be important in the control of automatic imitation (Brass et al., 2005, 2009; Wang et al., 2011b). Lastly, **Chapter 3** further elucidated the function of the MNS by demonstrating that at least one of the processes mediated by this system is the automatic motoric simulation of action kinematics; this is detailed in the updated model.

8.1.3 Future Directions

8.1.3.1 Relationship between objective and subjective biological motion processing

The updated neural model illustrated in Figure 8.2 gives rise to a number of questions for future investigation. One interesting question concerns the functional roles of dmPFC and pSTS in objective and subjective processing of biological motion. One method of ascertaining whether pSTS and dmPFC activations are necessary for subjective and objective processing of biological motion is to use transcranial direct current stimulation (tDCS) to disrupt function in these brain areas and assess the impact on measures of objective and subjective processing. The 'same' or 'different' task of **Chapter 5: Experiment 2** and the 'human' or 'robot' task of **Chapter 2** could be employed to assess objective and subjective processing respectively. The results of **Chapter 2** would predict that tDCS to pSTS should disrupt subjective and not objective processing, whereas the converse would be true for tDCS to dmPFC. However, it could be that feed-back from dmPFC to pSTS is necessary for animacy judgements. Likewise it may be that pSTS function is necessary for objective biological motion processing.

Interesting insights may also arise from investigations of the temporal evolution of these anterior and posterior activations in animacy judgment formation. For instance, it may be the case that the objective content of biological motion is first processed in pSTS, fed forward to dmPFC and subsequently the subjective-objective difference signal is computed in posterior regions (Figure 8.3 Model 1). An alternative temporal model is depicted in Figure 8.3 Model 2. Here the incoming sensory data is compared to a stored representation of human motion at early temporal stages; subsequently the objective sensory data, but not the judgment, is fed forward to anterior regions. A possible method of disambiguating these models is to employ MEG to record the temporal evolution of posterior and anterior activations relating to animacy judgments.

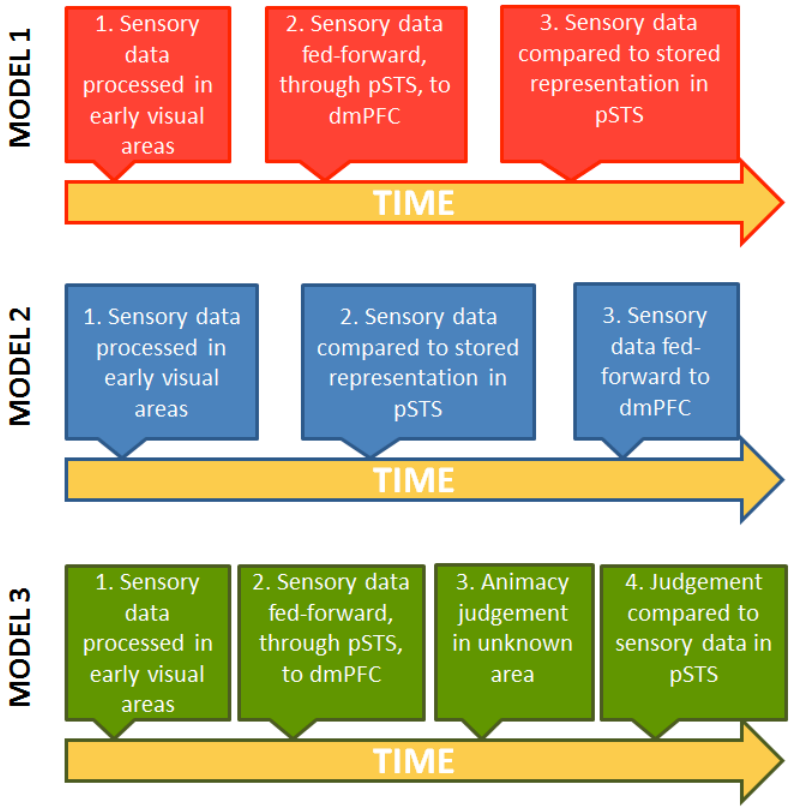

Figure 8.3. Hypothesised temporal models of animacy judgments

A further possibility, illustrated in Figure 8.3 Model 3, is that the animacy judgement is formed at another neural location and communicated to pSTS. Further fMRI investigations could employ more sensitive analysis techniques such as multivariate pattern analysis to elucidate whether there is a brain region, not identified by the current analysis, in which activity correlates with subjective judgements of animacy.

It is interesting to speculate about the possible *functions* of the pSTS subjective-objective difference signal. This signal can be considered to comprise two components: a sign (indicated, in Figure 8.4, by the direction (up or down) of the arrow), and a magnitude (indicated, in Figure 8.4, by the length of the arrow). The sign of the signal could indicate the judgement (human for positively signed and robot for negatively signed). The magnitude of the difference signal would be large when the discrepancy between subjective and objective is great, and small when the difference in minimal. Such a signal could play a role in categorical perceptual processing – modifying the representation of the motion so as to minimise within-category and maximise between-category perceptual differences. That is, when the difference between the stored representation and the in-coming sensory data is large the perceptual representation of the sensory data would need to be substantially modified to agree with the stored representation. When the difference between the stored representation and the incoming sensory data is

small the perceptual representation of the sensory data need only be minimally modified in order for it to agree with the stored representation. Whether the difference signal is involved in such a 'modification' process remains an intriguing question. Another possible role for the difference signal is in representing judgement uncertainty. That is, the further away the incoming sensory stimulus is from the stored representation, the more uncertain the judgement. Further studies may use techniques such as obtaining uncertainty judgements and assessing the effects of TMS to pSTS on objective and subjective biological motion tasks to further elucidate the functional significance of the subjective-objective difference signal.

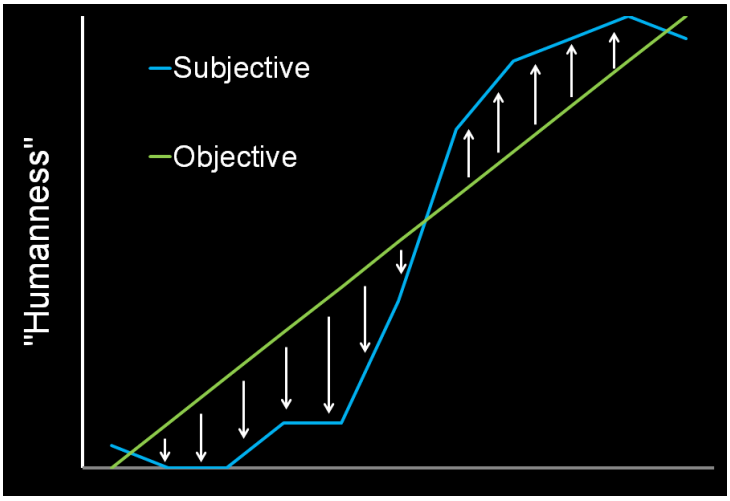

Figure 8.4. Difference between subjective (blue line) and objective (green line) judgments. Length of the white arrows represents the magnitude of the subjective-objective difference signal; direction represents the sign (up = positive, down = negative).

The recent finding that pSTS activity is attention dependent - pSTS activity is high if a biological stimulus is attended and low if the stimulus is unattended but, nevertheless, present (Safford et al., 2010) – raises the question of whether the suggested difference computation in pSTS is an automatic or attention dependent process. The same question may be asked of the kinematic processing that takes place in more anterior regions: that is, do we motorically simulate actions that we are not consciously attending to?

8.1.3.2 Relationship between biological motion processing and MNS activity

Another question that arises from the updated neural model illustrated in Figure 8.2 relates to the influence of animacy judgements on MNS activity. Stanley and colleagues (2007) have previously shown that belief about whether a stimulus represents human motion can impact on the extent to which that stimulus interferes with on-going action execution. In line with this, animacy judgements may modulate imitation in a bottom-up fashion by increasing communication between pSTS and IPL (Figure

8.5 Bottom-up model). It is also plausible that animacy judgements modulate imitation in a top-down fashion. That is, information about animacy judgements could be fed-forward from pSTS to mPFC and this region, which is known to be involved in the control of imitation, may influence activity in MNS areas such as IFG (Figure 8.5Figure 8.5 Top-down model). Dynamic Causal Modelling offers an analysis method that could be employed to investigate these models.

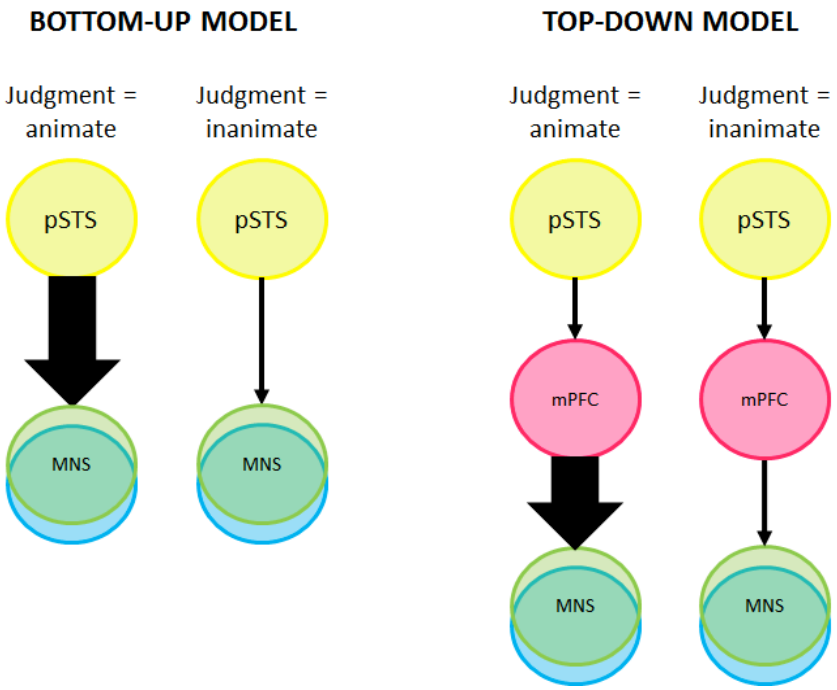

Figure 8.5. Possible models of the effect of animacy judgments on MNS activity.

Chapter 3 demonstrated that at least one function of MNS regions is the automatic simulation of action kinematics. An open question concerns how MNS regions obtain detailed information about action kinematics. As with animacy judgements there are at least two possibilities: a bottom-up route from pSTS to MNS areas and a top-down route from pSTS, via dmPFC to MNS areas.

8.2 ACTION PERCEPTION AND THE MODULATION OF IMITATION IN ASC

It has been suggested that a core impairment in ASC lies in the mechanisms that underpin imitation – the MNS (Williams et al., 2001; Oberman and Ramachandran, 2007). However, evidence both supports and opposes the hypothesis of a 'broken MNS' in ASC. This thesis took a wider view of the mechanisms that underpin imitation by investigating both input to the MNS (action perception) and modulation of the output from the MNS.

8.2.1 Findings

Chapter 4 focused on action perception in ASC demonstrating that individuals with ASC did not differ from control participants in thresholds for direction discrimination from point light depictions of either a walker, a translating rectangle or an unstructured object. This result corroborates the findings of Murphy et al. (2009) and extends these results to non-biological form-from-motion. However, these findings, of typical biological motion processing in ASC, contrast with previous reports (e.g. Blake et al. 2002, Kaiser et al., 2010a). It is possible that participants performed this task using a compensatory strategy (e.g. identifying sub-parts of the figures, and therefore side-stepping the requirement for biological motion processing and transforming the task into something like a visual search task). No such compensatory strategy could be employed in **Chapter 5: Experiment 1**wherein the task demanded processing of the velocity profile of the movement. Results from this chapter demonstrated that the control group were significantly more sensitive than the ASC group to perturbations to biological motion. Furthermore, whilst control participants were more sensitive to perturbations to biological relative to non-biological motion, this increased relative sensitivity to biological motion was not found in the ASC group; individuals with ASC were equally sensitive to perturbations to biological and non-biological motion.

The paradigms employed in **Chapter 4** and **Chapter 5: Experiment 1** differed in the extent to which they required stored knowledge about human movement. Judging the direction of motion of a PL walker does not require stored representations of human movement. In contrast 'picking the less natural' requires a stored representation of natural human motion. **Chapter 5: Experiment 2** comprised a modified version of **Chapter 5: Experiment 1** wherein participants were asked whether the two animations looked the 'same' or 'different'. It was found that, in this task, which does not require a stored representation of human motion, individuals with ASC did not differ from controls. Together these studies suggest the novel hypothesis that individuals with ASC have atypical stored representations of human motion. Indeed a number of studies have reported differences between ASC and control groups when the task has depended on such stored representations (e.g. judge whether a stimulus moves 'like a person': Blake et al., 2003; Kaiser et al., 2010a; Annaz et al., 2010).

Irrespective of the mechanism that underpins difficulties with biological motion processing in ASC such a difficulty could result in atypical effects of motion perception on action execution. **Chapter 6** investigated the effect of actor form (human or robot) and actor motion (biological motion or constant velocity) on the Interference Effect in adults with ASC. It has previously been reported that observing incongruent actions interferes with on-going action execution and that this effect is larger for actions

with biological form (i.e. human versus robot) and motion (i.e. MJ vs CV) than for actions with non-biological form and motion (Kilner et al., 2003a, 2007a). **Chapter 6** did not replicate the effect of motion: there was no significant difference in the Interference Effect generated by observation of biological (MJ) and non-biological (CV) movements for either control participants or individuals with ASC. It was suggested that this lack of an effect may be a result of presentation mode: **Chapter 6** employed computer animated virtual reality agents whereas Kilner and colleagues employed videos; it may be the case that our participants had sensorimotor experience with computer animated agents moving with both biological and non-biological motion.

Accurate processing of the form of movements also plays an important role in interference: control participants exhibit greater interference in response to movements with human as opposed to robot form (Kilner et al., 2003a). **Chapter 6** demonstrated that whereas control adults exhibited a greater Interference Effect in response to human form (human virtual agent and real human) compared to robot form (robot virtual agent) actors, individuals with ASC did not exhibit a significant Interference Effect whilst observing either a virtual human agent, real human or virtual robot agent. Taken at face value this result appears to support the broken MNS hypothesis of ASC. However, it is possible that this result is an example of atypical control over imitation in ASC: that is that human form acts as a 'pro-social prime' for control participants but not for individuals with ASC, elevating imitation levels in the control group alone.

Chapter 7 investigated whether the social modulation of imitation is atypical in ASC. Using a scrambled sentence task to first prime participants with either pro-social or non-social attitudes and an automatic imitation task to subsequently measure imitation, it was shown that the social modulation of imitation is atypical in ASC. Whereas imitation levels were higher for pro-socially primed relative to non-socially primed control participants, there was no difference between pro- and non- socially primed individuals with ASC. **Chapter 7** therefore comprises the first experimental demonstration that the modulation of imitation may be atypical in ASC.

Together, **Chapters 5, 6 and 7** demonstrate that, although atypical imitation can be observed in high-functioning adults with ASC (**Chapter 6**), action perception (**Chapter 5**) and the modulation of imitation (**Chapter 7**) may also be atypical. Problems with imitation may stem from difficulties with one of these components of the wider mechanisms that underpin imitation rather than a broken MNS per se.

8.2.2 Theoretical implications

The work in **Chapters 4 to 7** raises questions about the integrity of 3 components of our neural model of action perception and imitation which are illustrated as question marks in Figure 8.6. The first process of questionable integrity in ASC is biological motion processing: in particular whether subjective processing is impaired and objective processing preserved. The second is the modulation of imitation in ASC. This concern can be divided into two sub-concerns; one regarding the function of brain regions such as vmPFC which may underpin the effects of pro-social priming and the second regarding the influence of brain regions such as vmPFC on MNS regions. These three concerns are discussed in further detail in the following section.

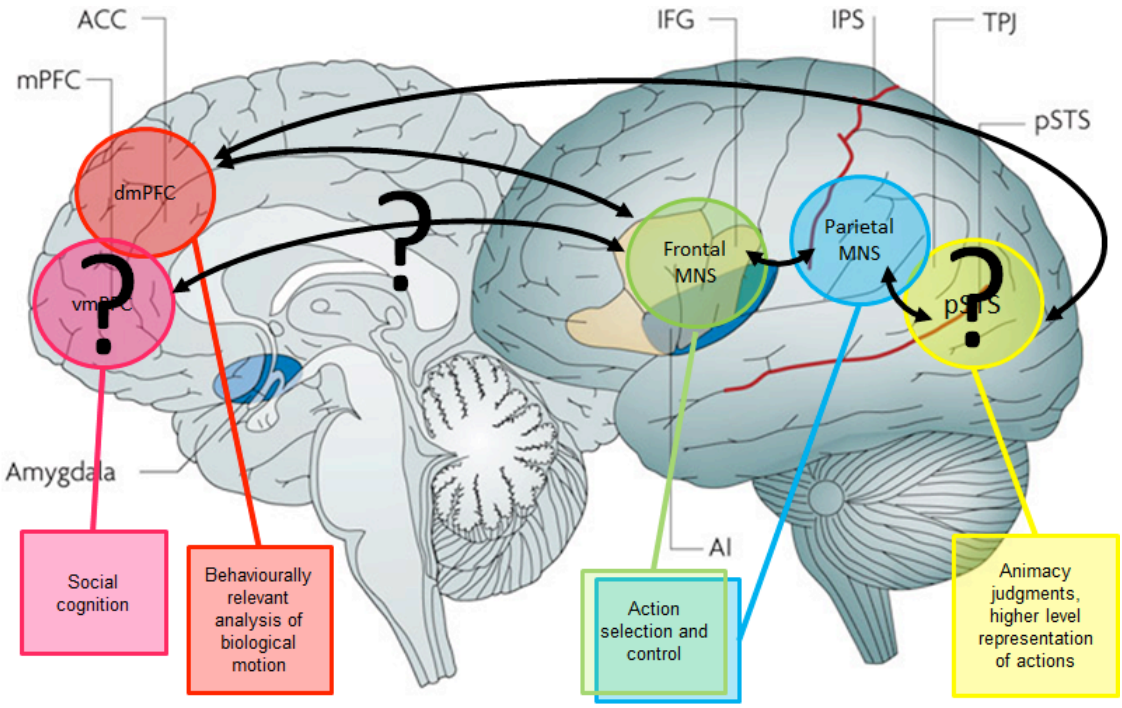

Figure 8.6. Atypicalities in the neural mechanisms of action perception and imitation in ASC suggested by the work in this thesis.

8.2.3 Future Directions.

8.2.3.1 Biological motion processing in ASC

Chapter 5 provided evidence that adults with ASC exhibit atypical action perception when the task depended on stored knowledge of natural human motion but not when the task required only 'same' or 'different' judgements. It was postulated that individuals with ASC have atypical stored representations of human motion. This hypothesis is in line with the relevant literature: studies which have reported differences between ASC and control groups have typically employed tasks which depended on stored

representations of human motion (e.g. judge whether a stimulus moves 'like a person': Blake et al., 2003; Kaiser et al., 2010a; Annaz et al., 2010). Studies which have reported intact processing of biological motion in ASC have typical employed tasks which do not depend on stored representations of human motion (e.g. 'judge the direction of motion': Murphy et al., 2009; **Chapter 4** of this thesis). Atypical subjective processing in the presence of typical objective processing in ASC is therefore a novel hypothesis, which would go some way towards explaining the current discrepancy in the biological motion processing literature.

An alternative possibility is that individuals with ASC have intact stored representations of human motion but have an atypical influence of stored representations on incoming sensory data (i.e. they know what a 'natural' human movement should look like but have difficulties comparing the observed stimulus to their stored knowledge). **Chapter 2** suggested that the pSTS is a key region in comparing stored representations of motion and incoming sensory data. It is possible that previous reports of pSTS hypoactivity in ASC (Herrington et al., 2007; Freitag et al., 2008) reflect difficulties in this comparison process. Further experiments are required to investigate these novel hypotheses and to relate them to the existing literature.

8.2.3.2 Relationship between biological motion processing and MNS activity in ASC

As discussed in section 8.1.3.2 subjective processing of biological motion and resulting animacy judgements may have bottom-up or top-down effects on MNS activity and may impact on measures of imitation such as the Interference Effect. For instance, in control participants, Stanley and colleagues (2007) demonstrated a significant Interference Effect when participants executed actions whilst observing the movements of a dot that they *believed* to depict human motion. However, if participants *believed* that the dot depicted computer-generated motion, no Interference Effect was observed. Therefore, subjective beliefs about observed movements can affect the extent to which observations impact on execution. This finding leads to the speculation that if individuals with ASC and control participants differ in their subjective judgements about what comprises a natural human motion this could have measurable consequences in terms of the Interference Effect. It is possible that, if individuals with ASC and control participants execute movements whilst observing motion-morphs (i.e. stimuli employed in Chapter 4 wherein the velocity profile of the movement is either 100% MJ, 100% CV or a linear combination of these two extremes) the generated Interference Effect would differ between the groups as a function of the extent to which the observed movement is judged to represent natural human motion (for example see Figure 8.7)

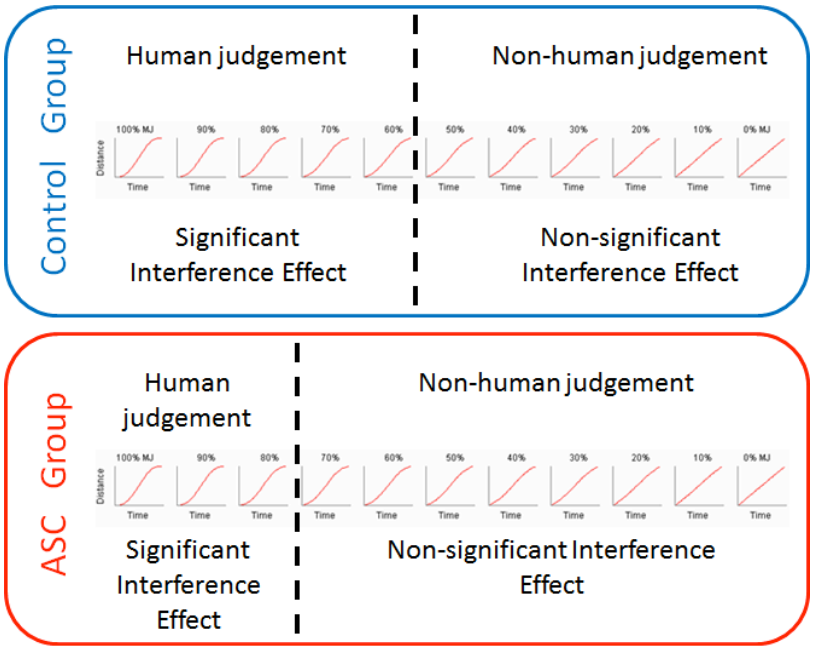

Figure 8.7. Interaction between biological motion processing and the Interference Effect. Figure illustrates one way in which atypical subjective processing of biological motion may result in an atypical Interference Effect of observed actions.

8.2.3.3 Modulation of imitation in ASC

Chapter 7 demonstrated that the social modulation of imitation is absent in individuals with ASC. Future work may investigate the neural basis of this effect. As discussed in the introduction, a working hypothesis would be that for control participants pro-social priming modulates activity in mPFC, which is involved in the control of imitation. It may therefore be predicted that, relative to control participants, individuals with ASC exhibit atypical mPFC responses to pro-social priming and hence atypical control over imitation. A related question concerns whether the lack of modulation of imitation in ASC is a result of atypical mPFC activity per se or atypical connectivity between mPFC and MNS areas.

8.2.4 Implications for treatment

Much effort is employed in developing imitation improvement programmes for individuals with ASC (Ingersoll, 2010; Zwaigenbaum and Howarth, 2011). An effective treatment program should target the mechanisms that underpin the atypical behaviour. This thesis suggests that training action perception and control of imitation may be important foci for imitation training programmes. With respect to action perception, recent studies with control adults have shown that it is possible to train individuals to discriminate biological movements that were previously indiscriminable (Jastorff et al., 2009), demonstrating promise for the training of action perception. The current thesis suggests that an important target may be training stored representations of natural human motion (**Chapter 5**).

With respect to training control over imitation, a recent study has shown that, in typical adults, imitation inhibition can be enhanced by training and that this type of training also enhances visual perspective taking (Santiesteban et al., under review). This study featured three groups of control adults: an imitation inhibition group, an imitation group and an inhibitory control group. The imitation and imitation-inhibition groups were both trained with videos of index or middle finger lifts. The imitation group were asked to perform the action they observed on the screen whereas the imitation-inhibition group were instructed that when they saw an index finger lift they should lift their middle finger, and when they saw a middle finger lift they should lift their index finger. The inhibitory control group were trained on a Stroop-like task in which the video hand remained static and a red or green circle appeared between the fingers; red and green stickers were placed on participants' index and middle fingers (placement counterbalanced between participants) and participants were instructed to lift their 'red finger' when a green circle appeared, and to lift their 'green finger' when a red circle appeared. The automatic imitation paradigm employed in **Chapter 7** of this thesis was used to acquire an index of automatic imitation following 40 minutes of training. Individuals trained to inhibit imitation showed reduced automatic imitation relative to the Stroop and the imitation groups (Santiesteban et al., under review) demonstrating that automatic imitation effects are susceptible to training. In addition, the imitation inhibition group demonstrated enhanced visual perspective taking on a task in which correct responding is achieved by taking the perspective of another agent. Santiesteban suggest that both imitation inhibition and visual perspective taking require self-other distinctions. This result suggests that imitation training may have advantageous effects for other aspects of social cognition that share common mechanisms. An interesting and novel question is whether the association between positive social attitudes and enhanced imitation can be trained. If so this may present a novel therapeutic target in ASC.

8.3 GENERAL LIMITATIONS AND FUTURE DIRECTIONS

8.3.1 Stimuli

Three stimulus types have been employed throughout this thesis: animations that move with either MJ biological motion, CV motion, or linear combinations of the two (**Chapters 2, 3, 5 and 6**); PLD stimuli (**Chapter 4)**; and disembodied hand videos (**Chapter 7**). With the exception of the PLD stimuli, which depicted whole body motion, results are limited to perception of hand/arm movements and have focused on a single action: vertical sinusoidal arm movements. Given that there is some evidence for somototopy in pSTS and MNS regions (Allison et al., 2000; Buccino et al., 2001) it could be that our results are limited to a hand movement specific network. Further work is necessary to investigate whether the current findings extrapolate to effectors other than the hand/arm. The study described in **Chapter 2**

focused only on biological motion and human / robot judgements. However, given that the pSTS has previously been implicated in complex judgements such as trustworthiness (Winston et al., 2002) future studies may attempt to extend the current findings to more complex judgements and may also employ more life-like stimuli such as the videos employed in **Chapter 3**.

8.3.2 Age group

Investigating the developmental timecourse of action perception and the modulation of imitation may inform on the aetiology of the difficulties discussed here in adults with ASC. With respect to action perception recent work from Annaz and colleagues (2010) showed that unlike TD children, those with ASC do not show developmental improvement, between the ages of 5 and 12, in their ability to judge whether PLDs '*moved like a person*'. The current thesis suggests that it may be interesting to investigate the parallel development of 'objective' and 'subjective' processing of biological motion, and to compare this development in children with ASC and controls.

The PFC has a delayed developmental profile relative to more posterior brain areas and is still developing in terms of both structure (Sowell et al., 1999; Giedd et al., 1999; Shaw et al., 2008) and function (Burnett et al., 2009; Dumontheil et al., 2010) throughout the adolescent years. This thesis implicated the dmPFC in objective processing of biological motion and previous studies have suggested that both dmPFC and vmPFC may be important in the control of imitation (Brass et al., 2005, 2009; Wang et al., 2011b). Further studies could investigate the development of these abilities and their neural correlates throughout adolescence. For instance, a study could investigate whether objective biological motion correlates with dmPFC activity in adolescents, as it does in adults, and whether the extent or location of this activity predicts performance on a measure of objective biological motion processing such as the 'same' or 'different' task described in **Chapter 5**.

With regard to the development of imitation, using the same paradigm described in **Chapter 7**, it was recently demonstrated that, whereas pro-socially primed adults exhibited a greater magnitude of automatic imitation than non-socially primed adults, adolescents did not exhibit social modulation of imitation (Cook and Bird, 2011). This result suggests that the control of imitation develops with age. A testable hypothesis, which follows on from the work of Annaz and colleagues (2010) in the biological motion field, is that the developmental trajectory of control over imitation is atypical in ASC. That is that the difference between ASC and control groups in the modulation of imitation emerges with age.

Further questions concern the major factors in the development of imitation modulation mechanisms in

the typical brain. That is, does control of imitation arise because of genetically pre-programmed development of prefrontal control regions and what is the function of experience (e.g. imitating whilst being in a pro-social frame-of-mind) in shaping these circuits? Answers to these questions would assist in predicting the extent to which experience and training can impact on the development of control of imitation.

8.3.3 ASC severity

This thesis tested only high-functioning individuals with ASC. This group represents only a small proportion of individuals with ASC; many have learning difficulties and other cognitive problems in addition to the core features. Although more general cognitive difficulties may affect performance on the paradigms employed in this thesis, it is possible, with careful experimental design, to measure the amount of variance in behavioural responses accounted for by a particular cognitive difficulty (e.g. biological motion processing). As such, future studies could investigate subjective and objective biological motion processing and the social modulation of imitation in low functioning individuals with ASC.

8.4 CONCLUDING REMARKS

This thesis used fMRI, MEG, movement recording and RT and accuracy analyses to address outstanding questions about the neural mechanisms that underpin action perception and imitation and the modulation of imitation in the typical brain and in adults with ASC.

Chapters 2 and 3 have added to current understanding about action perception brain regions and the MNS. It was demonstrated that activity in pSTS, which is commonly considered to comprise visual representations of action, represents the difference between a participant's subjective judgement about a MJ biological motion stimulus and the objective sensory data. This suggests a novel role for the pSTS in forming judgements about biological motion stimuli. With respect to the MNS it was demonstrated that activity over sensorimotor cortex is modulated dynamically during the observation of MJ biological motion. Therefore, the typical adult brain automatically simulates the kinematics of observed actions.

Chapters 4, 5, 6 and 7 investigated action perception and the modulation of imitation in ASC. **Chapter 4** showed that aspects of action perception are atypical in ASC. A novel hypothesis was proposed: individuals with ASC have a particular difficulty with subjective processing of MJ biological motion but preserved objective processing. **Chapter 6** reported that individuals with ASC also exhibit atypical imitation measured in terms of in the Interference Effect. Lastly, **Chapter 7** showed that, whereas pro-

social priming enhanced imitation in control participants this effect was absent in individuals with ASC. Taken together these studies suggest that action perception and the modulation of imitation are atypical in ASC hence evidence of atypical imitation should not be considered direct evidence for a broken MNS but rather may reflect atypicalities in one of these other components of the wider mechanisms that underpin imitation.

Chapter 9. References

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Chapter 2 is based on: Cook, J., Press, C., Saygin, A.P., Kilner, J. & Blakemore, SJ. Dissociable neural processing of objective and subjective components of biological motion. *Under review.*

Chapter 3 is based on: Based on: Press, C., Cook, J., Blakemore, SJ. & Kilner, J. (2011) Dynamic properties of the perception-action matching system. *Journal of Neuroscience*. 31(*8*):2792-2800.

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Chapter 6 is based on: Cook, J., Swapp, D., Pan, X., Bianchi-Berthouze, N. & Blakemore, SJ. Atypical interference effect of action observation in autism spectrum conditions. *Under review.*

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