

**Measuring and Modulating Mimicry:
Insights from Virtual Reality and Autism**

Paul Forbes

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I, Paul Forbes, 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.

Signed:

Date:

Abstract

Mimicry involves the unconscious imitation of other people's behaviour. The social top-down response modulation (STORM) model has suggested that mimicry is a socially strategic behaviour which is modulated according to the social context, for example, we mimic more when someone is looking at us or if we want to affiliate with them. There has been a long debate over whether mimicry is different in autism, a condition characterised by differences in social interaction. STORM predicts that autistic people can and do mimic but do not change their mimicry behaviour according to the social context. Using a range of mimicry measures this thesis aimed to test STORM's predictions. The first study employed a traditional reaction time measure of mimicry and demonstrated that direct gaze socially modulated mimicry responses in non-autistic adults but did not do so in autistic participants, in line with STORM's predictions. In the next two studies, I found that non-autistic participants mimicked the movement trajectory of both virtual characters and human actors during an imitation game. Autistic participants also mimicked but did so to a lesser extent. However, this type of mimicry was resistant to the effects of social cues, such as eye-gaze and animacy, contrary to the predictions of STORM. In a fourth study, I manipulated the rationality of an actor's movement trajectory and found that participants mimicked the trajectory even when the trajectory was rated as irrational. In a fifth study, I showed that people's tendency to mimic the movements of others could change the choices that participants had previously made in private. This tendency was modulated by the kinematics of the character's pointing movements. This thesis provides mixed support for STORM's predictions and I discuss the reasons why this might be. I also make suggestions for how to better measure and modulate mimicry.

Impact Statement

Copying other people is important for both learning and for connecting with others. There has been a long debate over whether there are differences in copying behaviours in autism - a condition affecting how people perceive the world and interact with others. This thesis investigated mimicry in autistic and non-autistic individuals. Mimicry is a particular type of copying behaviour which involves unconsciously copying the movements and actions of those around us. Investigating how mimicry might be different in autism can help us to understand the mechanisms which underlie the social difficulties associated with the condition.

Studying mimicry experimentally is a challenge as many measures of mimicry are either poorly controlled or not related to mimicry behaviours during everyday social interactions. This thesis used virtual reality to try and overcome some of these difficulties. By having participants interact with virtual characters, this enabled a high level of experimental control as the virtual characters could be programmed to behave consistently across participants. Virtual reality was used to create realistic social interactions similar to those in everyday life, for example, the virtual characters could respond to participants' behaviour to create a sense of interaction.

This thesis demonstrated the feasibility and challenges of using virtual reality to study human social interaction. For example, I showed that people mimicked the actions of a virtual character in a similar way to which they mimic people during real-life social interactions. Moreover, the mimicry differences some autistic individuals display during everyday social interactions also occurred when interacting with virtual characters. These findings demonstrate the plausibility of using virtual reality as a research tool and potentially as part of training and therapy programmes with both autistic and non-autistic individuals.

This thesis made a significant contribution to cognitive models of mimicry, and more generally, furthered our understanding of social cognition in autism. For example, the findings suggested that the basic mechanisms responsible for mimicry are likely to be intact in autism. However, autistic people may show differences in their responses to social cues, like eye-gaze, which affects the extent to which they mimic in different situations. Given the importance of copying behaviours during development and for connecting with others, these findings could have important implications for both educators and therapists.

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Chapter 1 - Introduction

1.1 Mimicry

1.1.1 What is mimicry?

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Figure 1-1 All-Ireland road bowls championship

Derek Bayes for *Sports Illustrated*. From Allport (1961; p.535).

“...as the performer makes his spring, many of the spectators...move their feet”

(Darwin, 1872; p. 40)

Darwin’s observation is clearly demonstrated in Figure 1-1. Notice how the spectators not only move their feet when the performer does but some also copy his posture and facial expression. This unconscious imitation of other people’s behaviour is called mimicry. Mimicry is ubiquitous; in a further example, Darwin (1872; p. 41) describes how a doctor informed him “that while attending women in labour he sometimes finds himself imitating the muscular efforts of the patient.” Mimicry is part

of a broader group of behaviours referred to as interpersonal coordination, which includes emulation, synchrony and entrainment (Bernieri & Rosenthal, 1991). Three features distinguish mimicry from these other types of interpersonal coordination. Firstly, mimicry is spontaneous so unconscious and unintentional. The doctor “finds himself imitating” so he was not initially aware that he was copying the patient’s muscular efforts. Similarly, the spectators in Figure 1-1 are likely to be unaware of their motoric similarity to the performer. The spontaneous nature of mimicry separates it from other types of copying behaviours, such as emulation (or conscious imitation). This is a deliberate and controlled behaviour which involves copying the explicit goal of an observed action, for example, this may occur when a parent is teaching their child how to tie their shoelaces (Hamilton, 2008). Secondly, mimicry must occur with some delay between the observed and executed behaviour so that there is a mimicker and a mimickee. For example, an audience may clap in unison (Néda, Ravasz, Brechet, Vicsek, & Barabási, 2000) or two people may rock at the same frequency in rocking chairs (Richardson, Marsh, Isenhower, Goodman, & Schmidt, 2007) – these behaviours are not mimicry but entrainment – the spontaneous temporal coordination of behaviours (Knoblich, Butterfill, & Sebanz, 2011). Finally, mimicry is defined by some similarity in the form of the observed and executed behaviour. So it is different from complementary actions, for example, we may spontaneously grasp a free newspaper which is offered to us as he enter an underground station. Here, the vendor’s action and our own action are different in form. The above examples concern motor mimicry - when people mimic the movements of others. This will form the crux of this thesis, but it is important to briefly consider the many forms mimicry can take.

Mimicry occurs in a wide range of contexts - from the sporting match to the hospital room – and it also takes on many forms. Chartrand and van Baaren (2009) have outlined four types of mimicry: facial, emotional, verbal, and behavioural. Facial

mimicry involves mimicry of other people's facial expressions and movements. For example, parents open their mouths when feeding their infants (O'Toole & Dubin, 1968) and when people view a picture of someone smiling increased activity in the zygomatic major (a muscle involved in smiling) can be observed just 500 ms following picture presentation (Dimberg & Thunberg, 1998; Dimberg, Thunberg, & Grunedal, 2002). Emotional mimicry refers to the contagion (or 'catching') of other people's emotional states (Hatfield, Cacioppo, & Rapson, 1993). For example, when participants viewed angry or fearful faces, this not only resulted in facial mimicry, but also increased muscle activity in the arm muscles involved in making a fist or a defensive posture (Moody, Reed, Van Bommel, App, & McIntosh, 2017).

Verbal mimicry is the unconscious imitation of various aspects of people's language. During conversations people use the same words as others, copy their accents, speech rate, and utterance length (Marielle Stel & Vonk, 2010), and it has recently been shown that verbal mimicry may extend to internet-based verbal exchanges (Kwon & Gruzd, 2017). Finally, motor mimicry, which is the focus of this thesis, is the unconscious imitation of other people's bodily movements. In their seminal work, Chartrand and Bargh (1999) found that when participants interacted with a confederate who was instructed to either rub their face or shake their foot, participants also engaged in these behaviours more. This was despite participants reporting that they did not notice the confederate's face rubbing or foot shaking. Mimicry has been demonstrated for a range of motor behaviours, such as yawning (Helt, Eigsti, Snyder, & Fein, 2010), body posture (Tia et al., 2011) and pen-playing (Mariëlle Stel, Rispens, Leliveld, & Lokhorst, 2011). Together, this mimicry has been termed the "chameleon effect" as people change their movements to blend in with those around them (Chartrand & Bargh, 1999). But what purpose does mimicry serve? After all, the spectators were not competing in the match and the doctor was not giving birth.

1.1.2 Why do people mimic?

Theories of human mimicry fall into three broad camps (Wang & Hamilton, 2012). Firstly, theorists have emphasised the important social functions of mimicry, for example, in creating harmonious interactions (Chartrand & Bargh, 1999). Secondly, simulation theories argued that mimicry helps us understand other people's mental states by recreating their states in ourselves, for example, if you see someone is angry and you clench your fists this may help you understand their anger (Gallese, 2009). Finally, epiphenomenological theories do not regard mimicry as socially "special" – instead, mimicry is a by-product of generic, associative learning mechanisms which we share with other animals (Heyes, 2001, 2011). I deal with each approach in turn before outlining the social top-down response modulation (STORM) model (Yin Wang & Hamilton, 2012), which will be the focus of my thesis. This argues that mimicry is implemented as a social strategy for self-advancement (Wang & Hamilton, 2012). I finish this section by summarising the relationship between the different theories.

Mimicry as social glue

Social glue theory emphasises that successful coexistence in social groups has been fundamental for human survival (Lakin, Jefferis, Cheng, & Chartrand, 2003). Mimicry serves as a tool to foster successful and harmonious interactions between members of these social groups. By mimicking others, we display our similarity to them resulting in a social connection. Social glue theory is supported by studies which have demonstrated a bidirectional relationship between mimicry and liking. When we mimic others they like us more and we mimic those we like more (Chartrand & Bargh, 1999). Social glue theory predicts that when there is a desire to affiliate or promote closeness mimicry is enhanced. For example, individuals who have been made to feel socially excluded mimic their interaction partners more (Lakin, Chartrand, & Arkin, 2008) as do

those who have a greater motivation to affiliate (Lakin & Chartrand, 2003). Social glue theory also argues that mimicry has prosocial consequences beyond the immediate interaction. For example, mimicry results in increased donations to charity (Stel, van Baaren, & Vonk, 2008) and increased helping behaviour even towards people not involved in the mimicry situation (R. B. Van Baaren, Holland, Kawakami, & Van Knippenberg, 2004). These findings suggest mimicry may result in a general prosocial orientation.

However, social glue theory has recently been questioned. For example, Hale and Hamilton (2016b) highlighted that the link between mimicry and liking may be unreliable with half of the published studies on this topic failing to find evidence for this link (Maddux, Mullen, & Galinsky, 2008; Van Swol, 2003; Verberne, Ham, Ponnada, & Midden, 2013). Moreover, alternative theories of mimicry and imitation suggest that it is not the similarity of the movements which results in the prosocial consequences of mimicry but rather the contingency between movements. For example, Catmur and Heyes (2013) directly manipulated the similarity and contingency between observed and performed movements and found that contingency, rather than similarity, mediated the prosocial outcomes, such as closeness, enjoyment of the task, and helping behaviour. Thus, the link between mimicry and harmonious interactions, such as increased liking and rapport, remains to be robustly established. Moreover, if mimicry does bring about prosocial consequences, it is unclear whether mimicry *per se* is required to bring about these effects (e.g. moving similar body parts), or, whether these effects are the result of more general processes, such as the contingency between the movement of the mimicker and mimickee.

Mimicry as simulation

Simulation accounts of mimicry are a broad set of theories which posit that in order to understand other people's mental states, humans simulate or recreate those

states in their own motor, somatosensory and affective systems (Gallese, 2007; Niedenthal, Mermillod, Maringer, & Hess, 2010; Pickering & Garrod, 2004). For example, Allport (1924) proposed that people who mimic someone's facial expression have a better understanding of its meaning than those who do not. In terms of language, Pickering and Garrod's (2004) interactive alignment account proposed that when individuals engage in dialogue their linguistic representations become automatically aligned. This alignment manifests itself at a range of linguistic levels, for example, conversation partners mimic each other's intonation, words and syntax (Branigan, Pickering, & Cleland, 2000). Pickering and Garrod (2004; p. 188) state that by reusing the representations activated during language comprehension, alignment removes the "computational burden" involved in representing the mental state of one's conversation partner.

Similar claims have been made for the mimicry of facial expressions. Niedenthal and colleagues suggested that producing the same facial expression as someone (e.g. a smile) plays a functional role in emotion recognition (e.g. identifying their joy) (Niedenthal et al., 2010; Wood, Lupyan, Sherrin, & Niedenthal, 2016). Wood et al. (2016) found that when participants applied a facemask which increased "feedback noise" from their own facial movements, the ability to discriminate between morphed images of angry and sad facial expressions was diminished compared to a control group who had moisturiser applied to their faces. These group differences were not seen when discriminating morphed images of horses and cows. However, facial mimicry does not appear necessary for emotion recognition as individuals with Moebius syndrome – a rare genetic condition resulting in congenital facial paralysis – are able to identify a range of facial expressions (Bogart & Matsumoto, 2010). Although, it is possible that facial mimicry is useful when making more subtle judgments about other's facial expressions (Hess & Fischer, 2013).

The discovery of human mirror neurons (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Kilner, Neal, Weiskopf, Friston, & Frith, 2009), cells which discharge both during the observation and execution of a particular action, appeared to lend biological credence to simulation theories (Gallese & Goldman, 1998; Gallese & Sinigaglia, 2011). For example, Carr, Iacoboni, Dubeau, Mazziotta and Lenzi (2003) asked participants to observe or imitate emotional facial expressions during functional magnetic resonance imaging (fMRI). Both observation and imitation revealed activation of a network including the mirror neuron system and limbic system connected by the insula. Therefore, despite not explicitly copying the observed facial expression, activation of the mirror neuron system was sufficient to trigger limbic system activity and the potential experience of the other's emotion (Iacoboni, 2008). Some simulation accounts of mimicry also claim that differences in the mechanisms responsible for mimicry (e.g. the mirror neuron system) can result in conditions associated with altered social cognition, such as autism (Iacoboni & Dapretto, 2006; Williams, Whiten, Suddendorf, & Perrett, 2001). Yet, despite the intuitive appeal of simulation accounts of mimicry (Southgate & Hamilton, 2008), the extent to which we use our own sensorimotor systems to simulate and understand the others' mental states remains controversial (Hickok, 2013).

Mimicry as epiphenomenon

Heyes' associative sequence learning (ASL) model proposed that mimicry develops via associative mechanisms (Heyes, 2001, 2011). For example, if an infant opens her mouth and at the same time sees someone opening their mouth then the infant's visual representation of mouth opening is connected with her motor representation of mouth opening (Heyes, 2016). The ASL model strongly contests the claim that humans can copy observed actions at birth (Oostenbroek et al., 2016; Ray & Heyes, 2011). Rather, it argues that mimicry develops through sensorimotor

contingencies which develop from a range of sources during development, such as self-observation, being copied by caregivers and synchronous actions. ASL states that the reason non-human animals do not mimic as readily is that they do not have the same opportunities to experience sensorimotor contingencies. For example, humans have a prolonged period of development and engage in activities which specifically promote copying behaviours, such as music, pretend play and dance. Heyes argues that ASL is different from “stimulus-response behaviourism” as mimicry can be context-dependent. We develop associations between observed and performed actions but also learn about the consequences of these associations in different contexts. Different consequences of mimicry in different contexts means the tendency to mimic can be inhibited or facilitated.

The fundamental assumption of ASL - that mimicry develops through long term visuomotor connections - is supported by studies demonstrating that it is possible to alter these connections following incompatible sensorimotor experience. If participants observe a hand-opening action and are then required to perform a hand-opening action (compatible trials) their reaction times are faster than when they observe hand-closing and are then required to perform hand-opening (incompatible trials). However, if participants are trained to perform hand-opening after having observed hand-closing this can abolish the quicker reaction times on compatible trials (Heyes, Bird, Johnson, & Haggard, 2005). Similar findings have been demonstrated for different body parts (e.g. hand and foot movements; Gillmeister, Catmur, Liepelt, Brass, & Heyes, 2008) and in studies where participants can freely choose their action - so are not given explicit instructions to make an incompatible action (Wiggett, Hudson, Tipper, & Downing, 2011). Recent work with newly sighted individuals, who lacked early visuomotor experience, has showed that these people fail to show mimicry responses even when tested months after cataract-removal surgery (McKyton, Ben-Zion, & Zohary, 2018).

These sources of evidence suggest mimicry is likely to develop through contingent visuomotor experiences. Despite this evidence in favour of ASL, the view that mimicry is not present at birth has been disputed (Meltzoff et al., 2018). Moreover, although ASL makes strong claims about how mimicry develops, it places less emphasis on the possible functions of mimicry.

Mimicry as social strategy

The social top-down response modulation (STORM) model (Wang & Hamilton, 2012) regards mimicry as an unconscious Machiavellian strategy used to manipulate our social world for self-advancement. STORM predicts that the implementation of mimicry is determined by the anticipated social consequences of mimicry and is thus tightly controlled by social cues. As outlined above, considerable evidence suggests that people change their mimicry behaviour depending on the social context – for example, people are more likely to mimic when they feel socially excluded (Lakin, Chartrand & Arkin, 2008), when interacting with attractive people (van Leeuwen, Veling, van Baaren & Dijksterhuis, 2009) or people they like (Stel et al., 2010). Moreover, participants scoring high on narcissism mimic high-status, but not low-status, individuals more than those low in narcissism (Ashton-James & Levordashka, 2013). The model does not dispute the claim that mimicry may foster harmonious social interactions (Chartrand & Bargh, 1999), but crucially, according to STORM, this is done for personal social gain. For example, people give more money to those that mimic them (R. B. van Baaren, Holland, Steenaert, & van Knippenberg, 2003) and are also more easily persuaded by them (Maddux et al., 2008). Karremans and Verwijmeren (2008) have demonstrated the sophistication with which mimicry is controlled by social cues. They found that males not involved in romantic relationships mimicked an attractive confederate more than those involved in a romantic relationship. In line with STORM, Karremans and Verwijmeren argued that in order to protect their relationships

from a relationship-threatening alternative, romantically-involved participants unconsciously regulated their mimicry. Moreover, those participants who were in romantic relationships and reported being closer to their partner mimicked the confederate to an even lesser extent.

Additional support for STORM comes from studies using stimulus-response compatibility (SRC) paradigms which are reaction time measures of mimicry (Brass, Bekkering, Wohlschläger, & Prinz, 2000; Heyes, 2011). As described above, during a typical SRC task participants observe an action and make either a congruent (e.g., observe hand opening, perform hand opening) or incongruent (e.g., observe hand closing, perform hand opening) pre-specified action. Responses to congruent actions are faster than those to incongruent actions, and this congruency effect is taken as a measure of the tendency to mimic. Like studies investigating naturalistic mimicry (e.g. nose touching or foot shaking during conversation), the congruency effect is modulated by social cues, including the presence of eye gaze (Wang, Newport, & Hamilton, 2011), emotional facial expressions (Rauchbauer, Majdandžić, Hummer, Windischberger, & Lamm, 2015), social priming (Leighton, Bird, Orsini, & Heyes, 2010; Wang & Hamilton, 2013), and, beliefs about the model's animacy (Liepelt & Brass, 2010).

The advantage of SRC paradigms over naturalistic mimicry measures is that they allow the neural mechanisms of mimicry to be explored. Wang and Hamilton (2012) have argued that neuroimaging data can distinguish between different theories of mimicry. The mirror neuron system, including the inferior frontal gyrus (IFG), inferior parietal cortex (IPL) and superior/middle temporal sulcus/gyrus (STS/MTG), has been implicated in the implementation of mimicry (Bien, Roebroek, Goebel, & Sack, 2009; Iacoboni et al., 1999). The brain's mentalising system, including the medial prefrontal cortex (mPFC) and temporoparietal junction (TPJ), has been implicated in processing other's mental states (Fletcher et al., 1995; Marsh & Hamilton, 2011; Van Overwalle &

Baetens, 2009). For example, the mentalising system is active when attributing intentions to cartoon characters (Brunet, Sarfati, Hardy-Baylé, & Decety, 2000) or moving objects (Castelli, Happé, Frith, & Frith, 2000) and when actively processing others' intentions during competitive games (Gallagher, Jack, Roepstorff, & Frith, 2002).

Wang and Hamilton argued that if the mirror neuron system influences the mentalising system during mimicry, this would support a simulation account. As the brain's responses to mimicry are facilitating the understanding of other's mental states. Conversely, if the mentalising system controls the mirror neuron system during mimicry this would lend support to STORM, as the brains regions involved in interpreting the social situation (e.g. other's mental states) controls mimicry. A final possibility is that the two systems operate independently of each other during mimicry tasks. This would lend support to view that mimicry is not socially special in anyway but develops through domain general mechanisms.

To test this Wang, Ramsey and Hamilton (2011) conducted an fMRI study using a SRC task during which the model had either direct or averted gaze. Previous behavioural studies using this paradigm showed that direct gaze specifically enhances mimicry responses (Wang et al., 2011). As demonstrated in previous fMRI studies, Wang et al. found mirror neuron system activation during mimicry responses (Iacoboni et al., 1999) and mPFC activation when the model gave direct gaze (Schilbach et al., 2006) or when participants had to inhibit their tendency to mimic (Brass, Ruby, & Spengler, 2009). Using dynamic causal modelling, they found strong connections from mPFC to the superior temporal sulcus (STS) and from mPFC to IFG suggesting the mPFC exerts control over the mirror neuron system. Secondly, they found that the connection strength from mPFC to STS was modulated by the interaction between direct gaze and mimicry. This suggested that mPFC controls mimicry by modulating

sensory input into the mirror neuron system. Wang and Hamilton argued that this provides considerable support for STORM as it suggests that the mentalising system uses social cues to modulate the mirror neuron system which implements mimicry.

Yet, STORM's claim that all mimicry is subject to strategic social modulation has been challenged. Firstly, certain social cues do not reliably modulate mimicry. For example, if mimicry is driven by a Machiavellian motivation to improve one's social standing then one would expect social cues, such as the power and status, to modulate mimicry. Yet a comprehensive study by Farmer and colleagues demonstrated that these social cues do not modulate the mimicry of hand movements (Farmer, Carr, Svartdal, Winkielman, & Hamilton, 2016). Secondly, STORM argues that all types of mimicry are socially modulated. But different measures of mimicry, for example, reaction time measures compared to naturalistic mimicry, may not be related to each other which suggests different types of mimicry may not be socially modulated in the same way (Genschow et al., 2017). I deal with these methodological challenges in more detail below.

1.1.3 Summary

Theories of mimicry fall into three broad categories. One group of theories have emphasised the social functions of mimicry, for example, social glue theory argues that mimicry fosters harmonious social interactions (Chartrand & Bargh, 1999) and STORM claims mimicry is a strategy to further our social standing (Wang & Hamilton, 2012). Simulation theories argue that mimicry helps us understand the mental states of others by automatically recreating those states in ourselves (Niedenthal et al., 2010; Pickering & Garrod, 2004). Finally, epiphenomenological theories of mimicry, namely ASL (Heyes, 2001; 2011), do not attach a particular function to mimicry but instead argue that mimicry develops through generic, associative learning which connect contingent

motor and visual representations. Although these theories provide different explanations as to why people mimic, they are not mutually exclusive. For example, mimicry may develop through sensorimotor contingencies but may also help us to understand someone else's emotional state. Similarly, social glue and STORM both focus on the social consequences of mimicry, yet, mimicry could have multiple social consequences both for the individual, in terms of increasing their social standing, and for the interaction, in terms of increased rapport. Moreover, different types of mimicry may have different functions. For example, simulation accounts of mimicry may be most relevant for facial mimicry (Hess & Fischer, 2013) and verbal mimicry (Adank, Hagoort, & Bekkering, 2010) but it is less clear how they apply to the mimicry of other types of actions (Farmer, Ciaunica, & Hamilton, 2018). In the next section, I turn to mimicry in autism spectrum conditions (from herein *autism*), which are characterised by differences in social cognition and behaviour (American Psychiatric Association, 2013). What predictions do these theories make for mimicry behaviours in autistic individuals?

1.2 Mimicry and Autism

Table 1-1 Diagnostic criteria for autism

A. Persistent deficits in social communication and interaction	B. Restricted, repetitive patterns of behaviour, interests, or activities
Examples	Examples
<p>A1. Deficits in social-emotional reciprocity</p> <ul style="list-style-type: none"> • One-sided conversation • Differences in joint attention or sharing • Reduced pleasure in social interactions 	<p>B1. Stereotyped or repetitive motor movements</p> <ul style="list-style-type: none"> • Idiosyncratic or overly formal language • Echolalia, repetitive or unusual hand, face or body movements
<p>A2. Deficits in nonverbal communicative behaviours</p> <ul style="list-style-type: none"> • Differences in use of eye-contact, gesture and facial expression • Unusual volume, pitch, or prosody of speech 	<p>B2. Insistence on sameness, inflexible adherence to routines, or ritualised behaviour</p> <ul style="list-style-type: none"> • Overreaction to trivial changes to routine • Difficulty with non-literal aspects of language e.g. irony
<p>A3. Deficits in developing, maintaining, and understanding relationships</p> <ul style="list-style-type: none"> • Lack of interest in others • Difficulties in adjusting behaviour to different social situations 	<p>B3. Highly restricted, fixated interests abnormal in intensity or focus</p> <ul style="list-style-type: none"> • Narrow focus on few topics, objects or activities • Preoccupations; unusual fears
<p>C. Differences in behaviour must be present early in development. Although these can be masked until later life when the social environment becomes increasingly demanding.</p> <p>D. There must be some limitation or impairment to everyday functioning.</p> <p>E. Differences are not better explained by intellectual disability or a global developmental delay.</p>	<p>B4. Hyper- or hypo-reactivity to sensory input or unusual interest in sensory environment</p> <ul style="list-style-type: none"> • Preoccupation with touch or texture • Extreme distress from usual smells, tastes, sounds or lights <p>Table 1-1. A summary of the diagnostic criteria for Autism Spectrum Disorder (adapted from DSM-5, American Psychiatric Association, 2013). For a diagnosis all three A criteria must be met (i.e. A1, A2 and A3), 2 out of the 4 B criteria and all conditions for C, D and E.</p>

Autism is a neurodevelopmental condition which affects how people perceive the world and interact with others (Hill & Frith, 2003). According to the fifth edition of the Diagnostic and Statistical Manual of Mental Disorders (DSM-5, American Psychiatric Association, 2013), autism, which affects around 1% of the population (Brugha et al., 2012), is characterised by difficulties in social communication and interaction, and, restricted and repetitive patterns of behaviour (see Table 1-1, for a summary of the diagnostic criteria). Autism has a strong genetic basis (Bailey et al., 1995; Steffenburg et al., 1989) and is often present early in development, for example, infants later diagnosed with autism often show differences in eye contact or may be less responsive to their own name (Lord et al., 2000; Lord, Rutter, DiLavore, Risi, & Gotham, 2012). Approximately 30% of autistic people have intellectual disability defined by an IQ score of less than 70 (Chakrabarti & Fombonne, 2001, 2005) and about 10% of autistic people have an additional psychiatric or neurological condition, for example, epilepsy, attention-deficit hyperactivity disorder, dyspraxia and anxiety are some of the most common comorbidities (Gillberg & Billstedt, 2000).

Several theories have offered different cognitive explanations of autism (Frith, 2012; Hill & Frith, 2003). Baron-Cohen, Leslie and Frith (1985) proposed that autistic individuals do not have an intuitive understanding of other people's mental states so show differences in their 'theory of mind' or the ability to 'mentalise'. Other theories, such as 'central coherence' (Happé & Frith, 2006), have argued that autistic people tend to process information locally rather than globally, thus they pay more attention to small details rather than the broader context. Executive dysfunction accounts propose that autism is associated with some of the symptoms seen in frontal patients, such as differences impulse control, planning, and cognitive flexibility (Ozonoff & Mcevoy, 1994; Ozonoff, Pennington, & Rogers, 1991). More recently, theories have emphasised differences in social motivation in autism, for example, autistic individuals may be less

likely to seek out social stimuli as they find it less rewarding (Chevallier, Kohls, Troiani, Brodtkin, & Schultz, 2012) Finally, Bayesian theories have suggested that autistic people show differences in predictive processing, for example, when perceiving the world autistic people may weight incoming sensory data more strongly than their prior information about the world (Palmer, Lawson, & Hohwy, 2017; Pellicano & Burr, 2012). As yet, not one theory has fully captured the diverse range of behaviours displayed by autistic individuals. Often, theories may provide a reasonable account of the social signs of the condition but fail to account for the non-social aspects, or vice-versa (Bolis, Balsters, Wenderoth, Becchio, & Schilbach, 2017; Frith, 2012). The aim of this thesis is to focus one aspect of the autistic phenotype - mimicry. It is hoped that by studying this behaviour in detail, it will shed light on the cognitive and neural mechanisms which may be responsible for the other social and non-social differences seen in the condition.

1.2.1 Are there mimicry differences in autism?

In what is believed to be one of the first clinical descriptions of autism (Manouilenko & Bejerot, 2015; Wolff, 1996), Ssucharewa (or *Sukhareva*; 1926) mentions mimicry three times in her case report of the six boys she observed at the Psychoneurological Department for Children in Moscow. Case 2 displayed “paradoxical mimicry” as the boy “laughs with a sad facial expression” (p. 123), Case 3 “mimics everyone” (p. 127), whilst, Case 6 showed “a certain lack of mimicry and expressive movements” (Ssucharewa, 1926; Wolff, 1996; p. 130). These cases highlight the diversity of mimicry differences in autism and characterising these differences has proved challenging. For example, as Ssucharewa noted, some autistic individuals (e.g. Case 6) show a reduced propensity to copy others (Hermans, van Wingen, Bos, Putman, & van Honk, 2009; McIntosh, Reichmann-Decker, Winkielman, & Wilbarger, 2006; Yoshimura, Sato, Uono, & Toichi, 2015), whereas some autistic individuals (e.g. Case

3) display echolalia and echopraxia - an *increased* tendency to involuntarily copy the speech and actions of others (American Psychiatric Association, 2013; Spengler, Bird, & Brass, 2010). In this section I highlight the different theories which have tried to formalise these mimicry differences in autism before outlining the specific hypotheses tested in this thesis.

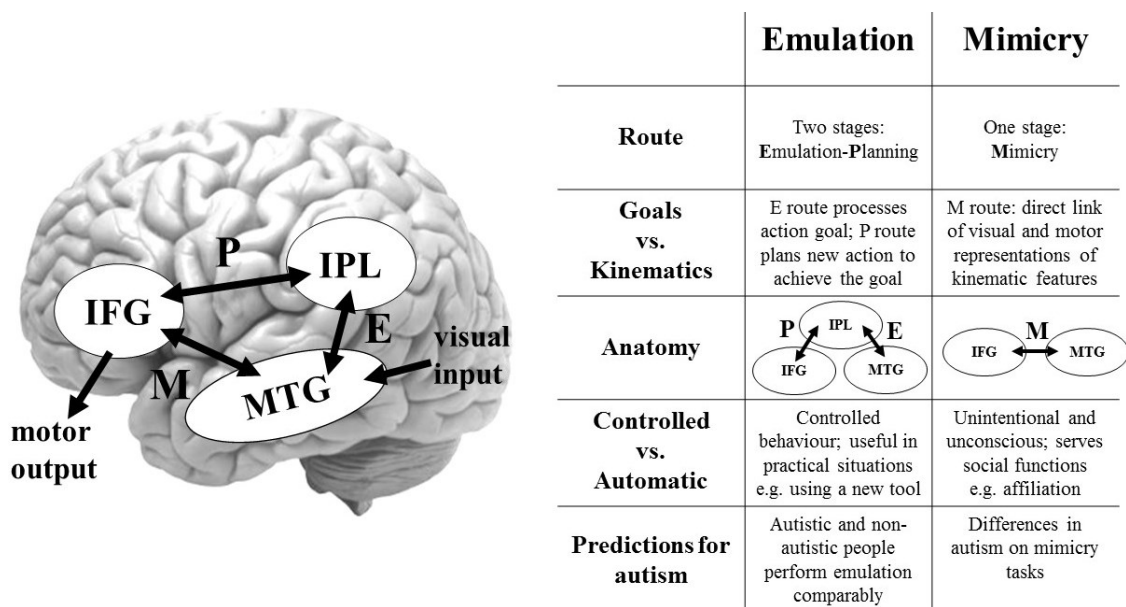


Figure 1-2 The EP-M Model (adapted from Hamilton, 2008)

1.2.2 Emulation vs. mimicry

Hamilton's (2008) Emulation/Planning-Mimicry (EP-M) model made a distinction between mimicry and emulation (see Figure 1-2). Mimicry involves implicitly and automatically copying the detailed kinematic features of an observed action, rather than just the action goal. Conversely, emulation is a controlled behaviour which involves copying the explicit goal of an observed action. Whereas mimicry is useful in situations with social motivations (e.g. establishing rapport), emulation is useful in practical situations (e.g. when learning how to use a tool). The EP-M model suggests that mimicry and emulation have distinct anatomical pathways within the mirror neuron system, the brain areas engaged when both observing and executing actions (Iacoboni et al., 1999; Rizzolatti & Craighero, 2004). Mimicry (the M route) involves a direct link between the visual input from an observed action in the middle

temporal gyrus (MTG) to motor output in the inferior frontal gyrus (IFG). Emulation of an observed action (the EP route) follows an indirect, two stage route: first, the action goal must be represented in the inferior parietal lobule (IPL), then, a new action must be planned from the IPL to the IFG. Neuroimaging studies have lent support to the model. Using a repetition suppression approach, Hamilton and Grafton (Hamilton & Grafton, 2006) found that observation of a repeated goal led to a suppression of activity in anterior intraparietal sulcus (aIPS), part of the EP route. This suppression did not occur when observing a series of novel goals. Moreover, Grafton and Hamilton (2007) again used a repetition suppression approach to demonstrate that aIPS represented the goal of the action (pick up bottle vs. pick up dumbbell), whereas, IFG and MTG represented the types of grasp used to pick up the object (finger-tip grasp on the top of the object vs. whole hand grip on the middle of the object).

In terms of autism, Hamilton (2008) proposed that autistic individuals perform well on emulation tasks but tend to perform differently on mimicry tasks compared to non-autistic participants. There is considerable support for Hamilton's proposal. For example, Hobson & Lee (1999) found that autistic participants were proficient in copying goal-directed actions, but tended not to copy the style with which the experimenter executed those actions. Similarly, McIntosh, Reichmann-Decker, Winkielman & Wilbarger (2006) found that, unlike non-autistic participants, autistic adolescents and adults did not spontaneously mimic happy and angry facial expressions. Yet, when explicitly instructed to copy an observed facial expression, autistic participants performed as non-autistic participants. Moreover, Wild, Poliakoff, Jerrison and Gowen (2012) found autistic participants were less sensitive to the duration, velocity and vertical amplitude of observed actions during an imitation task. Eye-tracking also revealed more goal-directed eye-movements in autism suggesting an over-reliance on goal-directed imitation strategies and a reduced propensity to mimic. A

meta-analysis of 53 studies investigating imitation abilities in autism supported Hamilton's proposal. It showed spared performance when copying only the goal of an action (i.e. emulation) but a reduced tendency to copy both the form (i.e. style) of an action (Edwards, 2014). In sum, Hamilton's EP-M model argued that autistic people can copy and understand the goals of observed actions but show differences in mimicry – the unconscious, automatic imitation of the kinematics features of others' actions.

1.2.3 Different mimicry or different modulation?

Despite the studies outlined above demonstrating a reduced propensity to mimic in autism, some studies suggest autistic people can mimic others and are sometimes sensitive to the kinematics features of other people's actions. For example, autistic adults show automatic imitation effects comparable to non-autistic participants in response to hand movements (Bird, Leighton, Press, & Heyes, 2007) and facial expressions (Press, Richardson, & Bird, 2010). Gowen, Stanley and Miall (2008) showed that autistic participants display comparable motor interference when observing incongruent arm movements which suggests some sensitivity to observed kinematics. In a recent meta-analysis which included over 200 autistic participants, Cracco et al, (2018) found no evidence for differences in automatic imitation. There are also reports of an increased propensity to show mimicry responses in autism. Spengler, Bird and Brass (2010) used an automatic imitation paradigm to show that autistic adults were less able to inhibit mimicry responses. These differences in the control of mimicry were related to activation in the mentalising areas, such as medial prefrontal cortex (mPFC), and the amount of autistic behaviours displayed during the Autism Diagnostic Observation Schedule (ADOS; Lord et al., 2000) – an autism diagnostic interview. The finding that the control of mimicry is related to the cognitive and neural mechanisms responsible for mentalising has been supported by neuroimaging studies in healthy participants (Brass et al., 2009) and those with frontal and temporoparietal lesions

(Spengler, von Cramon, & Brass, 2010). Finally, as outlined above, Wang et al. (2011) showed mPFC is sensitive to social cues, such as eye-gaze, and controls input to the neural mechanisms which implement mimicry.

Given these data, Hamilton (2008) acknowledged that it may not be mimicry *per se* which is different in autism but rather the control or modulation of mimicry. Wang and Hamilton's (2012) STORM model (outlined in Section 1) formalised this proposal. Specifically, the model argued that whilst non-autistic people socially modulate their mimicry for self-advancement, mimicry in autistic people is not modulated according to the social context. However, the basic cognitive and neural mechanisms responsible for mimicry are intact in autism. This model is easier to reconcile with reports of increased mimicry in autistic individuals either during experimental tasks (Spengler, Bird, et al., 2010) or in clinical observations (e.g. echopraxia and echolalia; American Psychiatric Association, 2013). STORM argues that the cognitive and neural mechanisms of mentalising are different in autism and this affects the control and social modulation of mimicry. First, I present evidence that autistic participants show reduced performance on mentalising tasks and associated differences in brain activation (e.g. mPFC and TPJ), before outlining studies which have suggested that the social modulation of mimicry may be different in autism.

Mentalising tasks involve processing other's mental states and a wealth of behavioural and neuroimaging studies have demonstrated differences on these tasks in autism (Marsh & Hamilton, 2011). Autistic children show reduced performance on false belief tasks (Baron-Cohen, 2000; Baron-Cohen et al., 1985; Frith, 2001) in which they have to dissociate their own beliefs (e.g. the marble is in the box) from another person's beliefs about the world (e.g. Sally thinks the marble is in the basket). Studies in autistic adults revealed differences in performance on implicit false belief tasks (Senju, 2012). During these tasks autistic adults' eye-movements suggest they do not spontaneously

attribute mental states to others although these participants may give the correct verbal response during explicit false belief tasks (Senju, Southgate, White, & Frith, 2009). Although, it is worth noting that the validity of some implicit mentalising tasks has recently been questioned (Kulke, von Duhn, Schneider, & Rakoczy, 2018).

In terms of neuroimaging, Castelli, Frith, Happe, and Frith (Castelli, Frith, Happé, & Frith, 2002) used positron emission tomography to show altered activity in mentalising regions in autistic adults whilst viewing animated shapes interpreted as having mental states (White, Coniston, Rogers, & Frith, 2011). Similarly, in fMRI studies, Gilbert and colleagues showed differences in mPFC activation in autistic adult when mentalising (Gilbert, Meuwese, Towgood, Frith, & Burgess, 2009) and, Marsh and Hamilton (2011) found that whilst mPFC distinguished between rational and irrational hand actions in non-autistic adults, this was not the case in autistic participants.

Wang and Hamilton's (2012) hypothesis that mimicry is not socially modulated in autism is supported by several studies employing stimulus-response compatibility paradigms. These showed that automatic imitation is intact in autism as shown by faster responses to congruent rather than incongruent actions, but modulation of this congruency effect by social cues may be different. For example, Cook and Bird (2012) showed pro-social priming relative to non-social priming led to an enhancement of automatic imitation in neurotypical participants but not in autistic participants. Similarly, Grecucci et al. (2013) found automatic imitation was enhanced in neurotypical participants, but not in autism, when preceded by emotional facial expressions. Moreover, Vivanti and Dissanayake (2014) found that non-autistic preschoolers imitated more frequently following direct gaze, whereas age-matched autistic children imitated to the same extent following direct and averted gaze.

Despite evidence in favour of STORM, it is important to acknowledge that not all mimicry differences in autism may be due to differences in social modulation. For example, Jiménez et al. (2015) aimed to reduce the social motivation to mimic by giving participants explicit instructions to focus on the goal of the observed action (Jiménez, Ortiz-Tudela, Méndez, & Lorda, 2015). However, despite this reduced social motivation to mimic, Jiménez et al. replicated a previous study (Jiménez, Lorda, & Méndez, 2014) and found that autistic children were still less likely to mimic. They concluded that some of the mimicry differences seen in autism are due to factors beyond differences in top-down social modulation. Given this controversy, the primary aim of the current thesis was to rigorously test a key prediction arising from STORM: autistic people can and do mimic others but do not modulate their mimicry strategically according to the social context.

1.2.3 Summary

Given the potential importance of copying behaviours, such as mimicry and imitation, during development, there has been a long debate concerning whether autistic people show differences in these behaviours. When considering these differences it is important to distinguish mimicry from other types of copying behaviours (Edwards, 2014; Hamilton, 2008). For example, a range of studies have demonstrated that autistic people understand the actions of others (Hamilton et al., 2007) and readily copy the goal of these actions (Wild et al., 2012). Thus, autistic people seem to emulate other people's actions in the same way as their non-autistic peers (Hamilton, 2013; Southgate, Gergely, & Csibra, 2008). Mimicry, however, involves the automatic and unconscious imitation of the kinematic features of other people's actions and, unlike emulation, is not goal-directed (Hamilton, 2008). Emerging evidence suggests that autistic people show differences in mimicry (Edwards, 2014) but characterising these differences has proved difficult. Some reports have suggested a reduced tendency to mimic (Hobson & Lee,

1999), others have showed an increased tendency to mimic (Spengler, Bird, et al., 2010), and some have suggested that the basic mechanisms for mimicry are intact in autism (Cracco et al., 2018). Wang and Hamilton's (2012) STORM model has argued that autistic people can and do mimic but show differences in their control of mimicry, specifically the social modulation of mimicry. Support for this prediction comes from studies showing that mentalising areas, such as mPFC, show different activation in autism (Gilbert et al., 2009; Marsh & Hamilton, 2011) and these regions have been strongly implicated in the control of mimicry (Wang et al., 2011). Although, several studies have provided indirect support for STORM (Cook & Bird, 2012; Grecucci et al., 2013), the theory remains controversial (Jiménez et al., 2015). The primary aim of the current thesis was to rigorously explore this key question arising from STORM: do social signals modulate mimicry in autism? In the next section I outline the diverse ways in which mimicry can be measured.

1.3 Measuring Mimicry

Mimicry falls within a broader category of social behaviours referred to as interpersonal coordination. This is the extent to which behaviours are non-random, patterned or synchronised in either timing or form during a social interaction (Bernieri & Rosenthal, 1991). As outlined above, mimicry is distinct from other forms of interpersonal coordination in that there must be some topographical or kinematic matching between the movements of the interaction partners, it must be automatic (i.e. unconscious), and, there must be some delay between the movement of one individual and the contingent movement of their interaction partner. In this thesis, I focus solely on measures concerning the mimicry of movements (motor mimicry) as opposed to verbal or emotional mimicry. Motor mimicry has been operationalised in a range of ways from simple frequency counts of discrete actions to more sophisticated kinematic analyses of

motion tracking data. I provide a critical overview of these different methods before outlining and justifying the methods used in this thesis.

1.3.1 Naturalistic mimicry

Naturalistic mimicry occurs during real-life social interactions and involves participants unconsciously copying the discrete action of an interaction partner. Naturalistic mimicry can be induced during social interactions by having a confederate perform a certain action (e.g. foot shaking) and counting the frequency with which a participant copies this. A confederate can also mimic the movements of a participant and the social consequences of this mimicry can be investigated, for example, whether mimicry results in greater rapport or other prosocial consequences. Alternatively, naturalistic mimicry does not have to be induced via a confederate but can instead be measured by determining the extent to which participants spontaneously coordinate their bodily movements during social interactions, for example, in terms of their posture or head movements.

In one of the first studies to induce mimicry using a confederate, Dabbs (1969) asked two participants to interview a confederate. The confederate interviewee mimicked the gestures and mannerisms of one of the participant interviewers and was subsequently evaluated more favourably by the interviewer who he had mimicked (e.g. he was considered better informed). Mimicry did not, however, result in more liking. Similarly, Chartrand and Bargh (1999) asked participants to take turns describing photos with another 'participant' who was actually a confederate. The confederate was instructed to either shake their foot or rub their face during the interaction. Participants shook their foot more when the confederate shook their foot during the interaction and the same results were found for face rubbing (Experiment 1). In a further experiment, Chartrand and Bargh (1999; Experiment 2) showed that those participants whose

movements and mannerisms were mimicked by a confederate rated the interaction as having gone more smoothly and liked the confederate more. Mimicry also seems to make participants more likely to help the mimicker. Participants whose body orientation and arm movements were mimicked by a confederate during a photo description task were more likely to agree to help the confederate than those participants she did not mimic. The confederate asked the participant whether they would read and critique a lengthy essay she had written and provide feedback within 48 hours – over three-quarters of the mimicked participants agreed but less than half of the non-mimicked participants did so (Guéguen, Martin, & Meineri, 2011)

Postural mirroring is a further measure of naturalistic mimicry which examines the extent to which people mimic the physical stance of others. For example, in a face-to-face interaction two people may have their opposite arms are in an identical position (LaFrance, 1985). Schefflen (1964) proposed that those who adopt a similar physical stance share a common psychological stance. This link between postural mirroring and relatedness or rapport has been reported in a range of studies. For example, Charney (1966) showed that “congruent postures” during psychotherapy sessions between the therapist and patient were related to instances of positive, interpersonal speech. This was supported by Trout and Rosenfeld (1980) who found that when the therapist mimicked the arm, hand and leg movements of their patients, their relationship was judged as having greater rapport by student raters. Moreover, in a seminar classroom the extent to which students adopted the postures of the teacher was positively correlated with student’s ratings of their involvement in the class (LaFrance & Broadbent, 1976).

Unlike other actions which are mimicked, such as foot-shaking or posture, head movements are tightly coupled with speech (Heylen et al., 2011), For example, people often nod their head when indicating their approval at something their interaction partner has said (Rosenthal & Jacobson, 1968). Thus, during social interactions head

movements are likely to be under more deliberate control than other types of body movements (Ramseyer & Tschacher, 2014). A range of techniques using motion tracking can be used to quantify the extent of head mimicry, including cross-correlation, wavelet analysis and recurrence (see Delaherche et al., 2012 for a review), and, as with other types of mimicry the extent of coordinated head movements may be related to the success of the interaction. For example, Ramseyer and Tschacher (2014) used motion energy analysis and cross-correlation to quantify the amount of head and body mimicry between the therapist and patient during psychotherapy sessions. They found that the amount of head mimicry predicted the overall success of the therapy.

However, not all studies have replicated these effects and the extent of head nodding may often be confounded by other factors during social interaction, such as the nature of the conversation (Rosenthal & Jacobson, 1968). For example, in one study participants synchronised their bodily sway during a photo description task but not their head movements (Shockley, Santana, & Fowler, 2003). Hale (2017) used wavelet analysis and found significant coupling of head movements at frequencies below 1.5 Hz but active *decoupling* of head movements at higher frequencies (1.5 – 5 Hz). But this coupling was not related to prosocial outcomes, such as rapport or trust, nor was it influenced by prosocial or antisocial priming.

Naturalistic mimicry can be measured for a range of body movements - from foot-shaking to head nodding. An advantage of naturalistic mimicry is that it captures mimicry during realistic social interactions, for example, during a conversation or therapy session. It is therefore one of the more ecologically valid ways to measure mimicry behaviours. Yet, rates of spontaneous mimicry during naturalistic interaction may be quite low so it may be quite hard to detect between conditions. Thus, confederates are used to induce mimicry. However, the use of confederates to induce mimicry is problematic as the confederate may not be blind to the experimental

condition; thus, their expectations could impact the behaviour of the participant across different mimicry conditions (Gilder & Heerey, 2018). For example, subtle differences in the confederate's eye-contact and social attention could confound the differences between conditions (Hale & Hamilton, 2016b).

A range of studies using a variety of analysis techniques (Delaherche et al., 2012) have tracked head movements during conversations and found a relationship between head mimicry and prosocial outcomes (e.g. the success of therapy; Ramseyer and Tschacher (2014). However, it is unclear what this head mimicry means. For example, nodding more during a conversation is related to positive impressions of counsellors and other interaction partners (Harrigan, 2008). Thus, if participants are nodding more during successful social interactions this increases the chances of finding greater head mimicry. Hence, it is possible that greater head mimicry is a serendipitous by-product of successful social interaction rather than a phenomenon which contributes towards them. Next, I turn to measures which have investigated mimicry under more controlled laboratory conditions.

1.3.2 Reaction time measures

In contrast to measures of motor mimicry in naturalistic settings which have high ecological validity (e.g. the frequency of face-touching during a conversation), reaction time measures aim to measure mimicry in a controlled laboratory setting using stimulus-response compatibility paradigms (Proctor & Vu, 2006). Whilst mimicry studies were traditionally conducted within social psychology, the advent of these reaction time measures approximately 20 years ago enabled the cognitive and neural mechanisms of mimicry to be investigated on a millisecond timescale (Brass et al., 2000; Stürmer, Aschersleben, & Prinz, 2000). Reaction time measures of mimicry require participants to make a response following a task-relevant stimulus, for example,

a blue colour cue means they must open their hands and a red colour cue means they must close their hand. At the same time a task-irrelevant stimulus appears showing a hand either opening or closing. When participants are required to open their hands (blue cue) and the task-irrelevant stimulus is compatible with this action (hand opening), reaction times are faster compared to conditions in which the task-irrelevant stimulus is incompatible with the required action (i.e. perform hand opening, observe hand closing) (Heyes, 2011; Stunner et al., 2000). Similar effects can be shown for index and middle finger movements during which the participants must move their index finger if they see the number 1 and their middle finger if they see the number 2. These numbers are superimposed on images of a hand moving either its index or middle finger (Brass et al., 2000). The differences between reaction times in compatible and incompatible trials are called congruency effects and this phenomenon has been called ‘automatic imitation’ (Heyes, 2011). Since these initial studies using hand and finger stimuli, automatic imitation has been demonstrated for compatible and incompatible mouth (Leighton & Heyes, 2010), foot (Gillmeister et al., 2008), and arm (Kilner, Paulignan, & Blakemore, 2003) movements.

Heyes (2011; p. 464) argued that naturalistic mimicry (Chartrand & Bargh, 1999) could be automatic imitation “in the wild” and thus taps into the same psychological processes – analogous to the relationship between silent reading and reading aloud. However, the extent to which reaction time measures are related to motor mimicry in naturalistic settings is not yet known and Ramsey (2018) has thus questioned the validity of automatic imitations as a measure of mimicry. For example, only one study has investigated the relationship between automatic imitation and naturalistic mimicry and found no evidence that these behaviours were correlated (Genschow et al., 2017). Yet, the claim that automatic imitation is related to mimicry

“in the wild” is supported by three lines of evidence which I deal with in turn (Heyes, 2011).

Firstly, automatic imitation is imitative in that it is based on the topographical, rather than a purely spatial or conceptual, matching between the observed and executed movement. Jansson et al. argued that the spatial compatibility between the observed and executed movement could be driving automatic imitation (Jansson, Wilson, Williams, & Mon-Williams, 2007). For example, participants may be quicker to make an upward movement after having observed something move upwards or are quicker to make a movement in the right side of space having observed something move on the right side of space. However, if the stimulus is presented orthogonally (Heyes et al., 2005; Wang et al., 2011) or flipped completely (Brass, Bekkering, & Prinz, 2001) relative to the participants viewpoint, automatic imitation effects still occur. A further way to control for spatial compatibility effects is to present a left hand on the screen in half the trials and a right hand in the other half (Catmur & Heyes, 2011). In the left-hand trials, spatial and imitative compatibility are congruent, whereas, in right-hand trials, spatial and imitative compatibility are incongruent. Such a design allows imitative compatibility to be separated from spatial compatibility. In a recent meta-analysis which systematically explored over 200 automatic imitation experiments, Cracco et al. (2018) concluded that spatial compatibility consistently contributed to automatic imitation effects but could not fully explain them. However, the imitative component of automatic imitation is 3 or 4 times smaller than the spatial component (Catmur & Heyes, 2011; Marsh, Bird, & Catmur, 2016). This suggests that automatic imitation effects have an imitative component so are at least partially due to the topographical matching between the observed and executed movement.

Jansson et al. (2007) have also argued that automatic imitation could be due to conceptual compatibility. Here, viewing hand opening, for example, activates a

semantic representation of “opening” resulting in an enhancement of congruent reaction times. The suggestion being that automatic imitation effects could occur independently of congruent motor representations. Yet, if this were the case then one would expect viewing hand opening to have similar effects on all types of opening movements (e.g. mouth opening) not just hand opening (Heyes, 2011). Yet, Leighton and Heyes (2010) did not find evidence to support this – rather, there were greater automatic imitation effects when it was specific to a particular effector. This speaks against purely conceptual compatibility effects. Thus, it appears automatic imitation depends to some extent on the topographic properties of the observed and executed body movements rather than just spatial or conceptual compatibility effects.

Secondly, Heyes (2011) claimed that automatic imitation is automatic as it occurs independent of intention and does not cease if attentional resources are compromised. Heyes argued that this automaticity makes automatic imitation comparable to naturalistic motor mimicry which people do not notice they are engaged in (Chartrand & Bargh, 1999). This claim is supported by studies which have increased attentional load and found that automatic imitation persisted under such conditions (Catmur, 2016). Moreover, when participants were given strong incentives not to automatically imitate, for example during competitive games like rock-paper-scissors (Cook, Bird, Lunser, Huck, & Heyes, 2012), they still did so even when this compromised financial payoffs (Belot, Crawford, Heyes, & Scheinkman, 2013). Yet, automaticity is multifaceted concept and includes factors such as speed, consciousness, intentionality and attention (Moors & De Houwer, 2006) - the extent to which automatic imitation meets all these criteria remains equivocal (Cracco et al., 2018).

Thirdly, it is claimed that automatic imitation is modulated by similar social cues to naturalistic mimicry (Wang and Hamilton, 2012). For example, social priming (Leighton et al., 2010), the appearance of the stimuli (Bird et al., 2007), beliefs about

the stimuli's animacy (Liepelt & Brass, 2010) and group membership (Rauchbauer et al., 2015) have all shown to modulate automatic imitation as have the presence of social cues, such as eye-gaze (Wang et al., 2011) and emotional facial expressions (Grecucci et al., 2013). However, these social cues vary in how consistently they modulate automatic imitation. For example, whilst eye-gaze has been shown to enhance automatic imitation across several studies (Marsh, Bird, & Catmur, 2016; Wang et al., 2011; Wang et al., 2011), power and status do modulate automatic imitation (Farmer et al., 2016) in the same way as naturalistic mimicry (Ashton-James & Levordashka, 2013; Cheng & Chartrand, 2003).

In sum, automatic imitation has enabled the cognitive and neural mechanisms of mimicry phenomenon to be studied on a millisecond timescale. The extent to which automatic imitation, measured using reaction time measures of mimicry, is distinct from naturalistic mimicry remains controversial (Cracco & Brass, 2018; Ramsey, 2018). Automatic imitation paradigms, such as the 'finger tapping' task (Brass et al., 2000), share several characteristics with naturalistic measures of mimicry, such as the frequency of with which a participant copies a confederate's face-touching (Chartrand & Bargh, 1999). Firstly, both require some topographical matching between the observed and executed movement (Brass et al., 2001). Secondly, both phenomena occur independent of intention so are to some extent considered automatic (Cook et al., 2012), and, finally, social cues modulate both processes (Wang & Hamilton, 2012). Yet, despite automatic imitation and mimicry measures sharing these similar features, there are fundamental differences between the two processes (Ramsey, 2018). Firstly, automatic imitation occurs on a millisecond timescale, whereas, during naturalistic mimicry the delay between the observed and executed action occurs over several seconds (e.g. 4 seconds according to Van Baaren, Janssen, Chartrand, & Dijksterhuis, 2009). Secondly, imitative responses to simple finger and hand movements, as indexed

by automatic imitation studies, are likely to develop primarily through self-observation ('non-social sensorimotor contingencies'; Farmer et al., 2018), whereas, naturalistic mimicry responses are much more likely to develop via social interaction ('social sensorimotor contingencies'; Farmer et al., 2018). Thus, how readily social cues modulate these different measures is likely to vary. Finally, Cracco and Brass (2018) have highlighted how these two processes rely on different mechanisms: automatic imitation is dependent on corticospinal facilitation of the observed action (Bardi, Gheza, & Brass, 2017), whilst naturalistic mimicry is the result of generalised sensorimotor arousal (van Schaik, Sacheli, Bekkering, Toni, & Aglioti, 2017). Thus, although automatic imitation tasks share some of the features of naturalistic mimicry tasks (Heyes, 2011), it is important to keep in mind these important differences between the two tasks (Ramsey, 2018). Moreover, only one study has investigated the relationship between automatic imitation and naturalistic motor mimicry and found that these phenomena were not correlated (Genschow et al., 2017).

1.3.3 Kinematic mimicry

The measures outlined so far have either manually coded mimicry from video recordings or have recorded participants' reaction times to press a key or move their hands. However, motion tracking technology has enabled researchers to capture the movements of participants in much greater detail. In terms of mimicry, motion tracking studies can examine the extent to which participants are sensitive to the kinematic features of a co-actor's movements. For example, are participants' own movements sensitive to the velocity or height of other people's movements? In such tasks participants are required to make a pre-specified movement and the extent to which this movement is influenced by another agent's kinematics can be measured.

In one such study, participants watched videos of an actor point to three locations with either a fast or slow velocity (Wild, Poliakoff, Jerrison, & Gowen, 2010).

Participants were then required to point to the same sequence of locations on a table in front of them. In half the videos there were targets at the locations (goal condition) whereas in the other half there were no targets (no-goal condition). Wild et al. found that in the no-goal condition participants mimicked the velocity of the actor's movements. That is, they moved with greater velocity in the fast compared to slow trials. In a follow up study, Wild et al. (2012) found that autistic participants did not mimic the velocity of the actors' movement in either the goal or no-goal condition (Wild et al., 2012). These studies demonstrated that participants mimic the kinematics features of other people's movement. Studies using moving dots, rather than human stimuli, have found a similar sensitivity to differences in observed kinematic profiles (Hayes, Dutoy, Elliott, Gowen, & Bennett, 2016). Participants' reach-to-grasp actions are also influenced by the kinematics of others' movements. For example, participants were asked to reach and grasp for an object having recently observed or whilst observing an experimenter grasp an object with a normal (80 mm) or exaggeratedly high (150 mm) trajectory (Hardwick & Edwards, 2011). Participants own reaching movements (i.e. their maximum wrist height) were higher whilst observing or having just observed the experimenter reach with an exaggerated trajectory. Thus, participants own movements are sensitive to the exaggerated kinematics of others' movements. Comparable findings have been reported for prehensile movements. When participants were required to grasp a cube whilst simultaneously observing an experimenter lifting a larger cube, participant's maximum grip aperture (the distance between their fingers) was greater (Dijkerman & Smit, 2007). This shows that participants' mimic the wrist trajectories and finger kinematics of those around them.

As with other types of mimicry, there is evidence to suggest that kinematic mimicry is influenced by contextual factors. For example, Bek, Poliakoff, Marshall, Trueman and Gowen (2016) employed the same paradigm as Wild et al. (2010; 2012)

and asked participants to either attend closely to the pointing movements of the actor (attention condition) or imagine performing the movements themselves (imagery condition). Compared to a control group, the participants pointing movements in the imagery and attention conditions were more closely matched to those of the model in terms of their kinematics, such as the duration, peak velocity and amplitude. Thus, the presence of goals (Wild et al., 2010), an autism diagnosis (Wild et al., 2012) as well as motor imagery and attention (Bek et al., 2016) all modulate the extent to which participant mimic the kinematics of others' movements. However, whether kinematic mimicry is modulated by social cues, such as eye-gaze or social engagement, remains unclear (Krishnan-Barman, Forbes, & Hamilton, 2017) and is one of the key questions explored in this thesis.

An advantage of using kinematic measures of mimicry is that motion tracking studies yield rich data allowing researchers to establish which movement parameters (e.g. velocity, peak height, grip aperture) have been mimicked and the extent to which they have been mimicked. Thus, when compared to reaction time measures, kinematic mimicry gives us a much more nuanced and detailed understanding of how people mimic each other during social interactions (Krishnan-Barman et al., 2017). However, although the influence of other people's kinematics on our own movements appears to be consistent, the extent to which they affect our movements is small and subtle. For example, in Hardwick and Edwards (2011) the difference between the experimenters normal and exaggerated trajectory was about 70 mm but the difference in the participant's movements between these conditions was just 3 mm so over 20 times smaller. Here, the participants' 'perturbed' movement trajectories in the exaggerated condition were much closer to the experimenter's movement trajectories in the normal condition, despite being slightly higher on average in this condition. Comparably small effects have been found for grip aperture mimicry despite large differences in the

observed movement (Dijkerman & Smit, 2007). Thus, kinematic mimicry is subtler than others forms of mimicry in which participants mimic the form of the observed movement more closely, for example, someone's posture or a discrete action, such as foot shaking.

1.3.4 Virtual reality




Virtual reality involves the computer stimulation of environments and has been made possible by advances in 3D computer graphics (Earnshaw, 1993). Whilst traditionally used for video games or training purposes (e.g. flight simulation), in the past two decades there has been an explosion of research within experimental psychology and neuroscience which has used virtual reality environments (Bohil, Alicea, & Biocca, 2011). Various technologies exist to implement virtual reality (for an outline of the key approaches see Table 1-2). Virtual reality environments may be particularly useful for studies investigating human social interactions which have been hampered by a trade-off between ecological validity and experimental control (Blascovich et al., 2002). That is, the more control researchers have over their variables of interest, the less naturalistic the experimental setting. Conversely, if the experimental setting is more naturalistic, the likelihood of extraneous variables confounding the dependent variables increases, as does the likelihood of replication difficulties. This trade-off between ecological validity and experimental control is exemplified in measures of mimicry. For example, during naturalistic mimicry it is unlikely that confederates keep their non-mimicry behaviour (e.g. eye contact) completely consistent across conditions although the situation (e.g. a live conversation) is realistic (Hale & Hamilton, 2016). Conversely, reaction time measures of mimicry, such as automatic imitation, allow mimicry to be indexed on a millisecond timescale but may not be related to mimicry processes outside the lab (Genschow et al., 2017). It is probable that this trade-off between ecological validity and experimental control has contributed to

the lack of reproducibility, generalisability and validity of social psychological experiments (Open Science Collaboration, 2015)

It has been argued that virtual reality provides a potential solution to this trade-off; virtual environments can be naturalistic yet are easily replicable and offer a high degree of control over the key variables (Blascovich et al., 2002). For example, virtual reality allows for ‘standardised social interaction partners’ so that the behaviour of the interaction partner is consistent across all participants and unaffected by their behaviour (Bombari, Schmid Mast, Canadas, & Bachmann, 2015; p. 2). Such consistency is difficult when using confederates (Kuhlen & Brennan, 2013). Moreover, virtual reality allows researchers to easily change one variable at a time and determine its impact on social behaviour. For example, changing important social features such the gender (Banakou, 2010), race (Peck, Seinfeld, Aglioti, & Slater, 2013) or age (Banakou, Groten, & Slater, 2013) of a virtual character often involves changing just one line of code. Manipulating such variables one at a time with human confederates and ensuring they are matched on other social qualities, such attractiveness or height, is much trickier (Pan & Hamilton, 2018).

Considerable evidence across multiple domains of social psychology and social neuroscience suggests that humans interact with and respond to virtual agents in a similar way to humans. For example, Bailenson, Blascovich, Beall and Loomis (2003) found that participants maintained a greater interpersonal distance between themselves and a virtual agent when the virtual agent engaged in mutual gaze compared to when they did not. These findings are comparable to what is found in real life social interactions – we keep a greater physical distance from those who are looking at us (Argyle & Dean, 1965).

Table 1-3 Examples of the difference virtual reality platforms

Name and example	Description	Advantages	Disadvantages
<p>Head mounted displays (HMDs)</p>  <p>e.g. in Pan et al. (2016) doctors took part in a virtual consultation in which the patient's daughter made strong demands for antibiotics. More experienced doctors were more likely to withstand the social pressure to unnecessarily prescribe the antibiotics.</p> <p>From Pan et al. (2016)</p>	<p>Participants wear a head mounted display which provides 3D stereovision (i.e. different input to each eye). Participants head movements are tracked and the visual scene in front of them updates accordingly. This allows for 360 degree vision so that participants vision of the non-virtual world is completely blocked.</p>	<ul style="list-style-type: none"> • Full immersion results in greater feelings of presence and copresence • The participant determines what to attend in the virtual world by moving their head • Head tracking data is provided “for free” as head movements are automatically recorded • Easy to implement and cheaper than CAVE systems 	<ul style="list-style-type: none"> • Low resolution means studies which require high-fidelity graphics are difficult • The manipulation of objects is technically challenged as participants cannot see the non-virtual world including their own body • Participants may experience motion sickness
<p>CAVE systems</p> <p>e.g. in Slater et al. (2013) football supporters were immersed in a virtual bar in which a man was attacked by a bystander. Participants were more likely to physically intervene when the victim was a supporter of the same football team as themselves.</p>  <p>From Slater et al. (2013)</p>	<p>Participants stand in a room (or ‘cave’) which has graphics displayed on multiple walls. Participants wear 3D glasses and motion sensors and the graphics update as they walk around the cave. Haptic devices can be installed to create a sense of physical realism.</p>	<ul style="list-style-type: none"> • Participants can see their own bodies which makes movement within the environment much easier • Participants can manipulate objects in the virtual environment • Allows for much bigger virtual worlds (e.g. a bar or classroom) 	<ul style="list-style-type: none"> • The non-virtual world is not blocked completely • Technically challenging and expensive
<p>Semi-immersive virtual reality</p> <p>e.g. in Pan and Hamilton (2015) participants played a drumming game with a virtual character to measure their imitative tendencies. Here the virtual world on the screen extended into the participant's world and the virtual character responded to participants' heads movements.</p>  <p>From Pan & Hamilton (2015)</p>	<p>These set-ups typically display the virtual environment on a large projector screen. The participants may be motion tracked and/or eye-tracked and the virtual environment can respond to these movements. 3D glasses are sometimes worn in these environments</p>	<ul style="list-style-type: none"> • Easily combined with neuroimaging methods • The manipulation of objects and one's own body is easier • Allows for augmented reality – combining both the real and virtual environments • Allows for higher resolution than HMDs so more subtle changes to the visual scene 	<ul style="list-style-type: none"> • Less immersive than HMDs and CAVE so participants can become more easily distracted by the non-virtual world • Participants feel less immersed than in other VR approaches may compromise the effect of the virtual world

Many other important findings from social psychology have been replicated in virtual environments. For example, as in real life social interactions, the presence and proximity of a virtual agents increases physiological arousal (Slater, Guger, et al., 2006), can induce psychosocial stress (Montero-López et al., 2016) and impair performance on untrained tasks (Hoyt, Blascovich, & Swinth, 2003). Virtual characters have also been used to study embodiment (Banakou et al., 2013), out-group biases (Hasler, Hirschberger, Shani-Sherman, & Friedman, 2014), altruism (Patil et al., 2017; Zanon, Novembre, Zangrando, Chittaro, & Silani, 2014), mimicry (Bailenson & Yee, 2005; Hasler et al., 2014), bystander behaviour (Hortensius, Neyret, Slater, & de Gelder, 2018), imitation (Pan & Hamilton, 2015), trust (Hale, Payne, Taylor, Paoletti, & De C Hamilton, 2018) and many other social psychological phenomenon (Bombari et al., 2015).

Virtual reality also allows researchers to investigate questions which would be impossible and/or unethical to investigate in real life (Bombari et al., 2015; Pan & Hamilton, 2018). For example, the Milgram paradigm has been implemented in virtual reality (e.g. Slater, Antley, et al., 2006), and virtual reality has been used to see whether people stop and help someone whilst fleeing a burning building (Zanon et al., 2014). Virtual reality enables low-cost and effective therapy to be implemented in a range of clinical populations including conditions associated with differences in social and affective cognition. For example, virtual reality has been used to provide social skills training to autistic adults (Georgescu, Kuzmanovic, Roth, Bente, & Vogeley, 2014; Smith et al., 2014), to assess and treat psychosis (Rus-Calafell, Garety, Sason, Craig, & Valmaggia, 2018) and post-traumatic stress disorders (Rothbaum et al., 2014). Virtual reality can also be used in vocational or sporting contexts to provide training. For example, in medical education virtual reality has been used in surgical training (Lahanas, Loukas, Smailis, & Georgiou, 2015) and to simulate clinical consultations

(Pan et al., 2016). Having provided a brief overview of the use of virtual reality in studies of human social interaction, I next review studies which have used virtual reality to study mimicry behaviours.

Virtual reality and mimicry

Virtual reality has been used in two ways to explore mimicry behaviours. The first approach involves motion tracking participants' movements and then having a virtual character mimic these movements. The consequences of this mimicry, compared to a no-mimicry condition, can then be investigated; for example, does mimicry lead to increased trust towards the virtual character or more prosocial behaviour? A second approach involves using virtual characters to induce mimicry in participants. For example, participants can play a simple game with a virtual character and the extent to which participants mimic the agent's movements can be examined. Do certain features of virtual characters result in more mimicry? Are we more likely to mimic virtual characters who are socially engaged rather than disengaged? I deal with these two approaches in turn.

Bailenson and Yee (2005) proposed that virtual characters who mimic participants ("digital chameleons") are more liked and more persuasive than virtual characters who do not mimic. In their study, participants wore a head mounted display and listened to a virtual agent deliver a persuasive message for 195 seconds. In one condition the virtual agent mimicked the head movements of the participant at a 4 seconds delay whereas in the no-mimicry condition the virtual agent's head movements were pre-recorded. Participants in the mimicry condition rated the virtual agent as more persuasive and also had a better impression of the agent than those in the no-mimicry condition. These results supported findings from some naturalistic mimicry paradigms using real confederates which demonstrated that mimicry may result in more positive

social evaluations (Chartrand & Bargh, 1999). In a study looking at the impact of virtual mimicry on attitudes towards outgroups, Hasler and colleagues asked Jewish Israeli participants to interact with a virtual character who was an outgroup member (i.e. Jamil, a Palestinian avatar). Participants had a conversation with Jamil about the Israeli-constructed security fences on the West Bank. Every time participants changed their sitting posture he either mimicked or counter-mimicked their movements with a 4 to 5 second delay (Hasler et al., 2014). Participants in the mimicry condition displayed more verbal expressions of empathy towards Palestinian suffering during the conversation. For those participants who had a low prior liking of Palestinians, they rated Jamil as more sympathetic than those participants in the counter-mimicry condition.

However, a number of studies using mimicking virtual characters have found less consistent support for the link between mimicry and prosocial effects (Hale & Hamilton, 2016a). Verberne, Ham, Ponnada and Midden (2013) asked participants to interact with a virtual agent which either mimicked or did not mimic participants' head movements. They investigated the effect of being mimicked in two tasks. In an investment game, there was no effect of mimicry on how much participants trusted or liked the virtual agent. In a route planner game, mimicked participants let the virtual agent plan more routes for them and liked the virtual agent more. These inconsistent effects of mimicry on liking and trust were replicated in a later study by the same group (Verberne, Ham, & Midden, 2015). Moreover, Hale and Hamilton (2016b, Study 2) systematically explored the effect of virtual mimicry on trust and rapport. In a pre-registered study, they found no effects of head and torso mimicry on rapport and trust ratings nor in a virtual maze which acted as an implicit measure of trust. Although these findings from virtual mimicry paradigms have yielded mixed results, they are similar to the effects seen in naturalistic mimicry studies using confederates. Here the relationship between mimicry and positive social evaluations is equivocal (Hale & Hamilton,

2016b). As outlined above, a great advantage of using pre-programmed virtual characters to mimic participants, it that all other factors in the interaction can be kept constant which is difficult when using human confederates. Thus, virtual mimicry may provide a more rigorous way to examine the impact of mimicry on social interactions.

Next, I turn to studies which have used virtual characters to induce mimicry in participants. As outlined above, pre-recorded videos of human actions have been widely used to induce mimicry behaviours (Genschow et al., 2017; Wild et al., 2010, 2012). In such paradigms, however, there is usually no potential for interactivity, that is, the behaviour of the person in the video is not influenced by the participant's behaviour (Schilbach, 2010). Virtual reality allows researchers to create a sense of interactivity. By motion tracking participants, the behaviour of the virtual character can be determined by that of the participant. This sense of interaction allows for more ecologically valid mimicry paradigms. For example, Pan and Hamilton (2015) asked participants to play a drum tapping game with a virtual character who was displayed on a large projector screen. The table in front of the participants extended into the virtual world on the screen so that the virtual character appeared to be sitting opposite the participants as the other end of the table (see Table 1-2). A sense of interaction was achieved by having the virtual character look at participants during their response period. The virtual character also waited for the participant to finish their turn before going on to the next trial. In the task, participants observed the virtual character tap three drums in a particular sequence and were then required to tap a sequence on their own set of drums. Sometimes the sequence the participants tapped was the same as the sequence the virtual character had just tapped (congruent trials) and sometimes it was different (incongruent trials). Participants were quicker to tap the first drum in the sequence on congruent compared to incongruent trials. When the virtual character was replaced by a ball, this congruency effect was reduced or absent. Pan and Hamilton thus

demonstrated that mimicry effects can be induced by virtual characters during ecologically valid, social interactions. Moreover, the finding that participants show stronger mimicry effects when interacting with a virtual character as opposed to a ball is in line with the animacy effects seen in automatic imitation paradigms (Liepelt & Brass, 2010). In another study by Vrijnsen and colleagues, participants wore a head mounted display and listened to a virtual character give an opinionated speech during which he made 10 pre-defined head movements. The extent to which participant mimicked these head movements within a 4 second period was coded. Participants with high self-reported social anxiety mimicked less than those with low self-reported anxiety (Vrijnsen, Lange, Becker, & Rinck, 2010). Both these studies demonstrate the feasibility of using virtual reality to induce mimicry.

It is important to consider the limitations of using virtual reality mimicry paradigms in terms of the place illusion and the plausibility illusion both of which determine the realism of virtual reality paradigms (Slater, 2009). Slater defines the place illusion (or ‘presence’) as the “feeling of being there” in the virtual environment, despite knowing explicitly that one is not there. This concept has been applied to virtual social interactions where ‘co-presence’ describes the sense of being there with someone and interacting with them rather than a computer screen (Garau et al., 2003). The place illusion and co-presence are largely dependent on the virtual reality platform. For example, a 3D virtual character in a headmounted display will usually result a greater place illusion (and co-presence) than viewing a 2D image on a projector screen. Moreover, such fully-immersive virtual reality systems ensure that the user cannot see the non-virtual world thereby further enhancing the place illusion. Pan and Slater (2011) directly compared the use of an immersive virtual reality system to a non-immersive desktop interface. In this study, participants experienced an attacker shooting people in an art gallery. Unsurprisingly, those in the immersive condition became more panicked

by the situation and also made more mistakes when trying to save virtual bystanders than those who experienced the scenario on a desktop computer. This suggests that those in the immersive condition had a greater sense of “being there.” However, in terms of mimicry, such fully-immersive virtual interfaces are difficult to implement as participants cannot see their own body. This makes hand and arm movements and the manipulation of objects difficult (Pan & Hamilton, 2018). That said, certain mimicry paradigms, such as head movement mimicry, are more easily implemented using head-mounted displays (e.g. Vrijssen et al., 2010).

The plausibility illusion is the extent to which participants believe that what is happening in virtual reality is really happening, despite knowing explicitly that it is not happening (Slater, 2009). The plausibility illusion is determined by the extent to which activities in the virtual environment are influenced by the participant’s behaviour. For example, if the participant gets too close to a virtual character, does the virtual character step away from them? In terms of mimicry paradigms, the plausibility illusion can be enhanced by creating a sense of interaction between the virtual character and the participants. For example, the participant’s head movements can be motion tracked and the virtual character can orient her head to look at the participant’s head (e.g. Pan and Hamilton, 2015). This creates a sense of social engagement (or even ‘eye-contact’) and enhances the plausibility illusion. However, although mimicry paradigms can create some sense of interaction through motion tracking, it cannot fully capture the subtleties of real life social interactions. For example, virtual characters facial expressions have been described as “wooden” (Vinayagamoorthy et al., 2006) and although virtual characters can respond to some aspects of a participant’s behaviour (e.g. head movements) responding appropriately to more subtle cues, such as facial expressions and gaze, remains a technical challenge (Pan and Hamilton, 2018).

1.3.5 Summary

Virtual reality is a useful tool for researchers interested in human social interaction as it allows for experimental control (i.e. standardised social interaction partners, Bombari et al., 2015) whilst simultaneously providing ecologically valid social interactions (Pan & Hamilton, 2018). Virtual characters and environments have been used to investigate a range of questions concerning human social interaction (Bombari et al., 2015). In terms of mimicry, several studies have programmed virtual characters to mimic participants movements and then investigated the social consequences (Bailenson & Yee, 2005; Hasler et al., 2014). These findings replicated the mixed results from real world mimicry paradigms where the relationship between mimicry and prosocial outcomes, such as increased trust and liking, is fragile (Hale & Hamilton, 2016). Whilst these studies used virtual characters to mimic participants, relatively few studies have tried to induce mimicry in participants using virtual characters. Those that have attempted to do so suggest that it is feasible – participants mimic virtual characters (Pan & Hamilton, 2015; Vrijssen et al., 2010). However, the realism of virtual social interactions is dependent on both the place illusion and plausibility illusion (Slater, 2009) both of which are constrained when studying mimicry behaviours. Firstly, it is difficult to implement mimicry paradigms in fully immersive platforms, and, secondly, virtual characters are only partially interactive.

1.4 Overview of Experimental Chapters

In this chapter I have outlined what mimicry is, the different forms it can take and theories which have tried to explain mimicry. I have highlighted how mimicry might be different in autistic people and why this might be. I have also evaluated the diverse ways in which mimicry can be measured. This thesis aims to explore how and when people mimic and to better characterise any mimicry differences in autistic

people. To do this I employed a range of mimicry measures including reaction times tasks, kinematic mimicry and virtual reality. Below I highlight the specific questions addressed in each chapter:

1. Does direct gaze modulate mimicry in autism?

Chapter 2 outlines a study which used a reaction time measure of mimicry to explore whether direct gaze modulates mimicry responses in autistic adults. This study aimed to test a key prediction arising from the STORM model (Wang and Hamilton, 2012): autistic people can and do mimic others but do not modulate their mimicry strategically according to the social context. The results of this study supported STORM's prediction.

2. Do people mimic virtual characters and is this mimicry modulated by social engagement?

Chapter 3 employed a kinematic measure of mimicry in a virtual reality paradigm to test whether autistic and non-autistic people mimic virtual characters and whether this mimicry is socially modulated. Again, this aimed to test STORM's predictions. I found that both autistic participants and neurotypical participants mimicked the kinematics of the virtual character's movements. However, autistic participants mimicked less and social engagement did not modulate mimicry in either group.

3. Why is mimicry not modulated in virtual reality?

Chapter 4 outlines two experiments which explored factors which may have accounted for a lack of social modulation of mimicry in Chapter 3. The first experiment used the same paradigm as in Chapter 3 but used videos of a human actor, as opposed to a virtual character, and manipulated how socially engaged she appeared. This aimed to increase the physical realism of the model. Participants mimicked the model but how

socially engaged the model appeared in the videos did not modulate mimicry. The second experiment manipulated the animacy of the model by including a condition in which participants interacted with a moving ball and a virtual character. Participants mimicked the kinematics of the ball and the virtual character to the same extent. Together these results suggest that the mimicry paradigm used in Chapter 3 and Chapter 4 is resistant to social modulation.

4. How does observed action rationality affect mimicry?

Chapter 5 tested whether the rationality of an observed action influenced the extent to which participants mimicked a model's movements. I found that participants' movements continued to be sensitive to observed movements even when these were rated as irrational. This experiment also demonstrated that participants code the environment of the model into their own movements even though their own environment may be different from that of the model.

5. Can people's tendency to mimic others' movements change their choices?

Chapter 6 tested whether people's tendency to mimic the movements of another agent could change the choices they had previously made in private. Participants first indicated which art pictures they preferred in private before making the same choices in a virtual art gallery. Participant's tendency to mimic the movements of a virtual character changed the choices they had previously made in private. In a follow up experiment using the same paradigm, I replicated this finding in a group of neurotypical participants and did not find any significant differences in the mimicry behaviour of autistic adults.

Chapter 2 - STORMy Interactions: Gaze and the Modulation of Mimicry in Autistic Adults

The results of Chapter 2 were published in *Psychonomic Bulletin and Review*:

Forbes, P. A. G., Wang, Y., & Hamilton, A. F. D. C. (2017). STORMy interactions: gaze and the modulation of mimicry in adults on the autism spectrum.

Psychonomic bulletin & review, 24(2), 529-535

2.1 Abstract

Mimicry involves unconsciously imitating the actions of others and is powerful and ubiquitous behaviour in social interactions. There has been a long debate over whether mimicry is different in people with autism and what the causes of any differences might be. Wang and Hamilton's (2012) social top-down response modulation (STORM) model proposed that autistic people can and do mimic but, unlike neurotypical participants, fail to modulate their mimicry according to the social context. The present study used an established mimicry paradigm to test this hypothesis. In neurotypical participants, direct gaze specifically enhanced congruent hand actions as previously found; in the autism sample, direct gaze lead to faster reaction times in both congruent and incongruent movements. This result shows that mimicry is intact in autism but is not socially modulated by gaze, as predicted by STORM.

2.2 Introduction

In this Chapter, I employed a reaction time measure of mimicry to investigate whether autistic people change their mimicry responses according to gaze cues. As outlined in the Chapter 1, people often unconsciously copy each other's actions, and this mimicry has been described as a powerful social glue (Chartrand & van Baaren, 2009). Individuals with a diagnosis of autism have impairments in social communication and

interaction (American Psychiatric Association, 2013) which may include differences in mimicry (Edwards 2014). The STORM model proposed that these mimicry differences may be due to difficulties in using social cues, like gaze, to modulate mimicry (Wang & Hamilton, 2012). Chapter 2 aimed to test this hypothesis using a well-established reaction time measure of mimicry. I first provide an overview of the importance of gaze as a social signal and how autistic people might process gaze differently. I then turn to STORM and its predictions for autism.

2.2.1 Gaze and autism

Gaze is an important social signal across a range of species and may be particularly important for humans. The white sclera of the human eye is the largest amongst primates and contrasts starkly with our coloured irises. This makes the detection of other people's gaze direction relatively easy for humans - it is clear when others are looking at us (Kobayashi & Kohshima, 1997). This unique morphology of the human eye may have evolved to allow cooperative social interaction in contrast to other species where direct gaze often signals threat (Tomasello, Hare, Lehmann, & Call, 2007). This proposal is supported by the finding that young infants show a sensitivity to gaze cues early in development with 3 to 6 month old infants already following other people's gaze direction (D'Entremont, Hains, & Muir, 1997).

Differences in the use of eye-contact are considered a major feature of autism (American Psychiatric Association, 2013). Given the importance of gaze for human social interaction, these differences in gaze processing in autism have been extensively studied (for a review, see Senju & Johnson, 2009). Elsabbagh et al. (2012) used EEG to show that event-related potentials (ERP) in response to dynamic eye-gaze shifts at 6-10 months predicted an autism diagnosis 36 months later in those infants with a family history of autistic traits. Similar ERP findings have been reported in older autistic

children (Senju, Tojo, Yaguchi, & Hasegawa, 2005). Some have suggested that altered neural responses to gaze cues could potentially act as a biomarker for autism (Pelphrey & McPartland, 2012).

These differences in the neural responses to direct compared to averted gaze are reflected in behavioural findings. For example, Senju and colleagues found that neurotypical participants were better at detecting direct compared to averted gaze. But this facilitative effect for direct gaze was not found in autistic children (Senju, Yaguchi, Tojo, & Hasegawa, 2003). Senju et al. proposed that these differences in detecting direct gaze may have downstream consequences on social and communicative development, such as differences in establishing joint attention. Moreover, in terms of gaze following, infants with a family history of autism were more likely to rely on head orientation cues rather than gaze cues when compared to infants without a family history of autism (Thorup, Nyström, Gredebäck, Bölte, & Falck-Ytter, 2016).

Finally, in addition to these differences in neural and behavioural responses to gaze, autistic individuals show altered physiological reactions. Helminen et al. (2017) measured changes in 2-5 year old children's heart rate in response to direct and averted gaze. Whilst heart rate deceleration was greater following direct compared to averted gaze for neurotypical and (non-autistic) developmentally delayed children, a matched autistic sample did not show these same physiological reactions.

In sum, gaze cues, such as eye-contact, provide a foundation for social cognition (Hamilton, 2016) as they exert a mixture of arousal, attentional, and social effects on the observer and facilitate downstream information processing, such as joint attention, ostensive communication and mimicry (Böckler, Timmermans, Sebanz, Vogeley, & Schilbach, 2014; Mundy, Kim, McIntyre, Lerro, & Jarrold, 2016). There is strong evidence from studies which have measured behavioural, neural and physiological

responses that the use and processing of gaze cues is different in autism (Senju & Johnson, 2009). However, the exact nature of these differences and its consequences on downstream information processing remain less well characterised. Next, I turn to studies which suggest that gaze cues modulate mimicry responses and how this modulation may be different in autism.

2.2.2 Gaze and mimicry

As detailed in Chapter 1, the STORM model proposed that social cues, like attractiveness (van Leeuwen, van Baaren, Martin, Dijksterhuis, & Bekkering, 2009), likeability (Mariëlle Stel et al., 2011) and feelings of social exclusion (Lakin et al., 2008), all modulate mimicry responses. But this modulation of mimicry by social cues may be different in autism. For example, neither pro-social priming (Cook & Bird, 2012) nor emotional facial expressions (Grecucci et al., 2013) enhance mimicry in autism.

In terms gaze, considerable evidence from a range of mimicry studies suggests that gaze cues modulate mimicry in non-autistic participants. In some of the earliest work to explore this, Bavelas, Black, Lemery and Mullet (1986) found that when a confederate seemingly incurred a painful injury, participants showed more motor mimicry (e.g. wincing) when he gave them eye-contact compared to when he did not. In terms of speech, participants who were looked at by a virtual agent later mimicked his intonation more than those who received averted gaze (Postma-Nilsenová, Brunninkhuis, & Postma, 2013). Recent developmental work has demonstrated direct gaze cues enhance facial mimicry in 4 month old infants (de Klerk, Hamilton, & Southgate, 2018) and enhance imitative performance in pre-schoolers, whereas, autistic pre-schoolers' imitative performance was the same in both direct and averted gaze conditions (Vivanti & Dissanayake, 2014).

Whilst the above studies have investigated mimicry in naturalistic settings, evidence from stimulus responses compatibility paradigms also converges on the conclusion that direct gaze enhances mimicry responses. In Wang, Newport and Hamilton (2011), participants saw either direct or averted gaze before performing a pre-specified action which was either congruent (mimicry) or incongruent (not mimicry) with an action on the screen. The results showed three effects – a main effect of congruency (congruent responses were faster than incongruent ones), and, a main effect of gaze (responses were faster following direct compared to averted gaze), and an interaction between gaze and mimicry (direct gaze enhanced congruent, but inhibited incongruent, responses). I consider different hypotheses in reference to each of these effects.

Firstly, previous studies have consistently demonstrated that the basic mechanisms of mimicry are intact in autism (Bird, Leighton, Press & Heyes, 2007), so we predicted a main effect of congruency in autistic participants. Secondly, autistic people seem to process and use eye-contact differently (Senju & Johnson, 2009). If all gaze processing mechanisms are different in autism, neither congruent nor incongruent responses should be affected by gaze. Finally, STORM predicts that *only* the interaction between gaze and mimicry should be absent in autism: autistic participants can mimic but do not use direct gaze as a social cue to control mimicry. This Chapter aimed to test these hypotheses.

2.3 Methods

2.3.1 Participants

Twenty-seven neurotypical adults and twenty-six autistic participants were recruited from the UCL Institute of Cognitive Neuroscience's 'autism@icn' participant database. We aimed for a sample size of twenty-five or more participants. The final

Table 2-1 A comparison of the ASC and NT samples

	ASC (n = 26)		NT (n = 27)		<i>t</i> test
	Mean (SD)	Range	Mean (SD)	Range	<i>p</i> value
Age (years)	28 (7)	18-48	27 (6)	18-40	<i>p</i> = 0.50
Fullscale IQ	120(12)	95-152	124(12)	99-151	<i>p</i> = 0.44
Verbal IQ	123(13)	100-155	125(12)	98-150	<i>p</i> = 0.85
Performance IQ	114(13)	87-132	118(13)	85-148	<i>p</i> = 0.34
ADOS total	8 (3)	4-17			
ADOS communication	3 (2)	0-6			
ADOS social interaction	6 (2)	2-11			
Gender	4 F; 22 M		5 F; 22 M		
Handedness	3 L; 23 R		3 L; 24 R		

sample size was determined by the availability of the participants on ‘autism@icn’ database during the testing period. Groups were matched on age, gender, handedness, and, verbal and performance IQ using either the Wechsler Adult Intelligence Scale (WAIS-III UK; Wechsler, 1999a) or Wechsler Abbreviated Scale of Intelligence (WASI-II, Wechsler, 1999b; Table 2-1). Autistic participants had a diagnosis of Asperger’s Syndrome (21), autism (3), or, autism spectrum disorder (2) from an independent clinician.

Autistic participants were assessed on module 4 of the Autism Diagnostic Observation Schedule (ADOS-G - Lord et al., 2000; ADOS-2 Lord et al., 2012) by a

trained researcher with research-reliability status. Seven participants met the ADOS classification for autism, eleven for autism spectrum, and, eight did not meet the classification of either autism or autism spectrum. Seven out of these eight reached the cut-off for autism spectrum on either the communication or reciprocal social interaction subscale, and, all eight had a clear diagnostic history from an independent clinician. All participants were financially reimbursed and gave written informed consent. All procedures were approved by the UCL Research Ethics Committee.

2.3.2 Procedure

Participants came into the lab as part of an autism@icn research day in which they completed several studies. For this study, they sat approximately 70 cm from the projector screen with their right elbow resting on the desk in front of them and their right hand in a semi-open position. To measure reaction times (RT), a Polhemus electromagnetic marker was attached to the inside of their right thumb and index finger. Participants completed Wang et al.'s (2010) stimulus-response compatibility paradigm exactly as in their study (Figure 2-1). At the beginning of each block participants were instructed to either open ('opening block') or close ('closing block') their hand as quickly as possible when they saw the actor's hand move, regardless of whether the actor opened or closed her hand on each trial. Thus, for each trial, the participants' pre-specified movements were either the same as the observed action (congruent trials; e.g. observe hand opening, perform hand opening) or the opposite of the observed action (incongruent trials; e.g. observe hand closing, perform hand closing).

Before each trial a fixation cross appeared on the screen for 300 ms. This was followed by a video which started with a female actor facing away from the viewer with her eyes closed and left hand in a static position across her face. She then opened her eyes and either moved her head towards the viewer (direct gaze) or turned her head

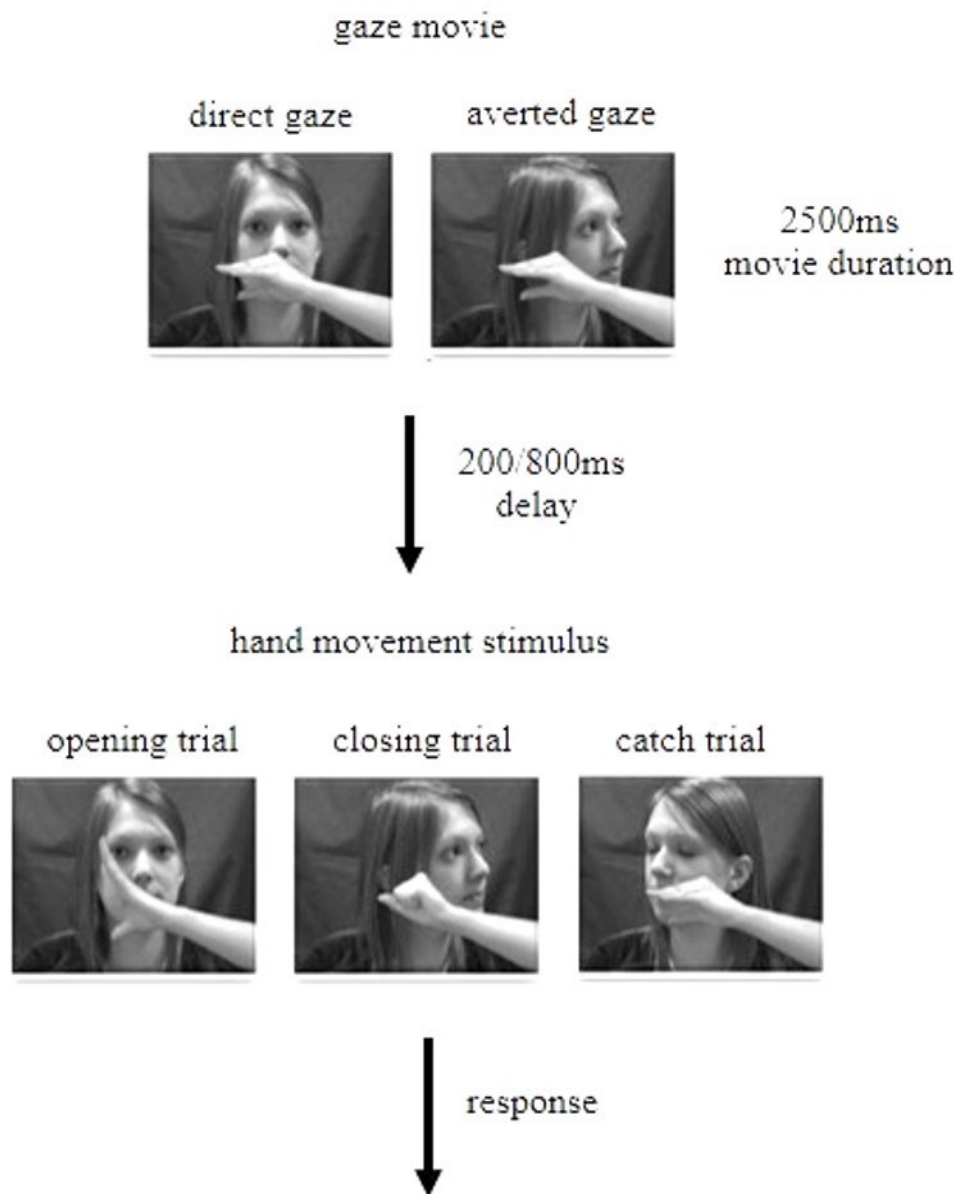


Figure 2-1 An example of the stimuli used and trial sequence (Adapted from Wang et al. 2010)

towards her left or right side (averted gaze). Following the head movement, the actor opened or closed her hand after a delay of either 200 ms or 800 ms (Figure 1). Videos appeared 50 cm x 43 cm on a 160 cm x 90 cm projector screen.

Participants completed 160 trials split across four blocks: two hand opening and two hand closing blocks presented alternately and randomised across participants. Within each block, 20% of trials were ‘catch’ trials during which the actor’s hand remained static. Participants were told to keep their hand static during these trials (i.e. not make the pre-specified movement). Participants were given approximately 5

minutes of practice before the experiment, during which they completed a shortened hand opening and hand closing block, and, were also made familiar with the catch trials. Data were recorded in Matlab and video presentation controlled using the Cogent toolbox. Analysis of hand aperture velocity was identical to that used by Wang et al. (2010) and allowed RTs to be calculated.

2.4 Results

2.4.1 Error rates

1.72% of trials were excluded as participants moved either too fast (<50 ms), too slow (>1000 ms), did not move at all or made the wrong pre-specified movement. An independent samples t-test revealed that there were no significant differences in proportion of trials excluded between NT and autistic participants ($p > 0.250$).

2.4.2 Neurotypical participants

One NT participant's mean RT was over 3 SD from the mean so was removed from the final analysis. Removal ensured the normality of the data but did not disrupt the matching between the groups. RTs were analysed using a two-way (gaze: directed/averted; congruency: congruent/incongruent) repeated measures ANOVA which revealed a significant main effect of congruency ($F_{1,25} = 47.3, p < 0.001, \eta_p^2 = 0.654$) with faster responses when making congruent as opposed to incongruent actions, and, a significant interaction between congruency and gaze ($F_{1,25} = 7.28, p = 0.012, \eta_p^2 = 0.225$). Post hoc t-tests showed that congruent responses were marginally significantly faster when preceded by direct gaze compared to averted gaze ($t_{25} = -1.73, p = 0.097, d = -0.117$), but this was not the case for incongruent responses ($t_{25} = 1.24, p = 0.227, d = 0.081$).

2.4.3 Autistic participants

The same analysis was applied to the autism group's RTs and revealed a main effect of gaze ($F_{1,25} = 7.05, p = 0.014, \eta_p^2 = 0.220$) with faster responses following direct gaze, and congruency ($F_{1,25} = 72.23, p < 0.001, \eta_p^2 = 0.743$) with faster responses when making congruent as opposed to incongruent responses. There was no significant interaction between gaze and congruency ($F_{1,25} = 0.014, p > .250, \eta_p^2 = 0.001$).

2.4.4 Group comparison

To explore group differences, RTs were analysed using an ANOVA with gaze and congruency as within-subject factors and group as a between-subject factor (Figure 2-4). This revealed a significant main effect of congruency ($F_{1,50} = 120.98, p < 0.001, \eta_p^2 = 0.708$) and group ($F_{1,50} = 13.26, p = 0.001, \eta_p^2 = 0.210$) with neurotypical participants responding faster than autism participants, and a marginally significant main effect of gaze ($F_{1,50} = 3.96, p = 0.052, \eta_p^2 = 0.073$) with a trend to faster responses following direct gaze. The interactions between gaze and group ($F_{1,50} = 4.03, p = 0.050, \eta_p^2 = 0.075$), gaze and congruency ($F_{1,50} = 3.19, p = 0.080, \eta_p^2 = 0.060$), and, gaze, congruency and group ($F_{1,50} = 3.02, p = 0.088, \eta_p^2 = 0.057$) were all approaching significance. The interaction between congruency and group ($F_{1,50} = 2.57, p = 0.115, \eta_p^2 = 0.049$) was not significant.

A key measure of the tendency to mimic is the congruency effect calculated as the mean RT to incongruent trials minus mean RT to congruent trials. However, as mean RT increases, the congruency effect also increases (Press, Bird, Flach & Heyes, 2005). Thus, when testing for modulators of this congruency effect, it is important to control for the confounding influence of mean RT (Butler, Ward & Ramsey, 2015). To deal with the slower mean RT in the autism group, we calculated a percentage

congruency effect (PCE) relative to overall mean RT for each participant using the following equation:

$$\text{Percentage Congruency Effect (PCE)} = \frac{\text{Mean Incongruent RT} - \text{Mean Congruent RT}}{\text{Overall Mean RT}} \times 100$$

This expressed how much faster participants' RTs were for congruent compared to incongruent trials in each gaze condition, relative to their overall mean RT. Using the PCE as a measure of the tendency to mimic, we can compare the influence of gaze on mimicry between groups (Figure 2-2).

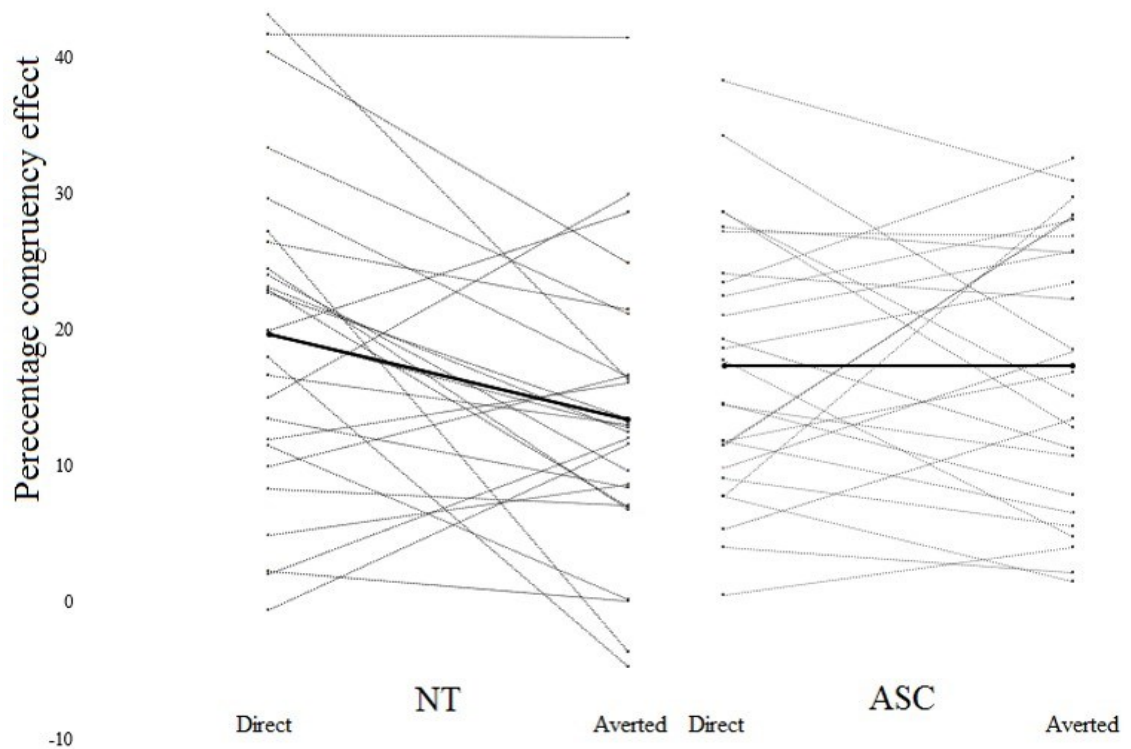


Figure 2-2 PCE for directed and averted gaze for each NT ($n=26$) and ASC ($n=26$) participant; means are in the thicker lines.

PCEs were analysed using an ANOVA with gaze as a within-subject factor and group as a between-subject factor. This revealed no main effect of group ($F_{1,50} = 0.153$, $p = 0.698$, $\eta_p^2 = 0.003$) but a significant main effect of gaze ($F_{1,50} = 4.25$, $p = 0.045$, $\eta_p^2 = 0.078$) and, importantly, there was a significant interaction between gaze and

group ($F_{1,50} = 4.28, p = 0.044, \eta_p^2 = 0.079$). Post-hoc t-tests revealed the PCE was greater in the direct gaze condition in NT participants ($t_{25} = 2.70, p = 0.012, d = 0.559$), but there was no difference in PCE between the two gaze conditions in the autism group ($t_{25} = -0.007, p > 0.250, d = 0.001$).

Table 2-2 A comparison of the ADOS subgroup and NT sample

	ASC (n = 18)		NT (n = 26)		t test
	Mean (SD)	Range	Mean (SD)	Range	p value
Age (years)	28 (5)	20-37	26 (6)	18-40	$p = 0.62$
Fullscale IQ	119 (14)	95-152	124 (13)	99-151	$p = 0.35$
Verbal IQ	123 (14)	100-155	125 (12)	98-150	$p = 0.65$
Performance IQ	112 (14)	87-132	118 (14)	85-148	$p = 0.28$
ADOS: total	10 (3)	7-17			
ADOS: communication	3 (1)	2-6			
ADOS: social interaction	7 (2)	4-11			
Gender	2 F; 16 M		5 F; 21 M		
Handedness	2 L; 16 R		3 L; 23 R		

Subgroup analysis

As 8 autistic participants did not meet the cut off for an ADOS classification of either autism spectrum or autism, the same analysis was conducted for the 18 participants who did meet cut off. These 18 did not differ from the NT group on age, verbal or performance IQ (Table 2). Analysis of RTs revealed a main effect of gaze ($F_{1,42} = 6.31, p = 0.016, \eta_p^2 = 0.131$), congruency ($F_{1,42} = 93.04, p < 0.001, \eta_p^2 = 0.689$) and group ($F_{1,42} = 13.21, p = 0.001, \eta_p^2 = 0.239$). The interaction between gaze

and group ($F_{1,42} = 6.40, p = 0.015, \eta_p^2 = 0.132$), and, the interaction between gaze, group and congruency were significant ($F_{1,42} = 4.24, p = 0.046, \eta_p^2 = 0.092$). The interaction between group and congruency ($F_{1,42} = 1.45, p = 0.235, \eta_p^2 = 0.033$), and, gaze and congruency ($F_{1,42} = 1.30, p > 0.250, \eta_p^2 = 0.030$) were not significant.

Analysis of PCE revealed no main effect of gaze ($F_{1,42} = 2.06, p = 0.159, \eta_p^2 = 0.047$) or group ($F_{1,42} < .001, p > 0.250, \eta_p^2 < 0.001$); but, as with the whole group analysis, showed a significant interaction between gaze and group ($F_{1,42} = 4.84, p = 0.033, \eta_p^2 = 0.103$). Post-hoc t-tests revealed that the PCE was greater in the direct gaze condition in NT participants ($t_{25} = 2.70, p = 0.012, d = 0.559$), but there was no difference in PCE between the direct and averted gaze conditions in autism ($t_{25} = -0.542, p > 0.250, d = -0.132$).

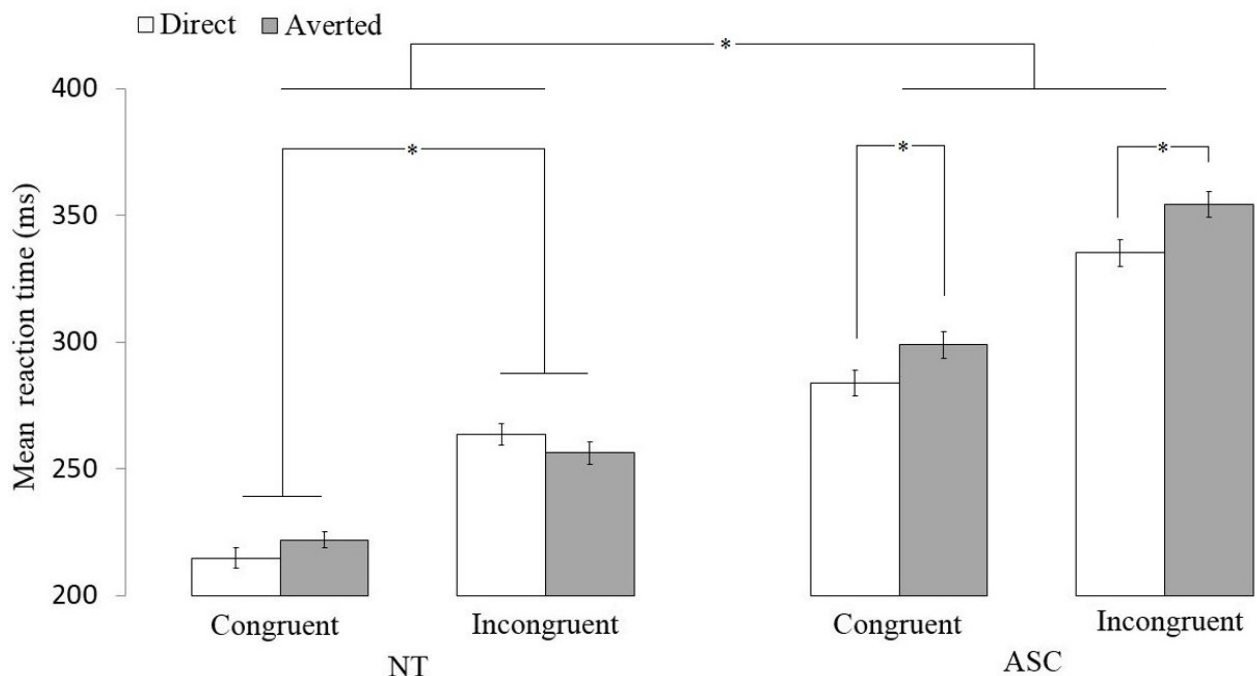


Figure 2-3 Mean RT (+/- SEM) for congruent and incongruent trials for direct and averted gaze for NT participants ($n=26$) and those reaching cut off for an autism spectrum or autism classification on ADOS ($n=18$)

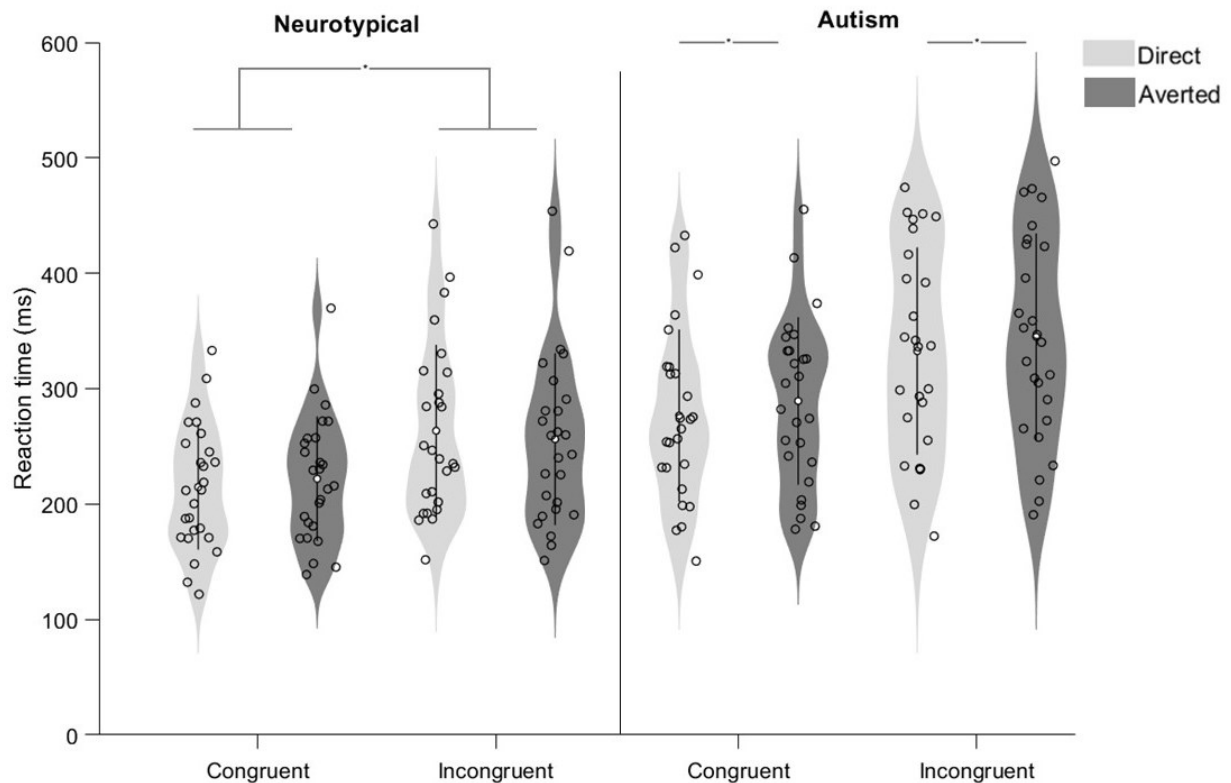


Figure 2-4 Mean RT (+/- SD) for congruent and incongruent trials for direct and averted gaze for neurotypical participants (n=26) and all autistic participants (n=26)

2.5 Discussion

Neurotypical and autistic adults performed a stimulus-response compatibility task measuring the tendency to mimic in the presence or absence of direct gaze. Neurotypical adults showed a stronger mimicry effect following direct gaze. Autistic adults mimicked but did not show this specifically social enhancement of mimicry by gaze. Instead, they showed faster RTs for both congruent and incongruent responses following direct gaze. I discuss our findings in terms of STORM and current theories of gaze processing in autism.

2.5.1 STORMy Interactions

Autistic participants demonstrated a reliable congruency effect which suggests the basic mechanisms responsible for imitative responses are intact in autism (Edwards, 2014). The data did not support the hypothesis that all gaze processing is disrupted in autism (Senju & Johnson, 2009) as a consistent main effect of gaze was found. All

responses were faster after direct compared to averted gaze in autism. In neurotypical participants, direct gaze enhanced congruent responses (i.e. mimicry) but slowed incongruent responses resulting in no overall effect of gaze. The general gaze effect suggests autistic people may sometimes use gaze as an alerting or attentional signal so are not entirely immune to signals from the eyes.

STORM predicted that if social top-down response modulation is different in autism, the interaction between gaze and congruency found in neurotypical participants would be absent in autism. The results support STORM, as in autism, the tendency to mimic was not enhanced following direct compared to averted gaze. This lack of social modulation of mimicry by gaze is consistent with previous studies showing neither pro-social priming (Cook & Bird, 2012) nor emotional facial expressions (Grecucci et al., 2013) enhance mimicry in autism. The findings also corroborate evidence from autistic pre-schoolers who imitated to the same extent in direct and averted gaze conditions, unlike their neurotypical peers who imitated more following direct gaze (Vivanti & Dissanayake, 2014).

2.5.2 Gaze processing in autism

The findings are consistent with previous studies which suggest that gaze cues do not have a social effect on downstream information processing in autism (Böckler et al., 2014; Mundy et al., 2016). Participants with autism differentiated between direct and averted gaze as all responses were faster in the direct gaze condition. This suggests that direct gaze may have had an attentional or alerting effect in participants with autism. However, direct gaze did not have a specifically social effect on mimicry as was found in neurotypical participants. This generic, non-social effect of gaze cues was also found by Ristic et al. (2005) who showed that autistic individuals were sensitive to gaze direction when it was spatially informative (i.e. it predicted the location of a cue).

However, unlike neurotypical individuals, those with autism were no longer sensitive to gaze direction when it was spatially uninformative (i.e. gaze direction predicted the location of the cue at chance levels). So, there may be sensitivity to gaze in autism as a generic spatial cue (or as an attentional or alerting stimulus as found in the present study), but not sensitivity to gaze cues as specifically social stimuli.

Recent neuroimaging studies further support the hypothesis that gaze cues do not have the same social impact in autism. In neurotypical participants, direct compared to averted gaze resulted in increased activity in areas involved in theory-of-mind processing, such as medial prefrontal cortex, temporoparietal junction, and, posterior superior temporal sulcus (Von Dem Hagen, Stoyanova, Rowe, Baron-Cohen, & Calder, 2014). Furthermore, activation of medial and orbital prefrontal regions has been shown to be positively correlated with gaze duration in neurotypicals (Kuzmanovic et al., 2009); in autism, however, these classic “social brain” areas were preferentially activated by *averted* as opposed to direct gaze (Georgescu et al., 2013; Von Dem Hagen et al., 2014). Together these behavioural and neuroimaging data suggest individuals with autism may show some sensitivity to gaze cues but might not reap all the social effects of these cues.

2.5.3 Conclusion

In this Chapter I showed that autistic people can unconsciously copy the actions of others but do not use important social cues, such as gaze, to determine when and what to mimic. Autistic participants were sensitive to direct gaze as an attentional or alerting stimulus but did not use gaze as a specifically social stimulus to modulate their mimicry. In Chapter 3, I aimed to test the predictions of STORM in a more ecologically valid, virtual reality environment.

Chapter 3 - Reduced Mimicry to Virtual Characters in Autism

The results of Chapter 3 were published in the *Journal of Autism and Developmental Disorders*:

Forbes, P. A. G., Pan, X., & Hamilton, A. F. D. C. (2016). Reduced mimicry to virtual reality virtual characters in Autism Spectrum Disorder. *Journal of autism and developmental disorders*, 46(12), 3788-3797.

3.1 Abstract

Increasing evidence suggests that autistic people can copy the goal of an observed action but show differences in their mimicry. For example, STORM predicts differences in the social modulation of mimicry in autism as was found in Chapter 2. The current Chapter aimed to test STORM in an ecologically valid, two-dimensional virtual reality environment. Participants played an imitation game with a socially engaged virtual character and socially disengaged virtual character. Despite being told only to copy the goal of the observed action, autistic participants and matched neurotypical participants mimicked the kinematics of the virtual characters' movements. However, autistic participants mimicked less. Social engagement did not modulate mimicry in either group. The results demonstrate the feasibility of using virtual reality to induce mimicry and suggest mimicry differences in autism may also occur when interacting with virtual characters. However, STORM's prediction that all mimicry is socially modulated was not supported.

3.2 Introduction

In Chapter 2, I showed that autistic people can and do mimic others but do not modulate their mimicry in response to important social cues, such as direct gaze. This is in line with the predictions of the STORM model which states that all mimicry is subject to social modulation, but this modulation is absent in autism. In Chapter 2, I employed a stimulus response compatibility paradigm which is a reaction time measure of mimicry. Although these paradigms can measure mimicry responses on a millisecond timescale, these automatic imitation studies have been criticised for their lack of validity (Cracco et al., 2018). That is, the extent to which they index mimicry ‘in the wild’ may be limited (Ramsey, 2018). Thus, Chapter 2 aimed to establish whether any potential differences in mimicry behaviour in autism could be investigated within a rich and ecologically valid, interactive virtual reality environment.

3.2.1 Mimicry as a social behaviour

Hamilton (2008) made an important distinction between mimicry and emulation. Mimicry involves implicitly and automatically copying the detailed kinematic features of an observed action, rather than just the action goal. Conversely, emulation involves copying the explicit goal of an observed action. Whilst emulation is useful in practical situations (e.g. when learning how to use a tool), Wang and Hamilton (2012) have argued that mimicry is fundamentally a social behaviour so modulated by social cues in a subtle and sophisticated manner. This has been captured in their social top-down response modulation (STORM) model (Wang & Hamilton, 2012). Mimicry has been measured using a range of approaches including naturalistic studies involving live confederates (e.g. Chartrand & Bargh, 1999), reaction time tasks using stimulus-response compatibility paradigms (e.g. Brass, Bekkering, Wohlschläger & Prinz, 2000), and kinematic studies using motion tracking (e.g. Castiello, Lusher, Mari, Edwards &

Humphreys, 2002). All these approaches have converged on the finding that a range of social cues, such as attractiveness of the interaction partner (van Leeuwen, Veling, van Baaren & Dijksterhuis, 2009), eye-contact (Wang, Newport & Hamilton, 2010), pro-social priming (Leighton, Bird, Orsini & Heyes, 2010; Wang & Hamilton, 2013), and, beliefs about the animacy of the interaction partner (Bird, Leighton, Press & Heyes, 2007; Castiello et al., 2002), modulate mimicry behaviours in neurotypical participants.

3.2.2 STORMy interactions: mimicry and autism

Autistic people have significant difficulties in everyday social interactions (American Psychiatric Association, 2013). Hamilton (2008) suggested that autistic participants perform well on emulation tasks, but tend to perform differently on mimicry tasks compared to neurotypical participants. For example, Hobson & Lee (1999) found that autistic participants were proficient in copying goal-directed actions, but tended not to copy the style with which the experimenter executed those actions. Similarly, McIntosh, Reichmann-Decker, Winkielman & Wilbarger (2006) found that, unlike neurotypical participants, autistic adolescents and adults did not spontaneously mimic happy and angry facial expressions. Yet, when explicitly instructed to copy an observed facial expression autistic participants performed as neurotypical participants. Moreover, Wild, Poliakoff, Jerrison and Gowen (2012) found autistic participants were less sensitive to the duration, velocity and vertical amplitude of observed actions during an imitation task. Eye-tracking also revealed more goal-directed eye-movements in autism suggesting an over-reliance on goal-directed imitation strategies in autism and a reduced propensity to mimic. A meta-analysis of 53 studies investigating imitation abilities in autism supported Hamilton's proposal. It showed spared performance when copying only the goal of an action (i.e. emulation) but impairments when copying both the form (i.e. style) and the goal of an action (Edwards, 2014).

The finding that mimicry is different in autism, a condition characterised by difficulties in social interaction, is in line with Wang and Hamilton's (2012) proposal that mimicry is fundamentally a social behaviour. It is important to note, however, that Hamilton (2008) has stressed that it is not mimicry *per se* which is impaired in autism, as autistic children and adults can and do spontaneously copy the actions of others. For example, some autistic individuals display echopraxia characterised by an increased tendency to involuntarily copy the actions of others (Spengler, Bird & Brass, 2010). Rather, it is the top-down social modulation of mimicry that is aberrant in autism. Hamilton's hypothesis has been supported by several recent studies using a stimulus-response compatibility paradigm. These show that automatic imitation is intact in autism as showed by faster responses to congruent rather than incongruent actions, but modulation of this congruency effect by social cues may be different or absent. For example, Cook and Bird (2012) showed pro-social priming relative to non-social priming led to an enhancement of automatic imitation in neurotypical participants but not in autistic participants. Similarly, Grecucci et al. (2013) found automatic imitation is enhanced in neurotypical participants, but not in autism, when preceded by emotional facial expressions. Finally, Chapter 2 (i.e. Forbes, Wang, & Hamilton, 2017) showed that direct gaze socially modulates mimicry responses in neurotypical participants but not in autism.

3.2.3 Using virtual reality to study mimicry

A significant limitation of previous studies investigating the social modulation of mimicry in autism is that they typically displayed isolated hand stimuli within a limited social context and measured participants' reaction times to make simple finger movements (Cook & Bird, 2012; Forbes, Wang, & Hamilton, 2017; Grecucci et al., 2013). The current study aimed to create a more ecologically valid mimicry paradigm by creating an interactive two-dimensional (2D), virtual reality environment. Pan and

Hamilton (2015) previously found that during a drum tapping game participants displayed a greater tendency to mimic when interacting with a virtual character compared to a bouncing ball. In their paradigm, a sense of interactivity was achieved by programming the virtual character to orient her head to the participant's head position when it was the participant's turn to respond. The virtual character was also responsive to the participant's movements as she would wait for the participant to finish their turn before starting her own.

We aimed to combine the virtual reality approach used by Pan and Hamilton (2015) with the kinematic approach used by Wild et al. (2012) to try and induce and socially modulate mimicry in adults with and without a diagnosis of autism. As virtual reality technologies become more accessible they are increasingly being used to teach and train social skills, such as job interview training, in autism (e.g. Smith et al., 2014; see Wang & Reid, 2011, for a review). It is therefore important to establish whether the behaviours autistic individuals display in everyday life, such as differences in eye-contact, gesture, and joint attention, also occur when interacting with and responding to virtual characters.

To investigate this with regards to mimicry differences, participants played a game with several virtual characters during which they observed the virtual character point to a series of three targets out of a possible four targets on the virtual table in front of them. Participants were given goal-orientated instructions as they were told to point to the same targets the virtual character pointed to on the table in front of them. However, the height of the virtual character's movements was manipulated to see whether participants' own movements were sensitive to the kinematics of the virtual characters' movements. Each participant played the game with a socially engaged and with a socially disengaged virtual character. The study aimed to explore three questions:

1. Would neurotypical participants mimic the virtual character despite being told only to copy the goal of the observed action?
2. If so, would this mimicry be modulated by the social engagement of the virtual character?
3. Would there be any differences in mimicry behaviour in autism?

3.3 Method

3.3.1 Participants

Twenty-five neurotypical participants and twenty-six autistic participants were recruited from the autism@icn database and, as in Chapter 2, were taking part in a research day during which they took part in multiple studies. Groups were matched on age, gender, handedness, and, verbal and performance IQ using either the Wechsler Adult Intelligence Scale (WAIS-III UK; Wechsler, 1999a) or Wechsler Abbreviated Scale of Intelligence (WASI-II, Wechsler, 1999b; Table 3-1). Autistic participants had a diagnosis of Asperger's Syndrome (20), autism (4), or, autism spectrum disorder (2) from an independent clinician.

Autistic participants were also tested on module 4 of the Autism Diagnostic Observation Schedule (ADOS-G - Lord et al., 2000) or ADOS-2 (Lord et al., 2012) by a trained researcher with research-reliability status. Seven participants met the ADOS classification for autism, twelve for autism spectrum, and, seven did not meet the classification of autism or autism spectrum. However, all seven who did not meet the cut off for an overall classification of autism or autism spectrum, reached the cut-off for autism spectrum on either the communication or reciprocal social interaction subscale. All participants were financially reimbursed for the time and gave written informed consent to participate. All procedures were approved by the local Research Ethics Committee.

Table 3-1 A comparison of the neurotypical and autism samples

	ASC (n = 26)	NT (n = 25)	t test
	Mean (SD)	Mean (SD)	p value
Age (years)	28 (6)	28 (6)	<i>p</i> = 0.66
Fullscale IQ	120(13)	122(15)	<i>p</i> = 0.62
Verbal IQ	123 (14)	124(15)	<i>p</i> = 0.91
Performance IQ	113(13)	115(15)	<i>p</i> = 0.58
ADOS total	9 (3)		
ADOS communication	3 (1)		
ADOS social interaction	6 (2)		
Gender	4 F; 22 M	6 F; 19 M	
Handedness	4 L; 22 R	3 L; 22 R	

3.3.2 Materials

All the virtual characters movements were animated with pre-recorded motion captured data. These data were recorded using an electromagnetic marker (Polhemus LIBERTY system, Colchester, USA) and mapped onto the virtual character using the software packages MotionBuilder (www.autodesk.com/motionbuilder) and Vizard (WorldViz Inc, Santa Barbara, USA). During motion capture, a piece of card with markings on it assisted the creation of the high (approximately 11cm peak height above the table) and low (3 cm) conditions. The speech for the engaged and socially disengaged virtual characters were recorded from two different female actors.

Participants sat approximately 70 cm from a 160 cm x 90 cm projector screen on which the virtual reality graphics were displayed in 2D. An electromagnetic marker (Polhemus LIBERTY system, Colchester, USA) was attached to the top of participants' right index finger and forehead. The marker on their index finger allowed their finger movements to be recorded, whilst the marker on their forehead allowed the socially engaged virtual character to give participant's eye-contact when smiling at them at the end of each trial. On the table in front of the participants, there was a piece of 81 cm x 66 cm blue card with four 6 cm diameter red circles stuck in the middle of it. The centre of the circles were 15 cm apart from each other and were 30 cm in front of the participants. These red circles acted as the targets. There was also a 6 cm x 4 cm piece of blue card stuck 10 cm in front of the participant which acted as the 'resting pad' where participants were required to place their right index finger when not moving. The physical world extended into the virtual world on the projector screen. Thus, the virtual character was also sat at a table with a piece of blue card with four red targets on it (Figure 3-1).

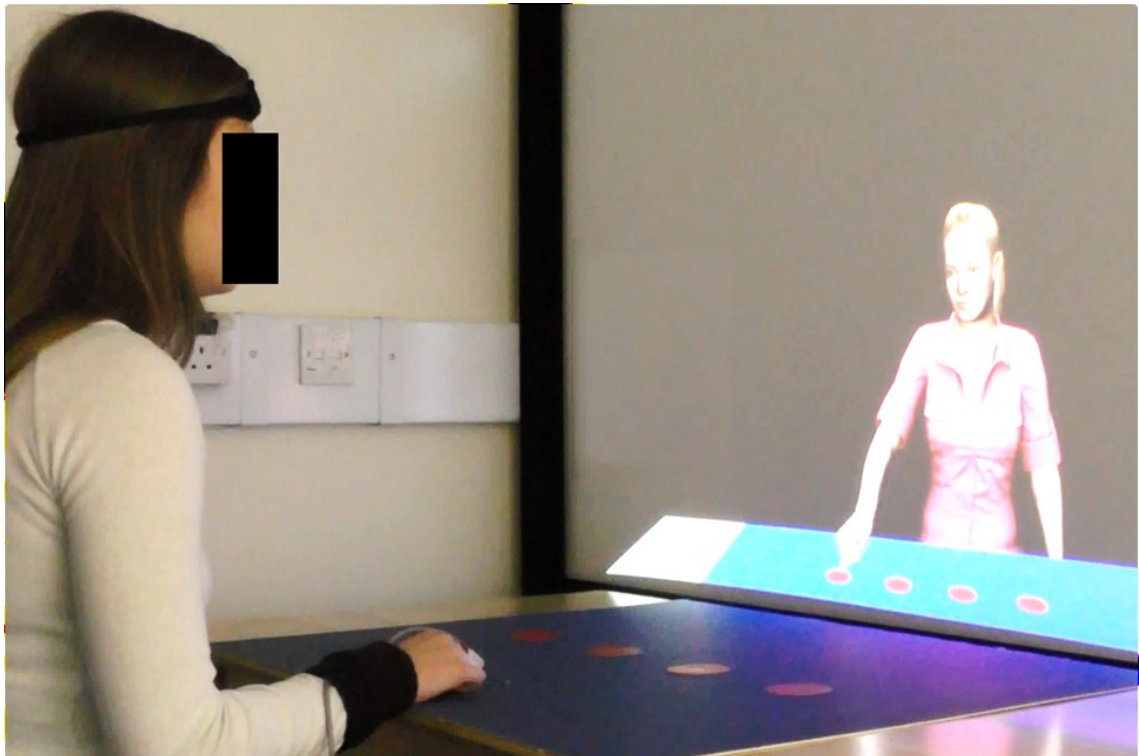


Figure 3-1 A demonstration of how the virtual world extended into the physical world

3.3.3 Experimental design

A 2 x 2 design was used with height (high/low) and engagement condition (engaged/disengaged) as within-subject factors and group (neurotypical/autism) as a between-subject factor. In each block there were 64 trials (32 high and 32 low) with 16 different movement combinations repeated four times.

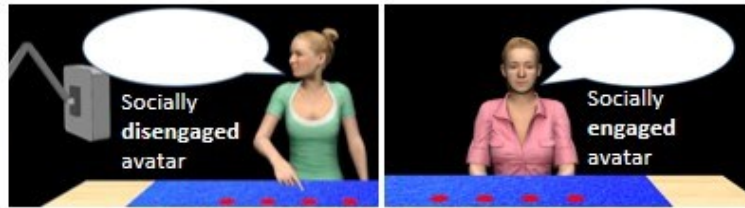
3.3.4 Procedure

Participants were told that they would be playing a game with two virtual characters, Jessie and Kate, but would first practice the game with another virtual character, Mike. Participants were told that the virtual characters' movements were based on the movements of people that had previously been in the lab. Before playing the game with Mike, Jessie or Kate, participants completed calibration during which they were required to place their right index finger into the middle of each of the four targets and the resting pad so that their locations could be recorded.

In the practice session with Mike, participants were told that they would hear a 'dong' sound which was the virtual character's cue to move. This 'dong' sound occurred at the beginning of each trial after a variable delay (1200 – 1800 ms). The virtual character would then point to three of the targets in front of them before returning to their resting position. A 'ding' sound then occurred after a variable delay (1200 – 1800 ms). This sound acted as the participants' cue to move and they were instructed to point to the same targets that the virtual character moved to. Once the participants completed their movements they were instructed to return to their resting pad and this triggered the next trial. The spatial correspondence between the virtual characters' and participants' targets was explained to the participants. For example, if the virtual character pointed to the target on her far left, participants should point to the

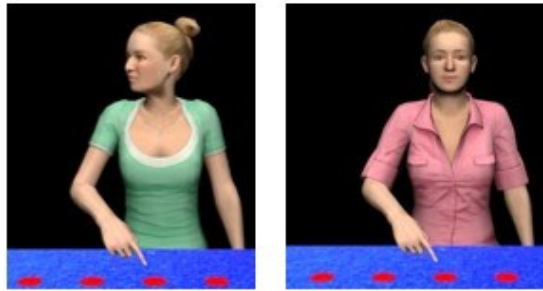
Introduction at the start of the block

"I'm going to be playing this game with you. But I have to watch this screen as well"



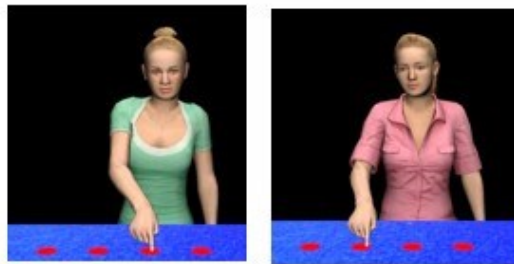
"I'm going to be playing this game with you. I'm really looking forward to it!"

Trial structure for the engaged and disengaged avatars



At the start of the trial the engaged avatar oriented her head to the motion tracker attached to the participant's forehead. The disengaged avatar looked at the screen to her right.

Variable delay (1200-1800 ms) before the avatar's cue to move: "dong"



The avatars pointed to a sequence of three targets

Avatar finishes movement



At the end of the movements, the engaged avatar looked up and smiled at the participant by orientating to the motion tracker attached to their forehead; the disengaged avatar looked at the screen.

Variable delay (1200-1800 ms) before participant's cue to move: "ding"

Figure 3-2 The trial structure for the socially engaged and socially disengaged virtual characters

target on their far right. Participants were given approximately 10 practice trials with Mike before the start of the experiment to ensure they understood the task instructions.

Participants then played the game with Kate and Jessie. For each participant, one virtual character was socially engaged and the other was socially disengaged (Figure 3-1). The order and engagement of the virtual characters was counter-balanced across participants. Before the game started, the socially engaged virtual character said,

“Hi, my name’s Kate/Jessie and I’m going to be playing this game with you. I’m really looking forward to it” and then smiled at the participant, whereas the social disengaged virtual character said,

“Hi, my name’s Kate/Jessie and I’m going to be playing this game with you. But I have to watch this as well” and then looked away at a virtual monitor to her right. The trial structure was then the same as for the practice session except that the socially engaged virtual character looked up and smiled at the participant and continued to look at them during their response. Conversely, the socially disengaged virtual character looked away at the monitor to her right after having completed her movements. So, she was not looking at the participant when they made their movements. Finally, in order to measure co-presence, after each game participants were asked to rate on a Likert scale from 1 (not at all) to 7 (very much so): “How much did you behave as if Jessie/Kate were real?”

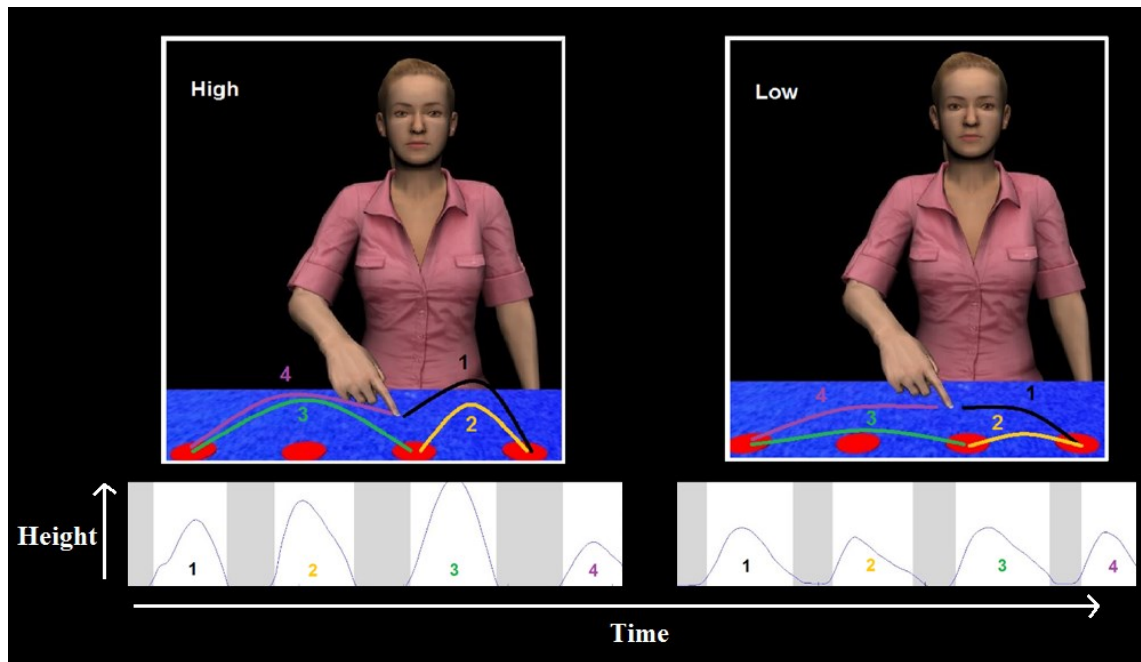


Figure 3-3 An example of a high and low trial (above) and a typical participant movement profile to these observed actions chunked into four movements (below). Only movements 2 and 3 were analysed

3.4 Results

3.4.1 Excluded data

The movement data were analysed using Matlab R2013b (MathsWorks, Natick, USA). Movement data were filtered with a Butterworth filter to remove high frequencies. Each participant's calibration data were used to chunk each trial into four movements: (1) the movement to the first target from the resting pad, (2) the movement to the second target; (3) the movement to the third target, (4) the movement back to the resting position (Figure 3-3). On 4.27% of trials, the data could not be chunked into four movements and these were excluded from the analysis. There were no significant differences between neurotypical and autistic participants in the number of trials that could not be chunked into four movements (Mean (SD): neurotypical 3.66% (5.35%); autism 4.87% (6.26%); $t_{49} = -0.741, p = 0.462$). On 3.13% of the trials participants failed to move to the correct targets. There were no significant differences between neurotypical and autism in the number of incorrect trials per block (Mean (SD): neurotypical 2.31% (1.93%); autism 3.90% (4.99%); $t_{32.61} = -1.516, p = 0.139$). By

combining these two exclusion criteria, the total proportion of trials excluded was 6.62%. There were no significant differences between the proportion of trials excluded between the two groups (Mean (SD): neurotypical 5.47% (5.39%), autism 7.72% (7.99%); $t_{49} = -1.176, p = 0.245$).

3.4.2 Peak height analysis

The mean peak height of the movements between the targets (the mean of movements 2 and 3) for each trial were subject to an ANOVA with engagement condition (engaged/disengaged) and height (high/low) as within-subject factors and group (neurotypical/autism) as a between-subject factor. This revealed a main effect of height ($F_{1,49} = 16.28, p < 0.001, \eta_p^2 = 0.249$). Post-hoc t-test revealed the peak height of participants' movements were significantly higher having observed the virtual character move with a high, compared to low, trajectory between the targets ($t_{50} = 3.89, p < 0.001$; Figure 3-4). This difference between the high and low observed actions was significant for both neurotypical ($t_{25} = 3.16, p = 0.004, d = 0.631$) and autistic ($t_{25} = 3.02, p = 0.006, d = 0.592$) participants. There was a marginally significant interaction between height and group ($F_{1,49} = 3.99, p = 0.051; \eta_p^2 = 0.075$; Figure 3-4). Neither the interaction between height and condition, or, height, condition and group were significant ($F < 0.8$; Figure 3-5).

3.4.3 Copresence

Overall participants' co-presence ratings were low (Figure 3-6). These scores were subject to a 2 x 2 ANOVA with engagement (engaged/disengaged) as a within-subject factor and group as a between-subject factor. This revealed a marginal effect of engagement ($F_{1,49} = 3.54, p = 0.066$) and group ($F_{1,49} = 3.21, p = 0.079$), but no interaction between engagement and group ($F_{1,49} = 0.004, p = 0.951$).

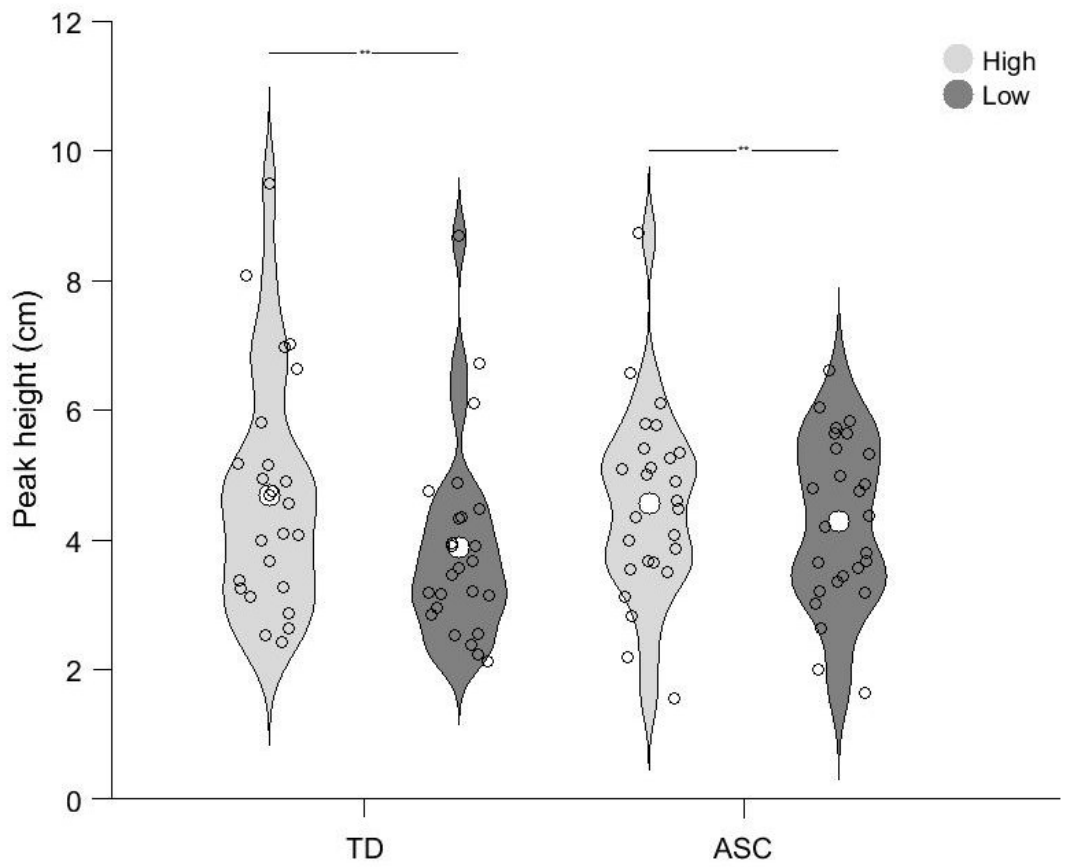


Figure 3-4 Mean peak heights between the targets in the high and low conditions.

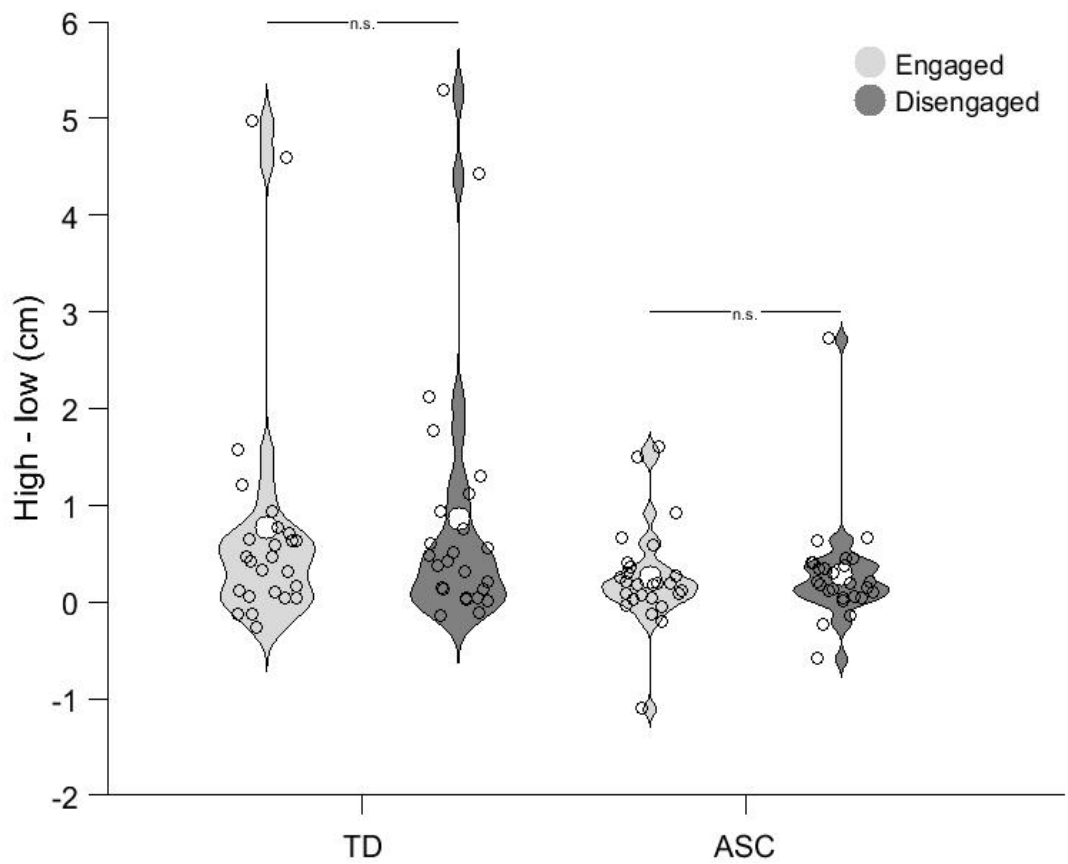


Figure 3-5 Mean difference between the high and low conditions for the engaged and disengaged conditions

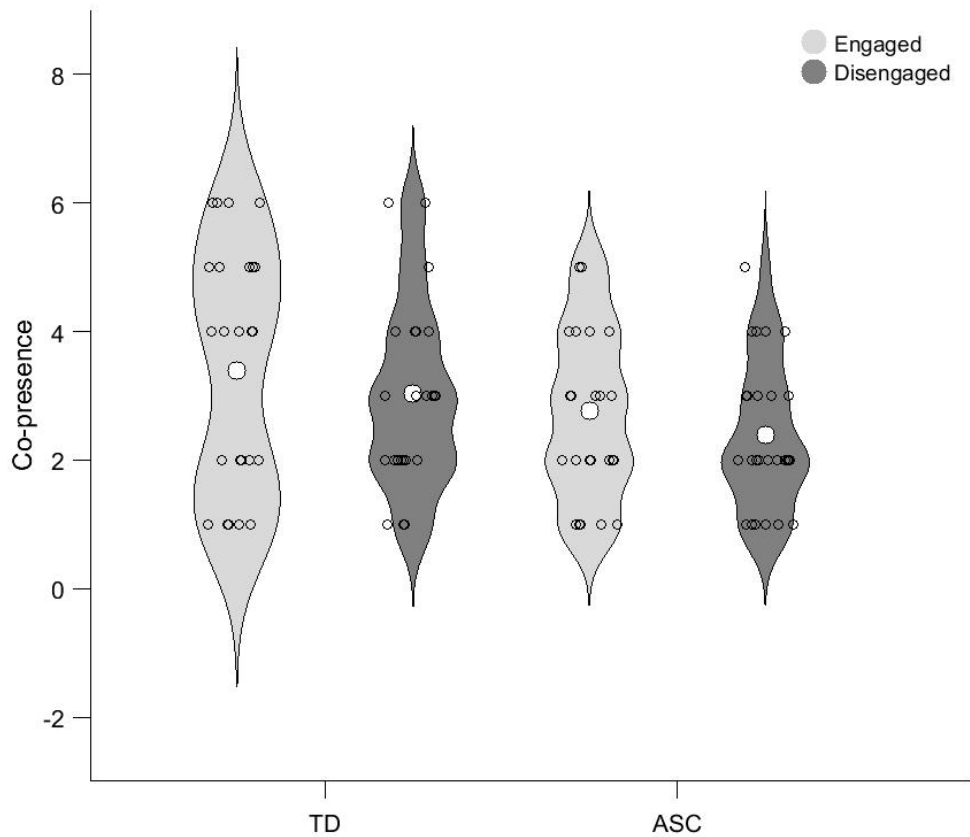


Figure 3-6 Mean copresence scores

3.5 Discussion

The study's primary aim was to use virtual reality to induce and socially modulate mimicry in neurotypical participants and to explore any differences in autism. Participants mimicked the kinematics of the virtual characters' movements despite being told only to copy the goal of the observed action. Autistic participants also mimicked but did so to a lesser extent. In neither group, however, was mimicry modulated by the social engagement of the virtual character. Possible reasons for this are discussed in further detail below.

3.5.1 A novel virtual mimicry paradigm

The results demonstrate that virtual characters can be used to induce mimicry in both neurotypical and autistic participants. Despite participants being told to point to the

same targets the virtual character pointed to, they were also sensitive to the kinematics of the observed action, rather than just the action goal. For example, on trials where the virtual character moved with a high trajectory between the targets, participants also tended to move with a higher trajectory compared to trials where the virtual character moved with a low trajectory. This supports previous kinematics studies, such as that by Wild et al. (2012), in which participants copied the vertical and horizontal amplitude of observed actions despite being given goal-orientated instructions. Previous studies investigating mimicry within a virtual reality setting had only explored reaction time measures of mimicry, such as a stimulus response compatibility paradigm (Pan & Hamilton, 2015). The present study extends this work by demonstrating that participants mimic the kinematics of virtual characters' movements. More generally, the present study adds to the growing number of studies which highlight the feasibility of virtual reality in the ecologically valid study of human social interaction (Bohil et al., 2011; Georgescu et al., 2014). Our virtual reality paradigm also has the potential to be used in combination with neuroimaging methods, such as functional near infrared spectroscopy, to elucidate the neural underpinnings of mimicry and how these might be different in autism (Pinti et al., 2015).

3.5.2 Reduced mimicry in autism

Both the neurotypical and autism group mimicked the virtual characters' movements, yet autistic participants did so to a lesser extent. This supports previous work demonstrating that autistic individuals can and do under certain conditions spontaneously mimic (Cook & Bird, 2012; Grecucci et al, 2013) but there is a reduced propensity do to so (Edwards, 2014). Most studies demonstrating a reduced propensity to mimic in autism investigated children (e.g. Jiménez, Lorda & Méndez, 2014) and those conducted with adolescence or adults have focused on facial mimicry (Hertzig, Snow, & Sherman, 1989; McIntosh et al., 2006). Thus, the current study extends this

work by showing that this reduced propensity to mimic in autism continues into adulthood, is not restricted to spontaneous facial mimicry, and, most interestingly, occurs in a virtual reality environment. Importantly, the groups did not differ in terms of their ability to copy the goal of the action (i.e. emulation) as there were no significant differences between the groups in the proportion of trials in which participants pointed to the incorrect targets. Again, this finding is supported by previous work showing intact emulation in autism (Edwards, 2014). Together, these findings support Hamilton's (2008) proposal of intact emulation yet differences in mimicry in autism. Finally, the finding that mimicry differences in autism occur when interacting with virtual characters has important practical and clinical implications for virtual reality training programmes, and, potentially, virtual reality diagnostic tools (Scassellati, 2005). It suggests that the behaviours autistic individuals display in everyday life also occur when interacting with and responding to virtual characters. Although, the limitations of our virtual reality approach are discussed below.

3.5.3 Unmodulated mimicry: copresence and social cues

Mimicry was not modulated by how socially engaged the virtual character was in either neurotypical or autistic participants. This is at odds with STORM and a series of previous studies which demonstrated that social cues, such eye-contact (Forbes et al., 2016), pro-social priming (Cook & Bird, 2012) and emotional facial expressions (Grecucci et al., 2013), modulate mimicry in neurotypical participants; yet, this modulation is reduced in autism. There are several possible reasons as to why the social manipulation did not modulate mimicry in the current study. Wang and Hamilton (2012) proposed that the effect of eye-contact on mimicry is mediated by an audience effect, whereby the enhancement occurs when participants feel the observer is maintaining social engagement with them throughout the response period. In the current study, the socially engaged virtual character gave participants eye-contact throughout

their response period so it is unclear why mimicry was not enhanced. One possible reason could be the lack of co-presence with the virtual characters; mean co-presence scores were low. Thus, if participants felt the virtual characters were unrealistic this may have nullified the impact of any social manipulation and caused low co-presence scores. The virtual characters' hand movements were motion captured so based on those of a human. This may account for the reliable mimicry effect as participants are likely to have regarded these movements as realistic. However, the virtual characters' head movements, and facial expressions, such as the socially engaged virtual character's smile, were key frame animated. Although, participants' qualitative experiences towards the virtual characters were not collected in the current study, in previous virtual reality studies participants have reported that the virtual characters "were slightly robotic without facial expression which lessened impact" (Pan et al., 2016; p. 11). Moreover, Moser et al. (2007) have highlighted differences in neural activation, such as reduced activation of the fusiform gyrus, when viewing a virtual character with emotional facial expressions compared to a human face displaying the same expressions. Thus, the present limitations of the virtual reality, especially with regards to realistic facial expressions, may have accounted for the lack of co-presence and the lack of social modulation in the present study.

The two-dimensional nature of the virtual reality environment may also have contributed to the low co-presence scores. Although the physical world of the participant continued into the virtual world on the screen in front of them, there was a tangible divide between the physical world of the participant and the virtual world of the virtual character. Schultze (2010; p. 439) has highlighted how "one key-determinant of co-presence is ... to jointly manipulate shared space and shared objects." Therefore, the current paradigm may benefit from being implemented in a fully immersive virtual reality setting, for example using a head-mounted display (HMD), such as the Oculus

Rift or HTC Vive. This would allow the participants to be embodied (i.e. have their own virtual character) and share the virtual space with the virtual character, for example, both virtual character and participant could point to the same virtual targets. However, studies using such an approach typically have the virtual targets positioned in mid-air without a table, but the kinematics of movements to such targets might differ.

Implementing our paradigm safely and effectively using an HMD with a physical table is technically challenging. A failure to embody participants accurately within a fully immersive HMD runs the risk of participants injuring their fingers on the table in front of them when pointing to the targets.

In the task there was some level of interaction between the virtual character and participant. For example, the virtual character did not start her turn until the participant had returned to the resting pad, and, after the engaged virtual character had finished her turn she oriented to a motion tracker attached to each participant's forehead thereby giving a sense of eye contact. Despite these advantages over simple video stimuli, participants were still watching animations on a screen in front of them. Reader and Holmes (2015) directly compared real life and video stimuli during an imitation task and found reduced object-directed imitation accuracy with the use of video stimuli. Furthermore, reduced activation of human motor cortex has been found when observing motor acts in videos compared to live movements (Järveläinen, Schürmann, Avikainen, & Hari, 2001). Again, the use of a fully immersive, three-dimensional environment, or, the use of real-life interaction partners may result in the social modulation of mimicry within the current paradigm.

3.5.4 Unmodulated mimicry: timing and task demands

In studies investigating social modulators of mimicry within a stimulus response compatibility paradigm, there is usually a small time window between the social

manipulation, the observed action and the subsequent response. For example, in Chapter 2, the delay between the social manipulation and observed action was either 200 or 800 ms. Participants were then required to respond as soon as they saw the actor's hand move in the video. Similarly, in Grecucci et al. (2013) the facial expression was presented for 500 ms, participants then observed the moving hand for 1105 ms before being required to respond. Finally, in Pan and Hamilton (2015; Experiment 2) the interaction between form (virtual character vs. ball) and congruency (i.e. mimicry) was only found on reaction times to tap the first, but not the last, drum in the sequence. Together these studies support the view that for certain social manipulations the delay between action observation and action performance needs to be minimised in order for the social manipulation to modulate mimicry. Future studies investigating social modulators of mimicry within the present paradigm may benefit from comparing the kinematics of movements to the first target.

The relatively high task demands in the current study may also have contributed to a lack of social modulation. Error rates in stimulus-response compatibility paradigms are typically less than 0.1% (e.g. Wang et al., 2010; Bird et al., 2007). In Pan and Hamilton's (2015) task mean error rates were between 1.2 - 1.5%. In the present study the error rate was approximately double this for the neurotypical participants (2.6%). The lower error rate in Pan and Hamilton (2015) is likely due to the lower memory demands of their task. The required drum sequence was displayed on a virtual tablet in front of the virtual character, whereas, in the current study participants had to memorise the correct three target sequence. Thus, the higher task demands in the present study may have nullified any potential social modulation of mimicry. Although, it is also possible that lower task demands will enhance mimicry as this could increase participants' ability to process the motion of the virtual character's movements (Rees,

Frith, & Lavie, 1997). Future studies could reduce the task demands by having participants point to fewer targets.

3.5.5 Conclusion

To conclude, we provide a novel paradigm which enables mimicry to be induced in a rich and ecologically valid, interactive virtual reality environment. Participants copied the kinematics of the virtual characters' movements, despite being instructed only to copy the goal of the observed action. The study reinforces Hamilton's (2008) proposal of intact emulation but differences in mimicry in autism as autistic participants showed reduced mimicry compared to neurotypical participants. The findings have implications for virtual reality training programmes and perhaps virtual reality diagnostic tools, as it suggests that behaviours autistic people display in everyday life also occur when interacting with virtual characters. Unlike previous studies investigating the modulation of mimicry, the social manipulation in the present study failed to modulate mimicry. There are several possible reasons as to why the social manipulation did not modulate mimicry, including the physical realism of the virtual characters and subtlety of the social manipulation. These factors were systematically explored in Chapter 4.

Chapter 4 - Modulating Mimicry? Physical Realism, Attention and Animacy

Parts of Chapter 4 were published in a review paper in *Neuropsychologia*:

Krishnan-Barman, S., Forbes, P. A. G., & Hamilton, A. F. D. C. (2017). How can the study of action kinematics inform our understanding of human social interaction? *Neuropsychologia*, *105*, 101-110.

4.1 Abstract

Chapter 3 found that both autistic and neurotypical participants mimicked the height of the virtual character's movements, but the autistic participants did so to a lesser extent. However, the social engagement of the virtual character did not modulate mimicry in either group which is inconsistent with the predictions of STORM. The first study (Experiment 1) presented in Chapter 4 aimed to address two potential confounds which could have accounted for this lack of social modulation: (1) the limited physical realism of the virtual character, and, (2) the lack of attention towards the social manipulation. To do this I replicated the paradigm employed in Chapter 3 but used videos of a human model rather than virtual characters. We also included 'catch' trials which required participants to attend to the model's face and thus the extent of her social engagement. Finally, I used a mixed, rather than a blocked design, to try and highlight the differences between the conditions (Brass, Derrfuss, Matthes-von Cramon, & von Cramon, 2003; Gowen & Poliakoff, 2012). The second study (Experiment 2) aimed to make the social manipulation less subtle. This was done by reducing the animacy of the stimuli - participants interacted with either a virtual character or moving ball. Participants mimicked all models in both experiments but there was no evidence that this mimicry was socially modulated.

4.2 Experiment 1. Increasing physical realism and attention

4.2.1 Introduction

Physical realism and social responses to virtual characters

The advantage of using virtual reality over video stimuli is that it can offer a sense of interaction, for example, by motion tracking participants and having the virtual character respond to their movements (Forbes, Pan, Hamilton, & Hamilton, 2016; Hamilton, Pan, Forbes, & Hale, 2016). However, virtual reality is to some extent limited by the realism of the virtual character's appearance. Mori's (1970) notion of the "uncanny valley" proposed that as the humanness of virtual characters increases, people show increased affinity towards them up to a certain level of humanness. At this point, as virtual characters fall just short of complete human-likeness, our affinity for them declines which is characterised by feelings of unease and eeriness. Mori suggested that presence of movement exacerbates this effect, or "steepens the slopes of the uncanny valley" (Mori, 1970; p. 34). Below I review the impact of virtual characters' physical realism on social interactions.

Garau et al. (2003) showed that if a virtual character moved with realistic eye movements then the greater realism of the virtual character's appearance was critical in determining the quality of the interaction. If the virtual character's appearance had lower-realism, then greater realism in its eye movements did not improve the quality of the interaction and could even lower it. With regards to mimicry, beliefs about the animacy of a stimulus have been shown to modulate automatic imitation (Liepelt & Brass, 2010). Thus, if the appearance of a virtual character results in it being deemed less animate, this could impact the social modulation of mimicry.

Perani et al. (2001) compared brain responses when participants viewed a real hand or a virtual hand grasping an object in which all stimuli, regardless of their

appearance, moved with biological motion (real kinematics). They found that areas involved in representing hand actions, such as posterior parietal cortex, were preferentially activated in response to viewing real, as opposed to, virtual hands. Given the dual role of these areas in both action observation and execution (Iacoboni et al., 1999), Perani et al. (2001) speculated that such differences in activation could have consequences for the imitation and mimicry of virtual characters. Similarly, regions of the ‘empathy of pain network’ (Singer et al., 2004), such as anterior cingulate cortex, show a dampened response when participants view cartoons as opposed to photos depicting others in pain (Gu & Han, 2007). This lends support to the view that virtual simulations and depictions of others’ behaviour may less reliably activate social brain regions when compared to real or video-recorded version of these behaviours.

Increasing physical realism through video stimuli

To deal with this issue, I aimed to recreate the same paradigm using recorded video stimuli of a human actor. Several studies have directly compared video stimuli and real stimuli and have found only subtle differences in social behaviour (Gullberg & Holmqvist, 2006). For example, Gullberg and Holmqvist (2006) compared participants’ gaze behaviour towards an interaction partner in real life and in two video conditions (life-size video and screen size). They found no reliable effects of either the size of the stimulus or the medium (real vs. video) on fixations – the face dominated as an area of fixation in all conditions and gestural features attracted fixations in all conditions. This suggests that certain social stimuli, such as faces, attract the attention of participants regardless of whether they are presented in real life or on a video. Additionally, Freeth, Foulsham and Kingstone (2013) asked participants to interact with an experimenter either live or via a video. Although they found some differences between the video and live conditions, many effects were consistent across the two conditions. For example, independent of condition, participants were more likely to look at the experimenter’s

face compared to her body and looked at her face more when being asked a question compared to when answering it. Freeth et al. concluded that the “similarities between live and video interactions demonstrate that many aspects of eye movement behaviours generalize between natural and artificial stimuli” (Freeth et al., 2013; p. 8).

Whilst these studies focused on gaze behaviour, a range of studies have demonstrated mimicry and automatic imitation effects using videos and even static images (Brass et al., 2001; Forbes & Hamilton, 2017; Forbes et al., 2016; Genschow et al., 2017; Stel et al., 2008; Wang & Hamilton, 2013b; Wild et al., 2010, 2012). For example, whereas Chartrand and Bargh (1999) used live confederates to induce mimicry, comparable effects have been observed using video recordings of a model who was either touching her nose or hair (e.g. Genschow et al., 2017). Similarly, Rohbanfard and Proteau (2013) found no differences in motor skill learning depending on whether the model was live or presented on a video. Moreover, young children successfully imitate after having observed videos of a model (Bandura, Ross, & Ross, 1963; Barr & Hayne, 1999; Hayne, Herbert, & Simcock, 2003) and non-human animals, such as dogs, have been shown to respond to videos of human actions (Pongrácz, Miklósi, Dóka, & Csányi, 2003) and may even copy them (Harr, Gilbert, & Phillips, 2009).

Yet, the use of video stimuli for the study of social cognition has been criticised (Reader & Holmes, 2015, 2016; Risko, Laidlaw, Freeth, Foulsham, & Kingstone, 2012; Schilbach, 2010). Reader and Holmes (2016) highlighted three sources of ‘nuisance variance’ when studying social interaction in constrained experimental settings, such as those which use video stimuli. These include the quality of the observed stimuli (visual fidelity), the role of gaze, and the extent to which the stimuli can provide a sense of interaction (social potential). Video stimuli contribute to all three (potentially interdependent) sources of ‘nuisance variance.’ For example, regarding visual fidelity,

Reader and Holmes' (2015) found that imitation was compromised when the model was presented via a live video stream compared to when the model was sat opposite the participant. In terms of gaze, Freeth, Foulsham and Kingstone (2013) asked participants to interact with an experimenter either live or via a video during which the confederate gave either direct or averted eye-contact. Only in the live setting did the confederate's gaze behaviour modify the participants' gaze behaviour. With regards to social potential, the mere presence of a seemingly passive bystander can influence participants' behaviour due to the bystander's potential to interact with them (Becchio, Sartori, & Castiello, 2010; Krishnan-Barman et al., 2017; Quesque, Lewkowicz, Delevoe-Turrell, & Coello, 2013). This potential for interaction and reciprocity is a defining feature of social interaction which may be hard to simulate using video stimuli (Risko et al., 2012; Schilbach, 2010). Finally, as with the literature on action observation in virtual reality, neuroimaging studies have revealed reduced motor cortex activation when participants viewed videos of motor acts compared to live movements (Järveläinen et al., 2001). Similarly children show mu wave suppression – a possible index of mirror system activity (Muthukumaraswamy, Johnson, & McNair, 2004) - when viewing live actions but not videos of those same actions (Ruyschaert, Warreyn, Wiersema, Metin, & Roeyers, 2013).

In sum, clearly the use of video stimuli to study social interaction is not a perfect substitute for a live agent (Reader & Holmes, 2015, 2016). However, a range of behaviours have been shown to be consistent across video and live conditions, including certain gaze behaviours (Gullberg & Holmqvist, 2006), imitation and mimicry (Brass et al., 2000; Genschow et al., 2017), and motor skill learning (Rohbanfard & Proteau, 2013). Thus, one of the aims of Experiment 1 was to establish whether the increased physical realism of the model, through the use of video stimuli, would result in the modulation of mimicry by social engagement.

Increasing attention

In Chapter 3, we did not control or monitor where participants were looking. Thus, it is possible that the lack of socially modulated mimicry was the result of participants not attending to the face and head of the virtual character. Participants were instructed to observe which targets the virtual character pointed to and then point to the same targets on the table in front of them. Thus, their attention may have been focused on the virtual character's hand movements rather than the rest of her body which conveyed the extent of social engagement. Several studies have shown that motor resonance and imitation are affected by the attentional state of the participant (Bek et al., 2016; Puglisi et al., 2017). To ensure that participants attended to the model's face and her degree of social engagement a letter appeared on the model's forehead on 20% of trials in Experiment 1. During these 'catch' trials, participants were instructed to state out loud the letter which appeared on the model's forehead.

The current study

The current study used the same sequential-pointing paradigm employed in Chapter 3 and aimed to increase the realism of the stimuli to assess whether this would result in the social modulation of mimicry. To do this, videos of a female model were recorded who pointed to sequences of three targets with either high or low movement trajectory. As before participants were instructed to point to the same targets as the person in the video. The engagement of the model was manipulated by having the actor either smile at participant's during the response period (engaged) or look away from the participant by turning her head to the side (disengaged). We included 'catch' trials to ensure that participants attended to the model's face and her degree of social engagement. We had two hypotheses: (1) participants would mimic the height of the model's movement trajectory; (2) the increased realism of the model's appearance and

the increased attention directed to her face would result in a differences in mimicry between the engaged and disengaged conditions.

4.2.2 Method

Participants

Eighteen (9 female) were obtained from my institute's participant database and had a mean (SD) age of 25 (8) years. All participants were right-handed, had normal or corrected to-normal vision and reported no history of neurological disorder. All were financially reimbursed for their time and gave written informed consent before participating. All procedures were approved by the UCL Research Ethics Committee.

Stimuli

Videos consisted of a female actor positioned behind a window frame, which appeared 48 cm × 40 cm on the projector screen. There was a horizontal bar across the centre of the window frame so the screen could be split into two (see Figure 4-1). The top half of every video was the same for all engaged trials and started with the actor looking up and smiling before looking down at her hand. At this point in the bottom half of the video, the actor moved from her resting position and pointed to three out of a possible four targets on the table in front of her. She then returned to the resting pad, looked up and smiled at the participants. The disengaged trials started with the model looking downwards and nodding her head. She then pointed to three targets before returning to her resting pad and looking to her right. The model held a neutral expression throughout the disengaged trials and did not look up at the participant (for timings, see Figure 4-1).

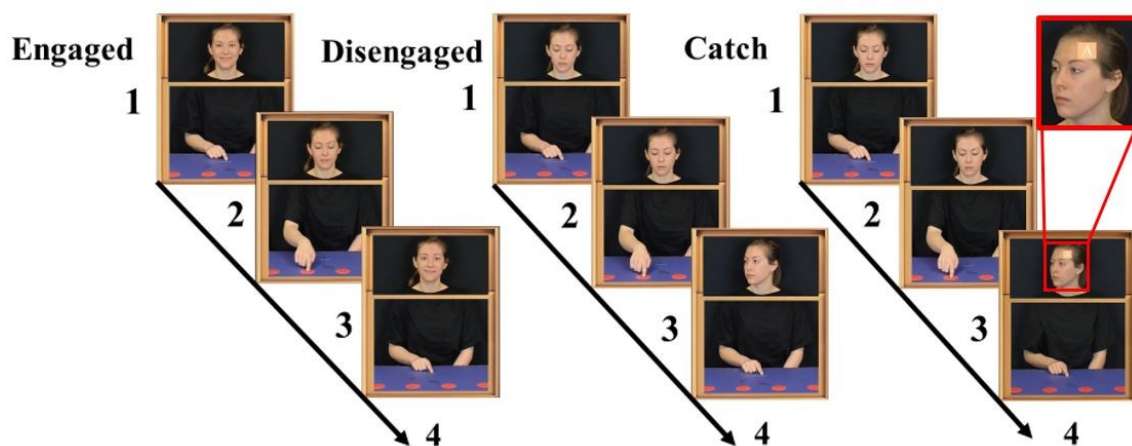


Figure 4-1 The trial structure for each condition

At 1 the actor rested her index finger on the resting position and either looked up and smiled at the participants (*Engaged*) or looked down and nodded with a neutral expression (2000 ms). At 2 the participant pointed to a combination of three red targets with either a high or low trajectory (4000 ms). At 3 she then returned to her resting position which was the participants' cue to move. The actor either smiled and looked up at participants (*Engaged*), or, look to her side with a neutral expression (*Disengaged*). The response period lasted 5000 ms during which participants were required to point to the same targets on the table in front of them. On catch trials a letter appeared on the actor's forehead at the start of the response period and participants stated out loud what this letter was.

The bottom half of the video was the same for both the engaged and disengaged trials and consisted of the model pointing to three different targets with either a high (2-3 cm) or low (8-9 cm) movement trajectory. There were eight different movement combinations which were repeated for each of the four conditions (32 trials). Each target was a red circle, which appeared 4 cm in diameter, and the centre of the targets appeared 10.5 cm away from each other on the projector screen.

To ensure participants attended the model's face, there were an additional 8 catch trials in each block. In these trials, a letter appeared on the model's forehead once she returned her finger to the resting pad. Participants were instructed to verbally respond to the letter which appeared on her forehead (e.g. if the letter was A, they should shout out 'a') but to proceed with their movements as normal. In total there were 40 trials within each block but the peak height of the movements during the 8 catch trials in each block were not analysed. Participants completed four blocks and the trials were fully randomised within each block.

Procedure

Participants sat approximately 70 cm from the projector screen. An electromagnetic marker (Polhemus LIBERTY system, Colchester, USA) was attached to participants' right index finger which enabled finger movements to be recorded. On the table in front of the participants, there was a piece of 81 cm × 66 cm blue card with four 6 cm diameter red circles stuck in the middle of it. The centre of the circles was 15 cm apart from each other and was 30 cm in front of the participants. These red circles acted as the targets. There was also a 6 cm × 4 cm piece of blue card stuck 10 cm in front of the participant which acted as the 'resting pad' where participants were required to place their right index finger when not moving.

Before the start of the experiment participants completed calibration: they placed their right index finger into the middle of each of the four targets and the resting pad so that the coordinates could be recorded. After calibration participants were given twelve practice trials. Participants were instructed to rest their finger on the resting pad in front of them. They were told to watch the actor in the video and see which three targets she pointed to, then, when she returned to her resting position, they should point to the same targets she pointed to in the same order. The spatial correspondence between the targets in the video and the targets in front of the participants was explained. For example, participants were told that if the actor in the video pointed to the target on her far left then participants should point to the target on their far right so that there was a spatial match between their targets. Participants were also informed that on some trials (i.e. the catch trials) a letter would appear on the model's forehead and they should state out loud the letter they see but proceed with their movements as in the other trials. During practice there were four catch trials.

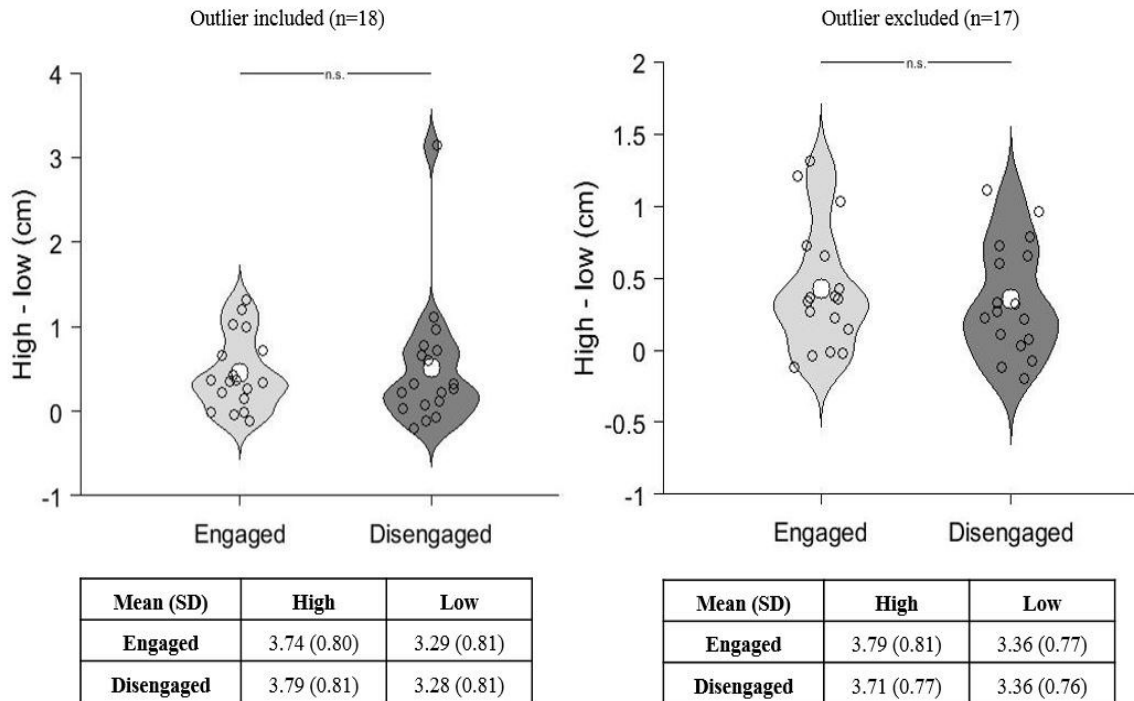


Figure 4-2 Mimicry (*high – low*) for the engaged and disengaged conditions

4.2.3 Results and discussion

Excluded data

On 1.0% (SD: 1.1%) of trials participants pointed to the wrong combination of targets. These error trials were excluded before the main analysis. Movement data were analysed using Matlab R2013b (MathsWorks, Natick, USA) and filtered with a Butterworth filter to remove high frequencies. Each participant's calibration data were used to chunk each trial into four movements: (1) the movement to the first target from the resting pad, (2) the movement to the second target; (3) the movement to the third target, (4) the movement back to the resting position. When a trial could not be chunked into four movements, it was removed from the analysis. This was then combined with the error trials to give a total percentage of excluded trials for each participant. The mean percentage of total excluded was 1.7% (SD: 2.6%).

Peak height analysis

The mean peak height of the movements between the targets (movements two and three) for each trial were subject to a repeated measures ANOVA with social engagement (engaged/disengaged) and height (high/low) as factors. Note, the mean length of movement two was larger than movement three due to the combination of targets the participants were required to point to; thus, movement has not included as a factor.

The analysis revealed a main effect of height ($F_{1,17} = 14.59$, $p = 0.001$, $\eta_p^2 = 0.462$), with the peak height of movements between the targets greater in the high (mean: 3.76 cm, SD: 0.75) compared to low (mean: 3.28 cm, SD: 0.80) condition. Post hoc paired samples t-tests revealed this was the case in both the engaged ($t_{17} = 4.43$, $p < 0.001$, $d = 1.043$) and disengaged condition ($t_{17} = 2.85$, $p = 0.011$, $d = 0.670$) (Figure 4-2). The main effect of engagement ($F_{1,17} = 0.074$, $p = 0.789$, $\eta_p^2 = 0.004$) and the interaction between height and engagement were not significant ($F_{1,17} = 0.123$, $p = 0.730$, $\eta_p^2 = 0.007$). A Bayesian paired samples t-test using JASP software, version 0.8.0.0 (JASP Team, 2017), compared mimicry (the difference in peak height between the high and low condition) in the engaged condition (mean: 0.458, SD: 0.439) to that in the disengaged condition (mean: 0.509, SD: 0.759). The Bayes Factor for this test ($BF_{10} = 0.257$) suggested moderate evidence in favour of the null hypothesis – no differences in mimicry between engaged and disengaged conditions.

Outlier removal

As can be seen in Figure 4-2 one of the participants was an outlier who showed a mimicry effect (3.14 cm) in the disengaged condition which was over three standard deviations from the mean for this condition. To ensure this outlier did not impact the results I performed an identical analysis with this participant removed.

This analysis revealed a main effect of height ($F_{1,16} = 18.63$, $p < 0.001$, $\eta_p^2 = 0.538$), with the peak height of movements between the targets greater in the high (mean: 3.75 cm, SD: 0.770) compared to low (mean: 3.36, cm, SD: 0.760) condition. Post hoc paired samples t-tests revealed this was the case in both the engaged ($t_{16} = 4.08$, $p < 0.001$, $d = 0.990$) and disengaged condition ($t_{16} = 3.75$, $p = 0.002$, $d = 0.910$) (Figure 4-2). The main effect of engagement ($F_{1,16} = 0.847$, $p = 0.371$, $\eta_p^2 = 0.050$) and the interaction between height and engagement were not significant ($F_{1,16} = 0.748$, $p = 0.400$, $\eta_p^2 = 0.045$). A Bayesian paired samples t-test using JASP software, version 0.8.0.0 (JASP Team, 2017), compared mimicry (the difference in peak height between the high and low condition) in the engaged condition (mean: 0.426, SD: 0.430) to that in the disengaged condition (mean: 0.354, SD: 0.389). The Bayes Factor for this test ($BF_{10} = 0.345$) suggested moderate evidence in favour of the null hypothesis – no differences in mimicry between the engaged and disengaged conditions.

Results Summary and Discussion

This experiment aimed to test whether the increased physical realism of the model and increased attention towards her face would result in the social modulation of mimicry. As in Chapter 3 we found that participants were sensitive to the peak height of the actor's movements. Participants moved with greater peak height between their targets after having observed the model move between her targets with a high compared to a low trajectory. This replicated previous work showing that mimicry and imitation can be reliably induced using video stimuli across a range of paradigms (Bandura et al., 1963; Forbes et al., 2017; Genschow et al., 2017; Wild et al., 2010, 2012). As in Chapter 3, the engagement of the model – whether she smiled at the participants (engaged) or looked away (disengaged) during the response period – did not modulate this mimicry. This was despite the increased physical realism of the model and the inclusion of 'catch' trials which aimed to increase the attention directed towards the

model's face and thus her extent of social engagement. Next, I present the results of Experiment 2 which employed the same sequential pointing paradigm as Experiment 1 but used a cruder social manipulation to try and modulate mimicry.

4.3. Experiment 2. Manipulating animacy

4.3.1 Introduction

Chapter 3 and Experiment 1 in this chapter demonstrated that modulating the social engagement of a virtual character or a human model did not alter mimicry in the sequential pointing task. One possibility is that the social manipulation was too subtle to induce differences in mimicry between the conditions. To address this possibility, Experiment 2 was conducted in which a virtual character was compared to a moving ball - a non-biological stimulus. The virtual character was animated as before, but the ball moved with non-biological motion (i.e. constant velocity) between the targets with either a high or low trajectory. The study aimed to explore whether the peak height of participants' movements would continue to be influenced by the height of a non-biological stimulus, and, if so, whether this effect was comparable to that induced by a virtual character. First, I outline studies which have compared mimicry responses to biological and non-biological stimuli.

Biological stimuli are animate human stimuli (or human-like stimuli e.g. virtual characters, humans) whereas non-biological stimuli are inanimate, non-human stimuli, such as abstract shapes or industrial robots. Two important features which separate animate stimuli from inanimate stimuli are their appearance and motion profiles. Animate objects, such as virtual characters, look like and take a similar form to humans, whereas inanimate objects, such as moving abstract shapes do not. Similarly, animate stimuli tend to move with a biological movement profile so contain variability and are non-linear according to the 'minimum-jerk' model (Flash & Hogan, 1985) . Conversely,

inanimate objects move with a constant velocity profile (Hogan, 1984). How do these features of the stimuli (e.g. their appearance and movement profile) impact mimicry responses?

Motor resonance describes the extent to which our motor systems are activated by the observation of other's actions (Blakemore & Frith, 2005). The extent to which motor resonance is modulated by the particular agent performing the action (e.g. whether the stimuli is biological) has been measured using three main approaches. Firstly, neuroimaging and neurostimulation techniques studies measure the extent of motor system activation during action observation (Gazzola, Rizzolatti, Wicker, & Keysers, 2007; Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004). Secondly, motor interference studies (Kilner, Paulignan, & Blakemore, 2003; Kilner, Hamilton, & Blakemore, 2007) test the extent to which an action in one plane (e.g. the vertical plane) is perturbed by the concurrent observation of a movement in the orthogonal plane (e.g. the horizontal plane). Finally, studies of mimicry (and automatic imitation) measure the extent to which imitative responses are stronger in response to particular actions. Although former two approaches have investigated the impact of stimuli appearance and movement profile on motor resonance, the results from such studies are equivocal (Cracco et al., 2018). Moreover, it has recently been suggested that motor interference tasks may be driven purely by spatial rather than imitative processes (Hardwick & Edwards, 2012). Thus, the current discussion will focus on studies which have tested mimicry responses towards animate and inanimate stimuli.

Press, Bird, Flach, and Heyes (2005) found larger congruency effects for a human hand compared to a robot hand in a stimulus response compatibility paradigm. This greater automatic imitation for biological compared to non-biological stimuli (or 'animacy bias') was later replicated and was shown to be present in autistic adults (Bird et al., 2007). Press et al. argued that this increased congruency effects for human rather

than nonhuman or non-biological stimuli can be explained by greater experience with human agents during development. This was supported by the finding that sensorimotor experience with robot actions enhanced automatic imitation for robot actions (Press, Gillmeister, & Heyes, 2007). Similarly, Pan and Hamilton (2015) found a greater congruency effect was seen for a human-like virtual character compared to a moving ball in a drumming task. Cracco et al.'s (2018) meta-analysis concluded that for reaction time measures of automatic imitation, congruency effects increased as models become more human-like.

In terms of kinematic mimicry responses, when neurotypical children reached to grasp a sphere the recent observation of a human performing the same action primed the execution of that action as shown by shorter movement duration and time to peak velocity. This priming did not occur after having observed a robot perform the action. For the autistic children the opposite was true - visuomotor priming occurred for the robot but not the human (Pierno, Mari, Lusher, & Castiello, 2008). Sparks, Sidari, Lyons and Kritikos (2016) demonstrated that the animacy of a non-biological stimulus can simply be implied by the visual presence of a human and this is sufficient to induce mimicry responses. Participants viewed a dot moving towards a dowel target with either a direct or exaggerated trajectory. If the dot turned green participants were required to reach and grip a dowel. If there was a still image of a female model in a 'ready-to-reach' posture in the background, then this resulted in motor resonance. That is, participants moved approximately 2 mm higher after having observed the dot move with an exaggerated trajectory. This did not occur if the image of the human was scrambled. Thus, visual cues implying animacy may also influence mimicry responses. Beliefs about animacy have also been shown to influence mimicry responses. In Liepelt and Brass (2010) participants saw a hand wearing a leather glove but those participants who believed this hand belonged to a human showed a larger congruency effect than those

who believed it was a wooden hand. Although, not all studies have found that beliefs about the animacy of the stimulus affect mimicry responses (Press, Gillmeister, & Heyes, 2006). In sum, studies using both automatic imitation (e.g. Press et al., 2005) and kinematic paradigms (e.g. Pierno et al., 2008) have suggested that mimicry responses are enhanced for animate compared to inanimate stimuli.

Current aims

The current study aimed to explore whether a non-biological stimulus – a ball moving with non-biological motion - would continue to induce mimicry in the point-to-point imitation paradigm employed in the previous experiments. Participant observed a ball move with constant velocity between the targets with either a high or low trajectory. This was compared to a human-like virtual character who was animated as in previous studies. The study aimed to address two questions:

(1) Would the peak height of participants' movements between the targets be influenced by the height of a non-biological stimulus?

(2) If so, would the mimicry induced by a non-biological stimulus be comparable to that induced by a virtual character?

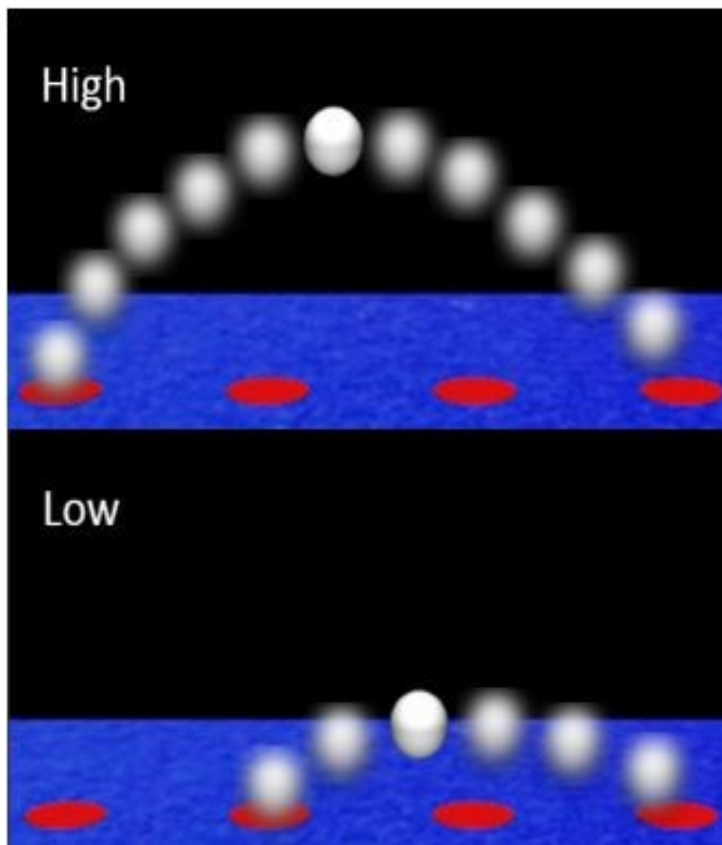


Figure 4-3 An example of the ball moving with a high and low movement trajectory

Instructions:

1. Place your index finger on the resting pad
2. Wait for a 'dong' sound
3. Watch Mike or a ball move to three targets
4. WAIT for the 'ding' sound
5. Move to the same targets that Mike or the ball moved to
6. Place your index finger back on the resting pad

Figure 4-4 Instructions given to the participants at the start of the task

4.3.2 Method

Participants

18 participants (4 male) with a mean (SD) age of 26 (7) years were recruited from the same participant database as in Experiment 1. All participants were right-handed, had normal or corrected-to-normal vision and reported no history of neurological disorder. All were financially reimbursed for their time and gave written informed consent before participating. All procedures were approved by the UCL Research Ethics Committee.

Procedure

Virtual Character

A male virtual character, called Mike, was animated using the same procedure as in Chapter 3. Participants were taking part in a two-part study. This experiment was the second part. They had previously interacted with Mike in a maze task in which we was programmed to be trustworthy. Participants rated Mike as more trustworthy and were more likely to follow his advice than a virtual character programmed to be untrustworthy (see Hale, Payne, Taylor, Paoletti & Hamilton, 2017; Experiment 1 for details). The position of the participant, the projector screen, the blue card with the participants' targets on it and the electromagnetic markers were also the same as in Experiment 1. Calibration was also completed as before.

The experiment started with Mike introducing himself to the participants and outlining the task instructions. Mike's voice was recorded by a male actor. A summary of the task instructions then appeared on the screen (Figure 4-4) and the experimenter ensured the participant understood the task instructions.

Ball

The ball's trajectories for the different movement combinations was generated using a custom-made script in Matlab (MathsWorks, Natick, USA). The ball moved with a constant tangential velocity (non-biological motion). As with the virtual character trials, every ball trial started with a 'dong' sound; after a variable delay (1200 – 1800 ms) the ball fell from a height of 25 cm above the table and landed on the first target. For the high trials the ball moved with a peak height of approximately 9 cm between the targets, for the low trials the ball moved with a peak height of approximately 3 cm between the targets (Figure 4-3). The ball then returned to its starting height of 25 cm above the final target. As with the virtual character trials, after a variable delay (1200–1800 ms) a 'ding' sound occurred which acted as the participants' cue to point to the same targets the ball landed on.

There were 128 trials in total – 64 (32 high, 32 low trials) for both the ball and the virtual character. The first trial was always a ball trial which was followed by a virtual character trial. The trial type then alternated between the ball and virtual character on each trial. Gowen and Poliakoff (Emma Gowen & Poliakoff, 2012) highlighted how in studies where biological and non-biological stimuli are mixed within the same block, motor resonance for the non-biological stimuli is more likely to be absent (e.g. Kilner et al., 2003). In contrast, a blocked design in which the biological and non-biological stimuli are presented in separate blocks, priming is more likely to be significant for non-biological stimuli (e.g. Brass et al., 2000). Gowen and Poliakoff argued that in mixed designs attention is drawn to the differences between the various types of stimuli resulting in a modulation of priming. Thus, in the current study a mixed design was used to highlight the differences between the stimuli and maximise the chances of finding mimicry differences between the virtual character and ball (Brass, Derrfuss, Matthes-von Cramon, & von Cramon, 2003).

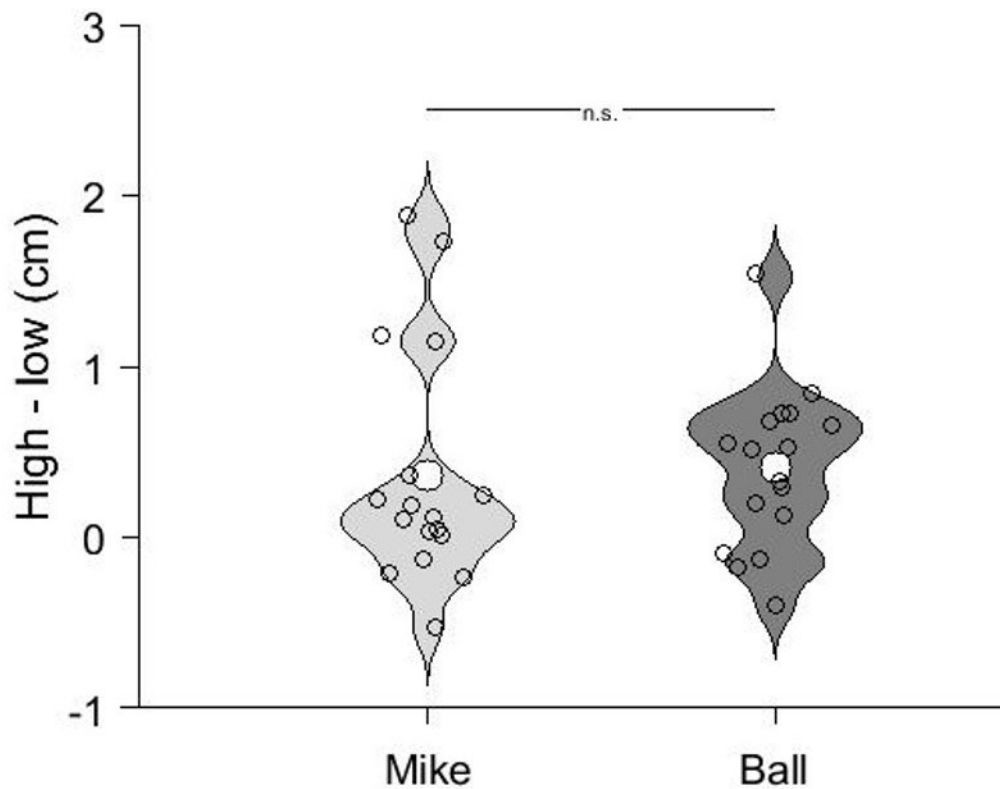
4.3.3 Results

Excluded data

On 3.9% (SD: 3.8%) of trials participants pointed to the wrong combination of targets. There were no significant differences in errors between the ball trials (Mean: 3.7%, SD: 3.9%) and virtual character trials (Mean: 4.1%, SD: 4.4%) as demonstrated by a paired samples t-test, $t_{17} = 0.437$, $p = 0.668$, $d = 0.103$. These error trials were excluded before the main analysis.

Movement data were analysed using Matlab R2013b (MathsWorks, Natick, USA) and filtered with a Butterworth filter to remove high frequencies. Each participant's calibration data were used to chunk each trial into four movements: (1) the movement to the first target from the resting pad, (2) the movement to the second target; (3) the movement to the third target, (4) the movement back to the resting position. When a trial could not be chunked into four movements, it was removed from the analysis. This was then combined with the error trials to give a total percentage of excluded trials for each participant.

When combined with the error trials, 52.6% of the trials were excluded for one participant. Given the high percentage of excluded trials, they were removed from the final analysis (although their inclusion did not change the results). After the removal of this participant, the mean percentage of total excluded trials was 10.4% (SD: 10.1%). Again, there were no significant differences between the total trials excluded for the ball trials (Mean: 10.4%, SD: 9.1%) compared to the virtual character trials (Mean: 10.5%, SD: 11.7%), $t_{16} = -0.067$, $p = 0.947$, $d = -0.016$.



Mean (SD)	High	Low
Ball	5.13 (1.88)	4.73 (1.68)
Avatar	4.82 (1.66)	4.45 (1.45)

Figure 4-5 Mimicry (high – low) for Mike and the Ball condition

Peak height analysis

The mean peak height of the movements between the targets (movements two and three) for each trial were subject to a repeated measures ANOVA with condition (ball/virtual character) and height (high/low) as factors. This revealed a main effect of height ($F_{1,16} = 9.08, p = 0.008, \eta_p^2 = 0.362$), with the peak height of movements between the targets greater in the high (mean: 4.97 cm, SD: 1.77) compared to low (mean: 4.59, SD: 1.55) condition. Post-hoc paired samples t-tests revealed this was the case for both the ball ($t_{16} = 3.56, p = 0.003, d = 0.863$) and the virtual character ($t_{16} = 2.16, p = 0.047, d = 0.523$) (Figure 4-5).

There was a main effect of condition ($F_{1,16} = 9.08$, $p = 0.008$, $\eta_p^2 = 0.362$) with the peak height of movements between the targets greater in the ball (mean: 4.93 cm, SD: 1.77 cm) compared to virtual character (mean: 4.63 cm, SD: 1.54 cm) condition. The interaction between height and condition was not significant ($F_{1,16} = 0.092$, $p = 0.765$, $\eta_p^2 = 0.006$). A Bayesian paired samples t-test using JASP software, version 0.8.0.0 (JASP Team, 2017), compared mimicry (the difference in peak height between the high and low condition) in the ball condition (mean: 0.404, SD: 0.471) to that in the virtual character condition (mean: 0.362, SD: 0.696). The Bayes Factor for this test ($BF_{10} = 0.259$) suggested moderate evidence in favour of the null hypothesis – no differences in mimicry between ball and virtual character condition.

4.3.4 Results summary and discussion

Experiment 2 aimed to explore whether the peak height of participants' movements would be influenced by the height of a non-biological stimulus, and, if so, whether this effect was comparable to that induced by a virtual character. Participants watched which combination of three targets either a virtual character or ball moved to and where then required to point to the same targets in the same order on the table in front of them. The virtual character and ball moved between the targets with either a high or low trajectory. The virtual character moved with biological motion; the ball moved with non-biological motion (i.e. constant velocity). As in previous studies, participants' movements between the targets were influenced by the height of the observed movement trajectory - the peak height of participants' movements were higher after having observed the stimulus move between the targets with a high, compared to a low, trajectory. This mimicry effect occurred in the virtual character (3.8 mm) and the ball condition (4.0 mm) and there were no significant differences between the two conditions. The results suggest that both biological and non-biological stimuli can induce mimicry in this point-to-point imitation task.

Experiment 2 is the first to demonstrate mimicry in response to non-biological stimuli in the point-to-point imitation task. This work replicates previous behavioural (Kilner, Hamilton, & Blakemore, 2007) and neuroimaging (Gazzola et al., 2007) findings which showed that our motor systems are activated by non-biological stimuli. No differences were found in mimicry induced by the virtual character compared to the ball. This was despite the ball moving with non-biological motion and a mixed, rather than blocked, design being used to try to highlight the differences between the two stimuli (Gowen & Poliakoff, 2012). This finding is in contrast to a host of other studies which found differences in motor resonance towards biological and non-biological stimuli in various behavioural paradigms (Bisio et al., 2014; Kilner et al., 2003; Pan & Hamilton, 2015; Pierno, Mari, Lusher, & Castiello, 2008). The General Discussion explores the potential reasons why no differences were found in mimicry for the two types of stimuli, in both Experiment 1 and Experiment 2.

4.4 General Discussion

The STORM model predicts that all mimicry is subject to top-down social modulation as important social cues determine what and when we mimic (Yin Wang & Hamilton, 2012). In Chapter 3, the social engagement of the virtual character did not change the extent to which participants mimicked her. In this chapter, I explored the reasons which may have accounted for this lack of social modulation, as many previous studies using a range of mimicry paradigms have found that social cues modulate mimicry (Wang & Hamilton, 2012). Experiment 1 showed that increasing the physical realism of the model and attempts to increase participants' attention to model's social engagement did not result in differences in mimicry between the engaged and disengaged conditions. Experiment 2 did not find any differences in mimicry when participants interacted with a moving ball compared to a virtual character. This suggests that animacy, at least in the sequential pointing task employed in this thesis, does not

modulate mimicry. This finding is at odds with reaction times measures of mimicry which have found increased mimicry responses to more animate models (Liepelt & Brass, 2010; Pan & Hamilton, 2015; Press et al., 2005). In the following section I try to account for these differences by highlighting differences in attention, anatomical matching and animacy between these previous studies and the task used here.

4.4.1 Attention

Gowen, Bradshaw, Galpin, Lawrence, & Poliakoff (2010) highlighted the importance of attention in bringing about motor resonance: “One possibility is that attentional resources are required to differentiate biological and non-biological stimuli; when attention is diffuse, too little attention is allocated to the stimulus and when attention is focussed on particular aspects of the movement, there are insufficient resources to differentiate the stimuli” (Gowen et al., 2010; p. 295). In the current paradigm, attention may have been too diffuse as participants were focusing on the combination of targets the ball or models moved to rather than the differences between the stimuli. Sparks et al. (2016) found a modulation of participant’s peak height if a biological stimulus was present, but not if she was absent. However, in their study the action was a simple, overlearned reach-to-grasp movement so attentional resources could be allocated towards the biological stimuli during action observation and execution. Similarly, in Pan and Hamilton (2015), participants were not explicitly told to watch the sequence of drums the virtual character or ball moved. Instead, participants were required to move to the sequence of drums displayed on the virtual tablet in front of them after the model had finished moving. The lack of attentional resources directed to the specific movements of the stimulus could have highlighted the differences between the two stimuli such that there were larger congruency effects for the virtual character compared to the ball.

The point-to-point imitation task used here is different to reaction time, motor interference and reach-to-grasp measures of motor resonance in several other ways. These differences may have further contributed to attentional differences in the current paradigm. Firstly, in stimulus response computability tasks there is a short (<1000 ms) delay between action observation and execution and in motor interference tasks (and in many reach-to-grasp paradigms) action observation and execution occur concurrently. In the point-to-point imitation task, however, the observed movement lasts approximately 5 seconds which is followed a variable delay (e.g. 1200 – 1800 ms) before the participant responds. Thus, the link between the source of the observed action and execution of the action is arguably less salient. Secondly, the point-to-point imitation task places relatively greater demands on working memory as participants must remember the combination of targets the agent moved to. Some work suggests that imitative responses are enhanced under higher working memory demands (van Leeuwen et al., 2009), or when working memory is impaired (Brass et al., 2003), as participants struggle to inhibit automatic responses. These heightened imitative responses under greater working memory demands could have concealed the subtle effects a non-biological agent may (or may not) have had on mimicry. Alternatively, increased working memory demands could draw attentional resources away from the differences between agents performing the action (Forbes et al., 2016; Gowen et al., 2010). Similarly, the action in the sequential pointing task is transitive, which may have resulted in greater goal-processing (Wild et al., 2010) and could have reduced attention towards the agent performing the action.

4.4.2 Anatomical vs. spatial matching

In Pan and Hamilton's (2015) drumming task, when there was a spatial mapping between the drums of the virtual character and those of the participant (Experiment 1), a greater congruency effect was seen for the virtual character compared to the ball but

only when participant's social evaluation of the virtual character was included in the analysis as a covariate. In the anatomical condition (Experiment 2) a greater congruency effect was seen for the virtual character compared to the ball even without controlling for participants' social evaluation of the virtual character. This suggests that when participants have to make the same anatomical movement as a biological agent this may enhance their motor resonance compared to that induced by a non-biological stimulus. In the current study, participants were asked to point to the same targets the virtual character pointed to but there was a spatial correspondence between the virtual character's targets and those of the participant. For example, if the virtual character pointed to the target on his far right, the participants were required to point to the target on their far left. This may be one factor which contributed to the lack of difference between the virtual character and the ball in the current study. Work presented in Chapter 5 suggests that participants have a tendency to make the same gross anatomical movements as a virtual character. Thus, it would be of interest to explore whether we see differences in the current paradigm when there is an anatomical matching between the model's targets and those of the participants.

4.4.3 Animacy

Several studies demonstrate that non-biological stimuli can induced motor resonance if participants believe the stimulus is based on human movements (Kilner et al., 2007; Liepelt & Brass, 2010b; Stanley, Gowen, & Miall, 2007). One further possibility therefore is that participants believed the ball was generated from or based on human movements. In Pan and Hamilton (2015) there were three separate balls above each of the three drums. These fell onto the drums to indicate the sequence. In the current study there was only one ball which moved between the targets. So, although the ball moved with non-biological motion, the ball moving between the targets, rather than just falling and landing on one target, may have increased the ball's sense of

animacy. However, it is worth highlighting that the participants in the current study had already interacted with Mike in a previous task in which they interviewed him and asked him for directions through a maze (Hale et al., 2018). Thus, although animacy ratings were not recorded, it seems unlikely participants would have deemed ball to be as animate as Mike.

The findings from Experiment 2 are at odds with findings from automatic imitation paradigms which show that as the similarity between the model and participant increases, congruency effects become larger (Cracco et al., 2018; Press, Bird, Flach, & Heyes, 2005b; Press et al., 2006, 2007). Thus, animacy beliefs may only impact mimicry responses in reaction time paradigms. Other mimicry measures, such as the mimicry of movement trajectory, may be more immune to animacy manipulations (Cracco et al., 2018). This is supported by the finding that different measures of mimicry may not be related to one another (Genschow et al., 2017).

4.4.4 Conclusion

To conclude, Experiment 1 tried to modulate mimicry by increasing the physical realism of the model and by attempting to increase participants' attention to her level of social engagement. Although, participants mimicked the model, mimicry responses were the same in the socially engaged and disengaged conditions. In Experiment 2, I tested participants' mimicry responses to a moving ball and a virtual character. Again, there were no differences in participants' mimicry towards the ball and the virtual character. The two experiments presented in this chapter combined with the experiment presented in Chapter 3 suggest that mimicry is not socially modulated in our sequential pointing paradigm. This is at odds with a range of studies using reaction time measures of mimicry. This raises the possibility that different mimicry measures may be tapping different processes with some certain mimicry responses more or less susceptible to

social modulation. In Chapter 5, I move away from trying to socially modulate mimicry and examine whether the rationality of the model's actions can influence mimicry.

Chapter 5 - Mimicry Responses Towards Irrational

Movement Trajectories

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Forbes, P. A., & Hamilton, A. F. D. C. (2017). Moving higher and higher: imitators' movements are sensitive to observed trajectories regardless of action rationality. *Experimental brain research*, 235(9), 2741-2753.

5.1 Abstract

Humans sometimes perform actions which, at least superficially, appear suboptimal to the goal they are trying to achieve. Despite being able to identify these irrational actions from an early age, humans display a curious tendency to copy them. The current study employed the same sequential pointing task as in previous chapters but manipulated the rationality of the observed action in two ways. Participants observed videos of a model point to a series of targets with either a low, high or 'superhigh' trajectory either in the presence or absence of obstacles between her targets. The participants' task was to watch which targets the model pointed to and then point to the same targets on the table in front of them. There were no obstacles between the participants' targets. Firstly, the peak height of participants' movements between their targets was sensitive to the height of the model's movements, even in the 'superhigh' condition where the model's action was rated as irrational. Secondly, participants showed obstacle priming – the peak height of participants' movements was higher after having observed the model move over obstacles to reach her targets, compared to when there were no obstacles between her targets. This suggests participants code the environment of co-actors into their own motor programs, even when this compromises the efficiency of their own movements.

5.2 Introduction

The preceding chapters tried to socially modulate mimicry responses within a sequential pointing imitation paradigm. These studies found that social cues, such as the model's social engagement (Chapter 3 and 4) and animacy (Chapter 4), did not modulate mimicry. In this chapter, I change tracks slightly and explore whether the rationality of the observed action influences mimicry responses.

Imagine you are at a wedding and the bride proposes a toast. You observe as she reaches over a coffee cup to pick up her glass. You then prepare to reach for your own glass. There is no cup obstructing your path to it. If human imitation is rational, your reach trajectory should not be perturbed by the recent observation of the bride's obstacle avoidance (Gergely & Csibra, 2003). Why move with higher trajectory when there is no need to? Yet, increasing evidence suggests that when moving within a social context, humans often perform actions which, at least superficially, appear suboptimal to the goal they are trying to achieve.

The ability to identify these seemingly irrational actions may be present early in development (Gergely & Csibra, 2003) and the observation of irrational, compared to rational, actions results in distinct patterns of neural activity (Brass, Schmitt, Spengler, & Gergely, 2007; Marsh, Mullett, Ropar, & Hamilton, 2014). Despite this competency in identifying irrational actions, humans display a curious tendency to both implicitly and explicitly copy them (McGuigan, Makinson, & Whiten, 2011; Marsh, Pearson, Ropar, & Hamilton, 2013; Griffiths & Tipper, 2009; Hardwick & Edwards, 2011).

In this chapter, I recorded participants' movements during the sequential pointing task and manipulated the rationality of the observed action in two ways (Wild, Poliakoff, Jerrison, & Gowen, 2012; Forbes, Pan, & Hamilton, 2016). Firstly, I aimed to establish whether participants' own movements would be sensitive to height of a

model's trajectory even when this was exaggeratedly high and rated as irrational.

Secondly, I aimed to establish whether participants code the environment of the model into their own motor programs, even when this compromises the efficiency of their own movements.

5.2.1 Rationality and overimitation

The ability to identify and reason about the rationality of a goal-directed action may be present from approximately 12 months of age (Gergely & Csibra, 2003; Kamewari, Kato, Kanda, Ishiguro, & Hiraki, 2005; Scott & Baillargeon, 2013; Sodian, Schoeppner, & Metz, 2004). In addition to this early competency in distinguishing rational from irrational actions, adult neuroimaging studies have revealed that the brain's mentalising system, specifically the temporoparietal junction, medial prefrontal cortex (Marsh & Hamilton, 2011) and superior temporal sulcus (Brass, Schmitt, Spengler, & Gergely, 2007), distinguish rational from irrational actions. Medial prefrontal cortex may be particularly attuned to unusual or irrational actions. Desmet and Brass (2015) showed that the observation of unusual *intentional* actions (e.g. an agent deliberately closes a box with her arm rather than her hand) was related to activation in the anterior medial prefrontal cortex, whilst the observation of unusual *accidental* actions (e.g. an agent bumps her arm against a box and closes it) was associated with activation in dorsal and posterior parts of medial prefrontal cortex (Desmet & Brass, 2015).

Given our early competency in identifying irrational actions and the brain's sensitivity to these types of actions, human's tendency to overimitate, that is, copy seemingly arbitrary and unnecessary features of an action, seems somewhat peculiar (McGuigan, Makinson, & Whiten, 2011). During a typical overimitation task, participants observe a model perform a causally irrelevant action, such as tapping on top

of a box, and subsequently copy this action when given the object. This is despite participants rating the action as “silly,” so not required to complete the end-goal of the action, such as retrieving a toy from the box (Marsh et al., 2013). Overimitation may be present from around approximately 18 months (Nielsen, 2006), shortly after infants show sensitivity to irrational actions (Gergely & Csibra, 2003). The tendency to overimitate then increases with age during childhood and persists into adulthood (McGuigan et al., 2011; Whiten et al., 2016). Whiten, McGuigan, Marshall-Pescini and Hopper (2009) have tried to explain overimitation in terms of a “copy all, refine later” strategy. Whilst in some circumstances (e.g. during overimitation tasks) this may result in the imitator performing inefficient actions, in general such a strategy may be adaptive as objects and tasks are often “casually opaque” (Lyons, Young, & Keil, 2007). For example, it is often not immediately clear how a novel object functions or what the particular requirements of a task are.

Overimitation tasks usually involve participants explicitly copying an unnecessary action performed on an object. However, studies of mimicry and imitation have shown that participants’ own movements are also sensitive to unnecessary and task irrelevant aspects of observed movement trajectories (Griffiths & Tipper, 2009; Hardwick & Edwards, 2011; Wild et al., 2010) For example, Hardwick and Edwards (2011) asked participants to perform reaching and grasping actions to an object after having observed, or whilst observing, an experimenter reaching with a normal, or an exaggeratedly high, trajectory. Despite being instructed to perform normal reaching movements throughout the experiment, participants’ maximum wrist height was approximately 3 mm higher after having observed, or whilst observing, the experimenter reach with an exaggeratedly high trajectory. Hardwick and Edwards concluded that even exaggerated movement kinematics have a small but significant effect on the observers’ own movements.

5.2.2 'Irrational' movements: learning and communicating

So what could be behind this tendency to copy and be influenced by irrational movements? Gergely & Csibra (2006) argued that during development ostensive pedagogical cues are vital in triggering and facilitating imitative learning (Gergely & Csibra, 2006). Infants adopt a 'pedagogical stance' whereby they attend to and are influenced by exaggerated (and seemingly irrational) movements. Brand, Baldwin, and Ashburn (2002) showed that caregivers display "motionese" - they enhance or exaggerate features within an action sequence to facilitate the infant's processing of that action. For example, a slow or curved trajectory towards a target can make the goal or intention of an action more salient. Nagai and Rohling (2007) argued that "motionese" can help infants to determine what to imitate. By using a saliency based attention model, which was sensitive to the color, intensity, orientation, flicker, and motion of the visual scene, they found that motionese could also be utilised by robots when determining what to imitate - even in the absence of existing knowledge about task-related actions or the action goals.

Whilst exaggerated movement trajectories are important for imitation and learning during development, more generally they be important for "joint action optimization" (Pezzulo, Donnarumma, & Dindo, 2013). Pezzulo et al. proposed that during joint actions co-actors move in such a way as to optimise the success of the interaction (e.g. moving a sofa) rather than their own movements within that interaction (e.g. moving their half of the sofa). This could mean changing one's own movements - and incurring a cost - to benefit the joint action. For example, an exaggerated trajectory requires more effort and potentially a more awkward position but if it signals to a co-actor which direction one is moving the sofa then this optimises the success of the joint goal. This theory was supported by Vesper, Schmitz, Safra, Sebanz, and Knoblich (2016) who showed that when pairs of participants were required to arrive at a target at

the same time, they exaggerated the curvature of their movements to communicate their arrival time.

Given the importance of exaggerated movement trajectories for learning and their role in joint action optimisation, this chapter aimed to test whether participants would mimic exaggerated and irrational movement trajectories even when this compromised the efficiency of their own movements. Alternatively, a mechanism could exist which evaluates the rationality of the observed movement trajectory so that participants own movements cease to be influenced by them. This could be similar to the mechanisms by which other ‘top down’ factors modulate imitative behaviours, such as the presence of goals (Wild et al., 2010) and the range of social cues outlined by STORM (Yin Wang & Hamilton, 2012). In the brain this ‘top-down’ control of imitative behaviours by social cues, such as eye contact, has been shown to be modulated by medial prefrontal cortex (Wang, Ramsey, & Hamilton, 2011). Given that medial prefrontal cortex responds to action rationality (Desmet & Brass, 2015; Marsh & Hamilton, 2011), it is plausible that a similar mechanism may also modulate the imitation of irrational movement trajectories.

5.2.3. Coding the environment of others into our own

When we move within a social context, we often encode our own environments in terms of other peoples’ points of view. For example, Frischen, Loach and Tipper (2009) asked participants to reach to a target in the presence of a distracter. In such tasks participants display negative priming - after having moved to the target, responses to the distracter (i.e. the previously ignored stimulus) are slowed (Tipper, 1985). This is due to participants initially inhibiting responses to the distracter. Frischen et al. (2009) found that when participants performed the task by themselves they displayed an egocentric frame of reference - negative priming was strongest for distracters closest to

their hand compared to those further from it. In contrast, when participants took turns to complete this task with another person, participants displayed an allocentric frame of reference – negative priming was strongest for distracters that were salient for the other person rather than themselves. They concluded that “observers are essentially processing their environment in the same way that the *other person* is encoding it as *they* are interacting with their surrounding” (Frischen et al., 2009; p. 218).

The finding that we may code the environments of others in our own action space was supported by Griffiths and Tipper (2009) who asked participants to reach for and lift up a target block in the presence or absence of an obstacle. On trials where there was no obstacle, but in the previous trial they had moved over an obstacle, participants’ reach trajectory was higher compared to trials where the previous trial contained no obstacle. When participants took turns to complete the task with another participant, they found that the obstacle avoidance of one participant influenced the reach trajectory of the other but only if the observed obstacle was in the peripersonal action space of the participant. If the obstacle was outside “the comfortable reach space of the observer” this had no effect on reach trajectory. However, this view was later challenged by Griffiths & Tipper (2012) who found that the observed obstacle avoidance could take place outside of the peripersonal space of the participant and induce obstacle priming but this was dependent on participants sharing their workspace with their co-actor and having a sense of ‘shared ownership’ over it. In their ‘shared workspace’ condition there was just one set of objects which the experimenter moved between the two participants after each trial. In contrast, when the participants had separate workspaces, so one participant had a yellow obstacle and target and the other had a blue set, obstacle priming did not occur.

Further constraints on obstacle priming have been outlined by Roberts et al. (2016). Participants watched videos of an actor perform horizontal or curvilinear

sinusoidal movements either in the presence or absence of a cylindrical object.

Participants' task was to perform continuous horizontal arm movements. The object in the video acted as either an obstacle, so required the actor in the video to move with a particular trajectory to avoid it, or as a distracter, so was present in the video but was not in the path of the actor's trajectory. As previously shown (Roberts, Hayes, Uji, & Bennett, 2014), participants' movement deviation in the vertical plane was greater when observing curvilinear compared to horizontal movements. When observing horizontal movements, however, deviation increased in the presence of an obstacle. Conversely, movement deviation was not modulated by the presence of an obstacle or distracter in the curvilinear condition. Roberts et al. (2016) proposed that the observed environmental context, such as the presence of an obstacle, only influences participants' own movements when the observed and executed actions are congruent (i.e. both actor and participant were performing horizontal movements).

The mechanism behind obstacle priming was recently explored by van der Wel and Fu (2015) who aimed to investigate whether obstacle priming was the result of entrainment or co-representation of the model's action (van der Wel & Fu, 2015). Entrainment refers to the unintentional, rhythmical synchronisation of two individuals' actions, for example, two people sat observing each other in rocking chairs tend rock together in synchrony (Knoblich, Sebanz, Nther Knoblich, & Sebanz, 2008; Richardson, Marsh, & Schmidt, 2005). Whereas, co-representation involves symbolically representing the goals and intentions of the co-actor (Sebanz, Knoblich, & Prinz, 2005). Van der Wel & Fu (2015) proposed that the mechanism may vary depending on the nature of the action.

They asked participants to move a dowel between two locations to the pace of a metronome. The metronome produced either a continuous sequence (a continuous looping of a tone every 850 ms) or a discrete sequence (two tones separated by 850 ms

with a pause following each set). This ensured participants produced either discrete or continuous movements with the dowel. Participants sat next to a confederate who moved his own dowel to a discrete or continuous sequence between his own two targets whilst the participant was performing the same movement. On some trials the confederate had an obstacle between his targets and on other trials there was no obstacle. The key manipulation was whether participants could see the action of the confederate. For discrete movements, obstacle priming - the difference between the participants' peak height when there was an obstacle between the confederate's targets compared to when there was no obstacle - was the same regardless of whether participants could see the actions of the confederate or not. For continuous movements, however, obstacle priming only occurred when participants could see the action of the confederate. Van der Wel & Fu (2015) argued that obstacle priming during continuous movements is due to entrainment and thus dependent on visual information; whilst during discrete movements, obstacle priming is driven by co-representation of the actor's task.

5.2.4 Current aims

Mimicry

The first aim of Experiment 1 was to test the limits of participants' mimicry responses to irrational movement trajectories. In the previous chapters we found that participants mimicked the height of a model's movement trajectories. This finding, that participants move slightly higher having observed a high compared to low movement trajectory, has also been replicated in the preceding chapters and by others (Forbes et al., 2016; Griffiths & Tipper, 2009; Hardwick & Edwards, 2011). In these studies, however, the manipulation of height was relatively subtle. For example, the difference between the high and low trajectory in Hardwick & Edwards (2011) was 7 cm, and 8

cm in Chapter 3. The current chapter aimed to establish whether participants' mimic the model's movement trajectory even when these were clearly exaggerated and rated as irrational. As before the height of the model's trajectory was manipulated so there was a low and high condition but I also included an additional "superhigh" condition. The peak height of the model's trajectory in the superhigh condition was 12 cm greater than that in the low condition. I aimed to test whether participants' own movements would continue to be sensitive to the trajectory in this superhigh condition. Experiment 2 was conducted to obtain rationality ratings of the movement trajectories to test whether the superhigh movements were deemed more irrational than the high and low movement trajectories.

Obstacle priming

Experiment 1 aimed to build on the obstacle priming literature in several ways. Firstly, in Roberts et al. (2016), participants were required to make a pre-specified, continuous, horizontal movement so the congruency between the observed and executed movement was determined by the experimental condition (i.e. whether they were observing horizontal or curvilinear movements). In the current study, participants observed videos of an actor pointing to a series of three targets out of a four possible targets. The actor in the video moved with a low, high or 'superhigh' (i.e. exaggeratedly high) trajectory either in the presence of absence of obstacles between her targets. The participants' task was to point to the same targets the actor pointed but there were no obstacles between the participants' targets. So, rather than being instructed to make a pre-specified movement, participants were given goal-orientated instructions (i.e. "point to the same targets she pointed to") and were free to point to these targets with a trajectory of their choosing. Here, much like during the toast at the wedding, the goal was pre-determined (i.e. pick up the glass / point to the targets), yet participants could decide for themselves how they achieved this goal. Thus, our aim was to establish

whether participants would be influenced by the observed obstacle even when the exact nature of the required movement was not explicitly pre-specified.

Our second aim concerned the location of model's obstacle. Griffiths & Tipper (2009, 2012) suggested that the observed obstacle needed to be within "the comfortable reach space of the observer" (i.e. their peripersonal action space) to have an effect on their movements (Griffiths & Tipper, 2009), or, participants must feel they are sharing their workspace with their co-actor (Griffiths & Tipper, 2012). In our task, participants sat 70 cm from a screen which displayed videos of an actor moving over obstacles to point to a series of targets. This ensured the obstacles were outside of the participant's peripersonal action space. Moreover, there was a clear divide between the workspace of the participant which was on the table in front of them and that of the actor whose workspace appeared on a screen in front of them. Whereas Griffiths and Tipper (2009, 2012) required participants to pick up a target block, we aimed to investigate obstacle priming within an imitative pointing paradigm (Forbes et al., 2016; Wild et al., 2010, 2012). We investigated whether obstacle priming would occur even when the obstacle was outside of the participants' peripersonal action space, and, when participants did not share a workspace with their co-actor. Finally, to ensure that any effects were not simply due to the visual saliency of the observed obstacle on the screen in front of the participants, we included a condition where the actor's obstacle was half the size.

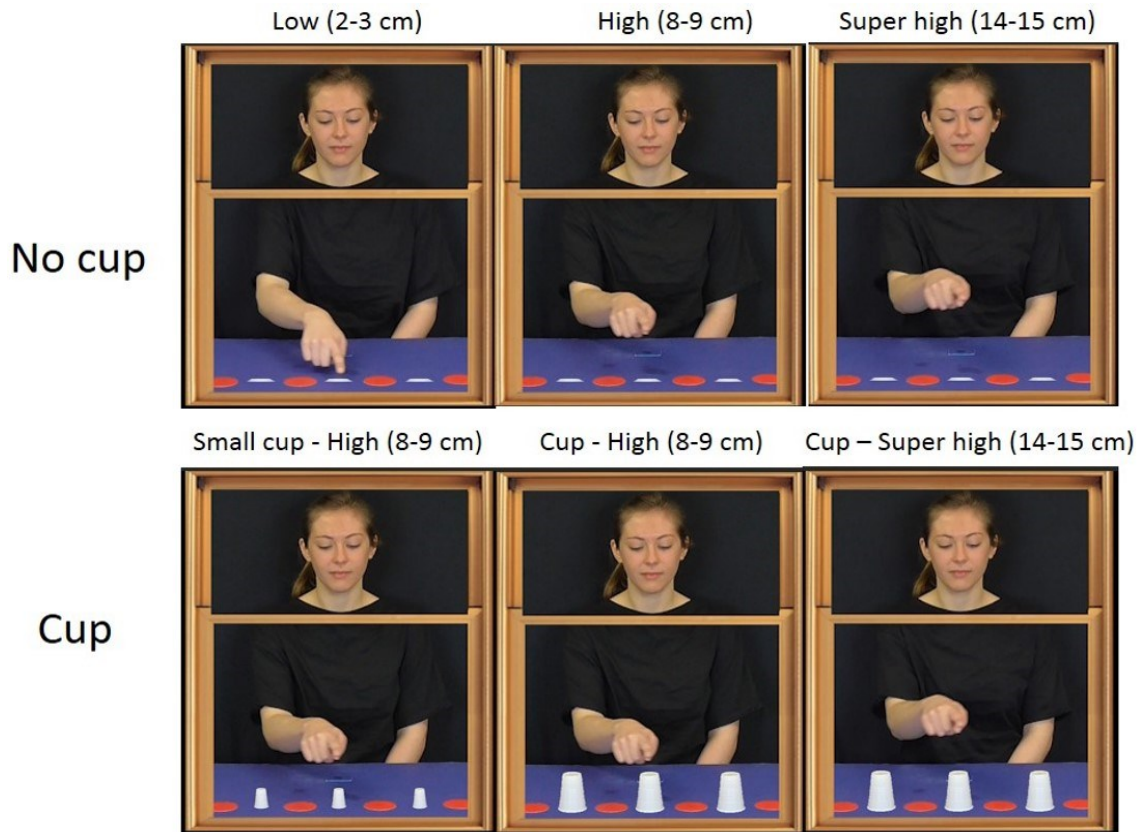


Figure 5-1 The six conditions; peak height for each condition is shown in parentheses

5.3 Experiment 1

5.3.1 Method

Participants

Participants (N = 27, 3 male) were obtained from the UCL Institute of Cognitive Neuroscience participant database and had a mean (\pm SD) age of 22.0 (\pm 2.9) years. All participants were right-handed, had normal or corrected-to-normal vision and reported no history of neurological disorder. All were financially reimbursed for their time and gave written informed consent before participating. All procedures were approved by the UCL Research Ethics Committee.



Figure 5-2 The experimental setup

Stimuli

Videos consisted of a female actor positioned behind a window frame, which appeared 48 cm x 40 cm on the projector screen. There was a horizontal bar across the centre of the window frame so the screen could be split in two (see Figure 5-1). The top half of every video was the same for all trials and started with the actor looking up and smiling before looking down at her hand. At this point in the bottom half of the video the actor moved from her resting position and pointed to three out of a possible four targets on the table in front of her in sequence. She then returned to the resting pad. Each target was a red circle, which appeared 4 cm in diameter, and the centre of the targets appeared 10.5 cm away from each other on the projector screen. There were 8 different movement combinations.

There were six different conditions (see Figure 5-1): 3 height conditions (low, high, superhigh) and 3 cup conditions (small cup, cup, superhigh cup). In the height conditions the actor moved above the table with a peak height of approximately 2-3 cm between the targets for low condition, 8-9 cm for the high condition and 14-15 cm for the superhigh condition. The initial movement to the first target and the fourth (final)

movement back to the resting pad were also manipulated to be either low, high or superhigh.

Between the targets in the height conditions there was a flat, white marker (4 cm diameter). There were three cup conditions. These used the same videos as for the high and superhigh videos except a cup (4 cm x 5.50 cm) was superimposed between the targets for the cup-high condition and cup-superhigh condition. The high-small cup condition used the high condition videos but the cup superimposed between the targets was half the size of the cups used in the other cup conditions. Videos were edited using Adobe Premier Pro CC 2015 (Adobe Systems, San Jose, CA, USA) and presented using Vizard (WorldViz Inc, Santa Barbara, USA).

Procedure

Participants sat approximately 70 cm from the projector screen (Figure 5-2). An electromagnetic marker (Polhemus LIBERTY system, Colchester, USA) was attached to participants' right index finger which enabled finger movements to be recorded. On the table in front of the participants, there was a piece of 81 cm x 66 cm blue card with four 6 cm diameter red circles stuck in the middle of it. The centre of the circles were 15 cm apart from each other and were 30 cm in front of the participants. These red circles acted as the targets. There was also a 6 cm x 4cm piece of blue card stuck 10 cm in front of the participant which acted as the 'resting pad' where participants were required to place their right index finger when not moving. There were no cups in front of the participants (Figure 5-2).

Before the start of the experiment participants completed calibration: they placed their right index finger into the middle of each of the four targets and the resting pad so that the coordinates could be recorded. After calibration participants were given 8 practice trials. All of the practice videos contained no cups. Participants were instructed

to rest their finger on the resting pad in front of them. They were told to watch the actor in the video and see which three targets she points to, then, when she returned to her resting position, they should point to the same targets she pointed to in the same order. The spatial correspondence between the targets in the video and the targets in front of the participants was explained. For example, participants were told that if the actor in the video pointed to the target on *her* far left then participants should point to the target on *their* far right so that there was a spatial match between their targets. After practice participants completed 3 identical blocks with 48 trials in each block (6 conditions x 8 different target combinations). Videos were presented in a randomised order.

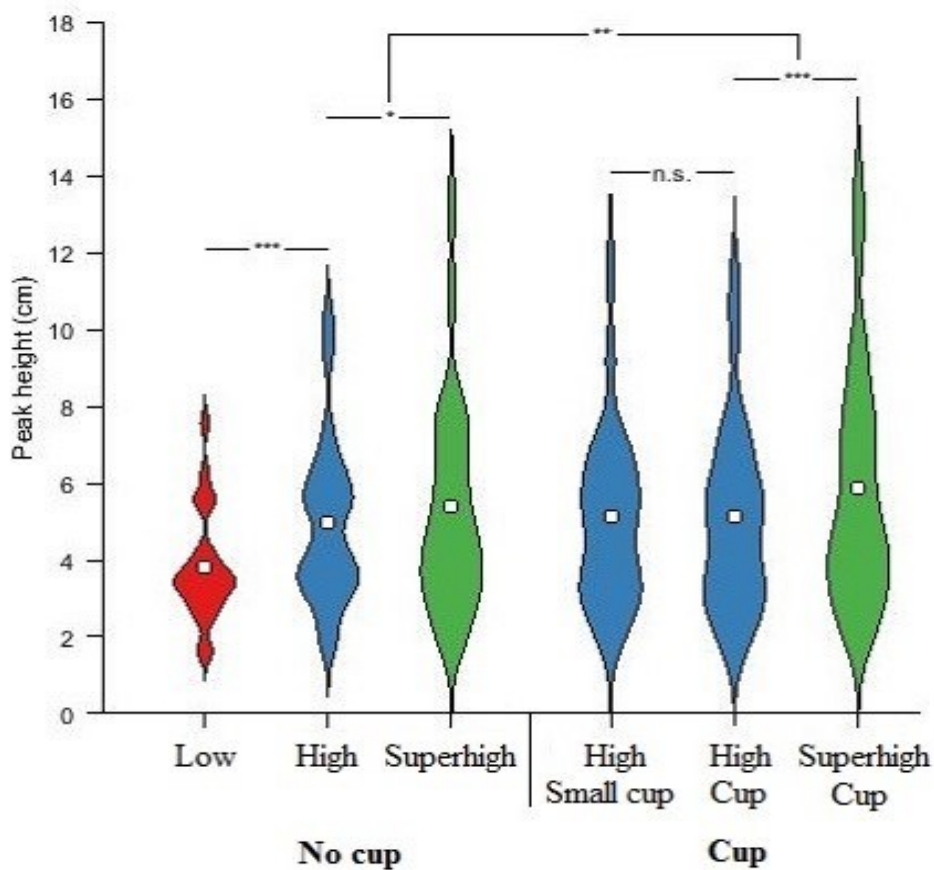


Figure 5-3 Mean peak height between the targets

Table 5-1 Mean and SD for each of the six conditions

Peak height (cm)	No cup low	No cup high	No cup superhigh	Small cup high	Cup high	Cup superhigh
Mean	3.82	4.96	5.40	5.14	5.12	5.89
SD	1.42	2.10	2.80	2.30	2.40	3.09

5.3.2 Results

Excluded data

The movement data were analysed using Matlab R2013b (MathsWorks, Natick, USA) and filtered with a Butterworth filter to remove high frequencies. For each trial each participant's data was chunked into four movements using their calibration file: (1) the movement to the first target from the resting pad, (2) the movement to the second target; (3) the movement to the third target, (4) the movement back to the resting pad. Three participants were excluded from the final analysis as over 10 % of their trials could not be chunked correctly (error rates: 25.5 %, 17.7 % and 14.6 %). The error rates for the other participants were all below 10% (mean = 1.8%, SD = 2.2%).

Peak height analysis

Mean peak height of the movements between the targets (mean of movements 2 and 3) for each condition for each participant were subject to repeated measures ANOVAs. Means for each condition are shown in Table 5-1.

Height

A one-way, repeated measures ANOVA was conducted with height (low, high, superhigh) as a factor. Epsilon (ϵ) = 0.597 as calculated to Greenhouse and Geisser (1959) was used to correct the one-way ANOVA. This revealed a main effect of height ($F_{1,194, 27.457} = 12.09, p = 0.001, \eta_p^2 = 0.344$; Figure 5-3). Post-hoc paired samples t-tests revealed the peak height of participants' movements were significantly higher in the

high condition [mean (SD): 4.96cm (2.10)] compared to low condition [mean (SD): 3.82 cm (1.42)], ($t_{23} = 3.824, p < 0.001, d = 0.781$), and significantly higher in the superhigh condition [mean (SD): 5.40cm (2.80)] compared to the high condition, ($t_{23} = 2.080, p = 0.049, d = 0.425$).

Cup

A 2 x 2 repeated measured ANOVA was conducted with height (high / superhigh) and cup (cup / no cup) as factors. This revealed a main effect of cup ($F_{1, 23} = 9.325, p = 0.006, \eta_p^2 = 0.288$) with participants displaying a greater peak height in the cup conditions [mean (SD): 5.50 cm (2.73)] compared to the no cup conditions [5.18 cm (2.42)], and, also a main effect of height ($F_{1, 23} = 13.189, p = 0.001, \eta_p^2 = 0.364$) with participants displaying a greater peak height for the superhigh compared to high conditions. There was no significant interaction between cup and height ($F_{1, 23} = 2.543, p = 0.124, \eta_p^2 = 0.100$). Finally, there were no significant differences between the high cup and high small cup condition as shown by paired samples t-test ($t_{23} = 0.350, p = 0.730, d = 0.071$)

5.4 Experiment 2

Experiment 2 was conducted to obtain rationality ratings of the movements in the low, high and superhigh conditions.

5.4.1 Method

Participants

One hundred participants (30 female, 3 left-handed) with a mean age of 27 years (range: 18-54) were recruited via the Prolific Academic website (<http://prolific.ac>). The study took approximately 5 minutes to complete and participants received £0.50 in

exchange for their participation. Ethical approval was granted by the UCL Research Ethics Committee and informed consent was obtained from all participants.

Stimuli and procedure

An example video for each of the three height conditions (low, high, superhigh) was shown to the participants. The same movement combination was used for all three height conditions. Participants were shown each video three times and asked to rate the rationality of the action in the video, using a battery of three statements (adapted from Marsh, Mullett, Ropar, & Hamilton, 2014). The statements were: (1) 'This action seems unnatural', (2) 'The action seems efficient' and (3) 'I would complete this action differently.' Participants were asked to watch the action and then indicate how much they agreed or disagreed with each statement on a 5 point scale. This created a total of 9 trials. The scores on these statements were summed, with the scores on statement 2 reversed scored, to produce an aggregated irrationality rating (with a maximum score of 15) for each of the three height conditions. The experiment can be seen here:

testable.org/t/81590f313

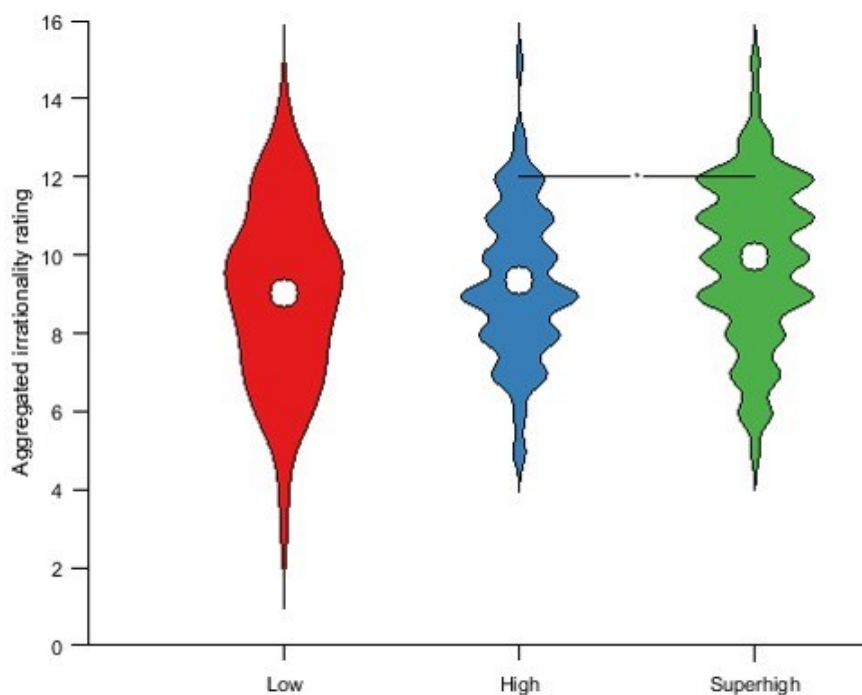


Figure 5-4 Mean aggregated irrationality ratings for the movements in the three conditions

5.4.2 Results

Excluded data

If a participant's response time was less than 5 seconds for at least one of the nine trials, then they responded before the end of the action in the video and their data were excluded from the analysis ($n=19$). Similarly if participants' response times were greater than 60 seconds for at least one of the nine trials, they were excluded from the analysis as it is likely they became distracted during the trial ($n=3$). One participant shown response times both shorter than 5 seconds and greater than 60 seconds, so the final sample consisted of 79 participants (25 female, 2 left-handed) with a mean age of 28 years (range: 18-54).

Irrationality rating

The aggregated irrationality ratings were subject to a one-way repeated measures ANOVA with height (low, high, superhigh) as a factor. Epsilon (ϵ) = 0.882 as calculated to Greenhouse and Geisser (1959) was used to correct the ANOVA. This revealed a main effect of height ($F_{1.76, 137.55} = 4.389, p = 0.018, \eta_p^2 = 0.053$; Figure 5). Post-hoc paired samples t-tests revealed the irrationality ratings were significantly greater ($t_{78} = 2.347, p = 0.021, d = 0.264$) for videos showing the superhigh movements [mean (SD): 9.95 (2.06)] compared to those showing high movements [mean (SD): 9.34 (1.91)]. There was no significant difference between the irrationality ratings for the high [mean (SD): 9.34 (1.91)] and low [mean (SD): 9.04 (2.27)] movement videos ($t_{78} = 0.970, p = 0.335, d = 0.109$).

5.5 Discussion

The current study used an established sequential pointing task to determine whether the rationality of an observed movement trajectory influenced the extent to

which participants mimicked it. Firstly, we found that participants' pointing movements between a series of targets were sensitive to the height of an actor's movement trajectory (Experiment 1), even when the observed movement trajectory was rated as irrational (Experiment 2). Secondly, I examined participants' movements after having observed an actor move over obstacles to reach her targets. Participants moved with an even higher trajectory between their own targets after having observed these videos, compared to videos in which there were no obstacles between the actor's targets. This was despite there being no obstacle between the participants' own targets throughout the experiment. This suggests participants' movements are not only influenced by the observed movement but also the environment within which the observed movement took place.

5.5.1 Moving higher and higher

I replicated the findings from previous chapters which show that participants mimicked the observed trajectories. That is, participants own movements were sensitive to the height of a recently observed movement trajectory (Forbes et al., 2016; Griffiths & Tipper, 2009; Hardwick & Edwards, 2011; Wild et al., 2010). The findings also extend this work in several important ways. In previous studies and in the previous chapters the difference between the high and low observed movement trajectories was relatively subtle (Forbes et al., 2016; Hardwick & Edwards, 2011). However, in the current chapter I showed that participants' movements continue to be sensitive to trajectories which are clearly exaggerated and rated as irrational. It is likely that the pedagogical (Gergely & Csibra, 2006) and communicative value (Pezzulo et al., 2013) of exaggerated movement trajectories could be driving participants' tendency to be influenced by them.

It is important to note that whilst the vast majority of participants moved higher in the high compared to low condition, fewer distinguished between the high and superhigh condition (although the difference in peak height reached statistical significance). Indeed, a minority of participants moved with a lower trajectory in the superhigh condition compared to the high condition. It remains to be seen what factors predict a breakdown of mimicry following the observation of exaggerated movement trajectories. The findings from Chapter 3 suggest that autistic people mimic the height of other people's movement trajectories to a lesser extent so it would be of interest to explore whether this is also the case in the superhigh condition. This would support theories which argue that imitative behaviours are more goal-directed in autism (Edwards, 2014; Hamilton, 2008).

Hardwick & Edwards (2011) required participants to make simple, overlearned reach-to-grasp movements towards an object. They proposed that participants' sensitivity to high movement trajectories during this task is in line with the goal directed theory of imitation (Bekkering, Wohlschläger, & Gattis, 2000). This theory states that imitators breakdown an observed movement into a hierarchy of goals, whereby goals of greater importance (e.g. pick up the cup) are imitated more readily than those deemed of lesser importance (e.g. pick up the cup by its handle). When the task is simple, such as during reach-to-grasp actions, observers have the cognitive resources to attend to and copy multiple goals within the goal hierarchy, for example, both the outcome and the kinematics of the observed movement. Conversely, if cognitive resources are limited, for example during early childhood or when the task is more demanding, imitators prioritise goals further up the goal hierarchy (Bekkering et al., 2000). Similarly, if a goal is made particularly salient then participants will imitate this goal more readily than goals further down the hierarchy (Wild et al., 2010).

The current task required participants to remember the sequence of the three targets the actor pointed and then point to their own targets in the same order. Our task was therefore more demanding than that of Hardwick & Edwards (2011). Despite this increased demand participants own movements were still sensitive to the peak height of the actor's movements. It is possible that the saliency of the movement trajectory resulted in participants' movements being sensitive to it, despite the increased cognitive load. Future studies could directly manipulate the saliency of the elevated trajectory and the task demands, for example, by having participants point to more targets, to directly test the goal-directed theory of imitation within this sequential pointing paradigm.

It is important to acknowledge a limitation of our study. Although participant rated the 'superhigh' action as slightly more irrational than the low or high actions (Figure 5-4), the low and high actions were still rated as somewhat irrational. This suggests that future work should record the real movements of actors who are blind to the experimental condition (e.g. Patel, Fleming, Kilner, 2012), rather than recording pantomimed actions as was done in the present study. For example, whereas we recorded videos of high movement trajectories and superimposed cups onto these videos, a better approach may be to record movements of an actor pointing to the targets *with* cups and then remove these cups in the videos.

5.5.2 Coding the environment of others into our own

The present findings are in line with previous work demonstrating that participants code the environment of the observed model, such as an obstacle in her action space, into their own action space (Frischen et al., 2009; Griffiths & Tipper, 2009, 2012; Roberts et al., 2017). These findings build on this previous work in several important ways. Roberts et al. (2016) required participants to make a pre-specified, continuous, horizontal movement whilst observing a model make either a congruent (horizontal) or incongruent (curvilinear) movement. The presence of an obstacle in the

video only influenced participants' own movements when both the model and participant were performing the same horizontal movements. Whilst the goal of the observed and executed movement was congruent in our study (i.e. "point to the same targets that she does"), participants were less constrained in terms of the nature of the movement they were required to perform. That is, the trajectory of their movements were not pre-determined as it was in Roberts et al. (2016). This suggests that even when there is not a direct matching between the observed and executed movement (i.e. they are not completely congruent) the environment of the model (i.e. the presence of obstacles) continues to influence participants' own movements.

Secondly, Griffiths & Tipper (2009) suggested when we view another person avoiding an obstacle to reach for a target object, for this obstacle to influence our own reaching movement, it must be within our peripersonal action space. In their study, when the obstacle was beyond the "comfortable reach space" of the participant their reach trajectory was not perturbed by the obstacle. In the current study, however, the obstacles between the actor's targets were displayed on a screen 70 cm in front of the participants. Thus, they were outside of their peripersonal space of the participants. Despite this, participants' movements between their own targets were higher after having observed the actor reach over obstacles to point to her targets, compared to when she moved with the same trajectory but there were no obstacles between her targets. This supports other work demonstrating that the proximity of the co-actor's obstacle does not influence obstacle priming (van der Wel & Fu, 2015).

Griffiths & Tipper (2012) later proposed that for obstacle priming to occur participants must share ownership of the workspace with a co-actor, even if the observed workspace is not within the peripersonal space of the participant. In the current study, there was a clear divide between the workspace of the participant (i.e. the table they were sat at) and the actor's workspace which was projected as a video onto a

screen in front of the participants. Despite this separation between the workspaces, obstacle priming still occurred.

One possibility however is that due to the visual similarity between the workspaces (i.e. workspace in the videos looked like the workspace on the table in front of participants), participants may have felt they were sharing the workspace with the actor. Griffiths and Tipper (2012) created a sense of ‘separatedness’ between the two workspaces by having one participant interact with a blue set of objects and the other interact with a yellow set. In the shared-workspace condition, participants interacted with the same workspace - after each trial the workspace was moved across the table from one participant to the other by the experimenter. When interpreted in the light of our current findings, it is possible that the visual similarity between the observed workspace and the participant’s own workspace in Griffiths and Tipper (2012) may have been sufficient to cause obstacle priming. Although, it remains unclear why this was not the case in Griffiths and Tipper (2009; Experiment 2).

It should also be stressed that in Griffiths & Tipper (2009, 2012) the observed action was not relevant to the participant’s own subsequent action. Participants were instructed to passively observe the other person’s action. This is in contrast to the present study where participants were explicitly instructed to attend to the sequence of targets the model pointed to and then point to the same targets on the table in front of them. Thus, the present study was more similar to a joint action task (Sebanz, Bekkering, & Knoblich, 2006), whereby the action of participants (i.e. the targets they pointed to) was dependent on the recently observed movements of the model. This greater attention to the model’s movements (Bek et al., 2016) and greater relevance of her movements to the participant’s task may also account for some of the differences in obstacle priming between the present study and those of Griffiths & Tipper (2009, 2012).

Van der Wel & Fu (2015) proposed that for discrete movements obstacle priming is due to the co-representation of the actor's task (Sebanz et al., 2005). Conversely, for continuous movements obstacle priming is the result of entrainment and thus dependent on receiving concurrent visual information from a co-actor (Richardson et al., 2005). Our task required the execution of discrete movements after the participants had observed the actor move to her targets. So when participants pointed to their own targets, this was in the absence of concurrent visual information about the actor's movements. Thus, our findings are generally in line with van der Wel and Fu's (2015) interpretation that when performing discrete movements participants co-represent the task of the co-actor during obstacle priming. However, a co-representation account fails to fully account for our findings. According to a co-representation account a smaller obstacle requires less adjustment yet there was no significant difference between the cup and small cup condition. Future studies should vary the size of the obstacle more systematically to directly test the co-representation account.

Finally, one possibility is that the continued presence of the obstacles on the screen in front of participants during their response period caused distractor interference (Tipper, Howard, & Jackson, 1997). However, this interpretation is unlikely. Firstly, the obstacles were small (5.5cm x 4 cm) and appeared 70 cm from the participants so well outside of their peripersonal action space. Secondly, as highlighted above, the saliency of the distractor has been shown to impact the extent of distractor interference (Tipper, Howard, & Houghton, 1998), yet when the size of the obstacle was halved (small cup condition) this did not impact the extent of obstacle priming. In addition, whilst automatic imitation of movement trajectories is at least partially due to spatial effects (i.e. the observed movements being higher up in space; Hardwick & Edwards, 2012), the higher movements in the cup compared to the no cup conditions, speaks against a purely spatial effect. Here the movements in the videos were same height, yet

participants moved higher in the cup condition. If the effects were purely spatial, we would not expect to see these differences.

5.5.3 Conclusion

To conclude, this chapter showed that participants' movements between a series of targets were sensitive to the height of observed movement trajectories, even when these were irrational - unnecessarily and exaggeratedly high. That is, participants continued to mimic the movements of the model even in the superhigh condition. Secondly, the presence of obstacles between the model's targets resulted in participants moving with an even higher trajectory between their own targets, despite their being no obstacles between them. This obstacle priming suggests that participants code the environment of a co-actor into their own action space. The results are consistent with previous work demonstrating obstacle priming is not dependent on the obstacles being within the peripersonal space of the participant (Griffiths & Tipper, 2012). The results also suggest that obstacle priming during the observation and execution of discrete movements is likely to depend upon participants co-representing the task of the model (van der Wel & Fu, 2015). In the next chapter, I investigate whether people's tendency to mimic others' movement can influence their choices.

Chapter 6 - The Way Others Move Influences What We Choose

6.1 Abstract

Whether pointing at a menu item or rifling through a clothes rack, when we choose we often move. We investigated whether people's tendency to copy the movements of others could influence their choices. Participants saw pairs of pictures in private and indicated which one they preferred. They then entered a virtual art gallery and saw the same pictures pairs in the presence of a virtual character. Having observed the virtual character point to indicate her preference with either a high or low movement trajectory, participants indicated their preference. There was either an anatomical or spatial correspondence between the participant's pictures and those of the virtual character. We found that participants copied the movement made by the virtual character rather than her action goal (i.e. her choice of picture). This resulted in a shift towards the virtual character's preferences in the anatomical condition but away from her preferences in the spatial condition. This effect was driven by the observation of the virtual character's high pointing movements. In a further experiment, we did not find any significant differences in imitation behaviour in autism, although autistic participants were less consistent in their choices. Our findings demonstrate that we are not only influenced by other's choices but also the types of movements others make to indicate those choices.

6.2 Introduction

In the previous chapters, participants demonstrated a consistent tendency to copy the movements of a range of other agents. Participants mimicked the movements of a virtual character (Chapter 3), a moving ball (Chapter 4) and also those of a human

model (Chapter 2, Chapter 5) even when her movements were rated as irrational (Chapter 5). In this chapter, we explored what consequences this tendency to mimic others may have. For example, copying the movements of others has been shown to override strong financial incentives to avoid imitative behaviours during competitive games (Belot et al., 2013; Naber, Vaziri Pashkam, & Nakayama, 2013). Specifically, this chapter explored whether the tendency to mimic the movements of others could change the choices that participants had previously made in private.

Imagine you are at a restaurant with a friend and the waiter is taking your order. Your friend points emphatically at the menu indicating the particular meal she wants. When the waiter asks you what you want you point at the same item on the menu. Why did you make the same choice as your friend?

Typical explanations offered by theories of social influence (e.g. Cialdini & Goldstein, 2004) stress your desire to affiliate with your friend and/or your belief that she has superior knowledge to you (perhaps she has been to the restaurant before). In support of this explanation a range of studies have demonstrated that our choices are influenced by our affiliative motives (Izuma & Adolphs, 2013; Midgley, Dowling, & Morrison, 1989) and by others' perceived expertise (Lauring et al., 2016; Plassmann, O'Doherty, Shiv, & Rangel, 2008). Yet, a limitation of these studies is that the social context is only implied (Berns, Capra, Moore, & Noussair, 2010; Campbell-Meiklejohn, Bach, Roepstorff, Dolan, & Frith, 2010; Plassmann et al., 2008). That is, although participants are informed of the choices of a particular person or group, they do not witness others indicating those preferences. However, as with you and your friend at the restaurant, people often move to indicate their preferences to others, or, as Schall (2001) highlighted "often one does one thing (order a meal) by doing something else (point at the menu)" (Schall, 2001).

Thus, it could be that when we observe others making choices, we are not only influenced by their choices (i.e. their action goal) but also the types of movements they make to indicate their choices. This is what we explored in the current study – when we make choices in the presence of others, are our choices influenced by the types of movements others make to indicate those choices? This distinction between copying the choice (or goal) of an action compared to a particular movement maps onto an influential theory of imitation (Bekkering et al., 2000; Wohlschläger, Gattis, & Bekkering, 2003). Thus, we place our study of social influence in the context of motor studies of imitation, and consider what these might predict about people’s imitative tendencies. In the literature review below, we consider how people’s choices might be influenced by the goal of another’s action, by the topographical matching between the model and imitator’s action, and by social cues conveyed in the kinematics of the action. We can draw on these theories to build our hypothesis of how people’s choices will be influenced by seeing another’s actions.

6.2.1 Coping goals vs. kinematics

The theory of goal-directed imitation (GOADI; Wohlschläger et al., 2003) states that during imitation people decompose an action into a hierarchy of goals in which the ends of an action (e.g. the particular item your friend pointed to on the menu) are further up the hierarchy than the means (e.g. the particular movement your friend made to indicate her choice). Actions at the top of the hierarchy are more readily imitated and, according to the ideomotor principle, the selected goal activates the motor programme most readily associated with it (Prinz, 1990). GOADI is largely supported by studies which have characterised people’s errors and movements during imitation tasks. These show both that children are primarily concerned with copying the goal of an observed action (e.g. touch ear) and are less concerned about the kinematics of the action (e.g. touch ear with a crosslateral movement) (Bekkering et al., 2000). Similarly, studies

which have recorded participants' kinematics during imitation tasks show that when goals are present participants do not copy the speed of the model's action, but are more likely to do so when the goals are absent (Wild et al., 2010, 2012).

In line with this, studies of mimetic desire show that people tend to choose the same item as others (Lebreton, Kawa, Forgeot d'Arc, Daunizeau, & Pessiglione, 2012), and tend to like things that others like (Campbell-Meiklejohn et al., 2010). Together these findings suggest that imitation behaviour is driven by the goal of an action, and that kinematic information is often ignored. One goal of the present study was to test if this is true in a rich virtual reality context.

6.2.2 Imitating anatomically vs. spatially

When imitating other people we can copy the topography of their action (match their movement anatomically), or, we can match their movement spatially (make a movement to the same spatial location). When there is a topographical matching between the movement of a model and that of an imitator, imitation is enhanced. For example, Brass et al. (2001) showed that participants are faster at imitating finger movements when the observed hand is presented in the same configuration as their own. Similarly, Ramenzoni, Sebanz and Knoblich (2015) found that the ability to tap synchronously with a model was modulated by the topographical congruency between the model and participants' hands. Automatic imitation effects are also strongest when they are effector-specific; for example, participants are faster to make hand opening movements having observed hand opening compared to mouth opening (Leighton & Heyes, 2010). Pan and Hamilton (2015) found that participants showed a greater tendency to copy another agent when they could map the actions of another agent onto their own body. They asked participants to perform simple tapping sequences with three drums which were either the same (congruent) or different (incongruent) from the

sequences performed by a virtual character or a bouncing ball. There was either a spatial or anatomical matching between the drums of the virtual character (or ball) and those of the participant. In the spatial condition, the participants displayed no imitative advantage for the virtual character compared to the ball. It was only in the anatomical condition - when there was a topographical match between participants and virtual character - that participants showed an imitative advantage for the virtual character. These studies demonstrate that imitative tendencies are enhanced when there is a topographical matching between the movements of the model and that of the imitator. The current study investigated whether people's tendency to match the movements of another agent topographically could influence their choices.

6.2.3 Communicative kinematics

The fact that we change our movements according to the social context was noticed by Darwin who highlighted how we often “wish to make certain gestures conspicuous or demonstrative” (Darwin, 1872). The advent of motion tracking technologies has provided us with a detailed understanding of these differences (Krishnan-Barman et al., 2017). Peeters et al. (2013) showed that, when participants had a communicative intent, the duration of their pointing movement was longer as was the time they spent at the apex of the point (Peeters, Chu, Holler, Özyürek, & Hagoort, 2013). Similarly, Cleret de Langavant et al. (2011b) showed that the trajectory and endpoint variability of pointing movements changed depending on the whether social context was communicative or not. These findings are consistent with a range of studies which have demonstrated that the kinematic features of other people's movements can reveal a wealth of information about their psychological states (Becchio, Koul, Ansuini, Bertone, & Cavallo, 2017; Krishnan-Barman et al., 2017). For example, actors who intend to cooperate will move with a slower and exaggerated trajectory (Quesque, Delevoye-Turrell, & Coello, 2015; Vesper, Schmitz, Safra, Sebanz,

& Knoblich, 2016) and when participants observe another agent make a movement more quickly, they rate their decision as more confident (Patel, Fleming, & Kilner, 2012). In sum, when we are in the presence of people we often change the kinematics of our movements in order to communicate with them. For example, to return to our restaurant example, your friend may want to draw the waiter's attention to her choice so points at the menu with a slow and exaggerated movement trajectory. What remains unknown, however, is the extent to which these differences in kinematics influence people's tendency to copy others' movements.

6.2.4 Current study

Knowledge of other people's choices (without any observation of their action) can influence our own choices (Campbell-Meiklejohn et al., 2010; Izuma & Adolphs, 2013). The aim of the current study was to test if this effect varies when more detailed information is available about the kinematics of the other person's action. A review of previous studies of imitation behaviour highlights three key findings which can lead to predictions for our task:

(1) when instructed to copy a model's action participants tend to copy the goal ahead of the kinematics (Wohlschläger et al., 2003). This aligns with social influence models which suggest that people tend to like things that others like (Campbell-Meiklejohn et al., 2010; Izuma & Adolphs, 2013).

(2) during imitation if there is a topographical (i.e. anatomical) match between the observed and executed movement, imitation is enhanced (Pan & Hamilton, 2015).

(3) when we aim to communicate with others we modulate the kinematic features of our actions (Peeters et al., 2013).

The current study aimed to explore imitation and social influence in an ecologically valid, virtual reality setting. Many previous studies of imitation have

usually involved just one goal (e.g. touch ear; Bekkering et al., 2000) or no goal at all (Wild et al., 2010). These studies have found that when a goal is present we prioritise copying the goal of the action rather than the type of movement made to achieve the goal (Bekkering et al., 2000; Wohlschläger et al., 2003). If no goal is present in the observed action, we pay more attention to the type of movement made and imitate this more reliably. But what happens when we have a choice of goals as is common in many everyday situations, such as in a restaurant (Gattis, 2002)? Do we still copy the observed goal at the expense of the movement, or, does the type of movement influence our movements and our choices?

To test this, participants were shown pairs of art pictures and indicated which one they preferred. They then entered a virtual art gallery and saw the same picture pairs in the presence of a virtual character who sat opposite them. In the art gallery, the virtual character pointed to the picture she preferred before the participant indicated their preference. In the art gallery there were two conditions (Figure 2). In the spatial condition, there was a spatial correspondence between the picture pairs of the virtual character and those of the participant so choosing the same picture as the virtual character meant making a different movement to her. In the anatomical condition, there was an anatomical correspondence between the picture pairs of the participants and those of the virtual character so choosing the same picture meant making the same movement.

The primary aim of Experiment 1 was to test whether seeing the choices of the virtual character could change the choices participants had made in private. We can contrast two main hypotheses:

Goal hypothesis – if participants copy the virtual character’s goal (i.e. her choice of picture), then in both the anatomical and spatial conditions participants should shift

their choices to match those of the virtual character (Campbell-Meiklejohn et al., 2010; Wohlschläger et al., 2003).

Movement hypothesis – if participants copy the virtual character’s movements, then in the anatomical condition participants should shift their preferences towards those of the virtual character as making the same movement as the virtual character involved making the same choice as her. Whereas, in the spatial condition, participants should shift their preferences away from those of the virtual character as making the same movement as the virtual character involved making a different choice to her (Figure 2).

The study’s second aim was to test whether the kinematic properties of the virtual character’s pointing movements, specifically the height of her point trajectory, could also influence people’s movements and choices. If the virtual character pointed with an exaggeratedly high trajectory, which has been shown to be communicative (Peeters et al., 2013), would participants be more likely to copy the goal of the observed action (i.e. the picture choice) or the type of movement made?

6.3 Experiment 1

6.3.1 Methods

Design and participants

The study followed a 2 x 2 design with configuration (anatomical vs. spatial) and height (high vs. low) as within-subject factors. The dependent variable was shift – how much participants shifted their preference either towards or away from those of the virtual character from the private to the social setting.

39 participants (25 female) with a mean age of 29 years (SD = 10 years; range 18-59) were recruited from the UCL Institute of Cognitive Neuroscience participant

database. All participants were right-handed, had normal or corrected-to-normal vision and reported no history of neurological disorder. All were financially reimbursed for their time and gave written informed consent before participating. All procedures were approved by the UCL Research Ethics Committee.

Materials

80 picture pairs in total were selected from a sample of 240 images (120 landscape and 120 abstract) which were rated by an independent group of 20 participants on their complexity, concreteness, attractiveness, valence, affectivity and interest using a 7-point scale. The luminance and contrast were also calculated for each image using MATLAB (MathsWorks, Natick, USA). The best matched 40 landscape pictures and the best matched 40 abstract pictures were then selected for the current study. All 80 picture pairs were presented in the private setting. In the social setting 40 of these were presented in the anatomical condition and 40 in the spatial condition. The same pictures always appeared in the anatomical and spatial conditions for all participants. In both the spatial and anatomical condition, the virtual character pointed with a high trajectory to indicate her preference on 20 trials and with a low trajectory on the other 20 trials. The landscape and abstract pictures pairs were distributed evenly across all the conditions.

The virtual character's movements were animated using pre-recorded motion capture data from a female actor using three magnetic markers (Polhemus LIBERTY system, Colchester, USA) attached to the head, the top of spine, and right index finger. When recording the movements, the actor was instructed to look from side-to-side before pointing with either a high or low movement trajectory (peak height of approximately 16 cm or 2 cm, respectively). The motion capture data was mapped on to

the virtual character using MotionBuilder (<http://www.autodesk.com/motionbuilder>) and Vizard (WorldViz Inc, Santa Barbara, USA).

Procedure

Private setting.

In the private setting participants sat in front of a 61 cm monitor and saw each picture pair for 5 seconds before the picture pairs disappeared. A question then appeared which said “Which picture do you prefer?” and participants had 2 seconds to indicate their preference by pressing the ‘a’ key on a keyboard if they preferred the picture on the left of the screen or the ‘l’ key for the picture on the right of the screen. A fixation cross appeared for 500 ms before the next picture pair appeared (see Figure 6-1). Responses were recorded in MATLAB and picture presentation was controlled using the Cogent toolbox (<http://www.vislab.ucl.ac.uk/cogent.php>). Each picture was presented on an 11.5 cm x 11.5 cm area with any excess spaced filled black (see Figure 6-1).

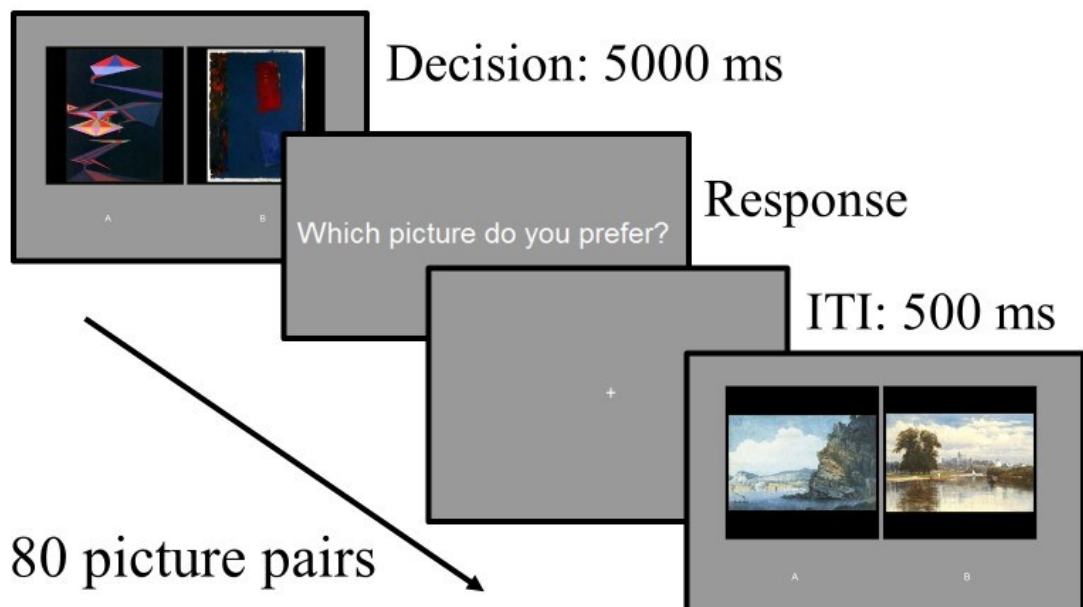


Figure 6-1 The private task trial structure

In Experiment 1 participants had 2 seconds to respond to indicate their preference. As some participants did not respond within 2 seconds in Experiment 1, this response period was unlimited in Experiment 2. ITI = inter-trial interval

Social setting.

After making their choices in the private setting participants made the same choices in the social setting - the virtual art gallery. Participants sat at a table on a stool and had a magnetic marker (Polhemus LIBERTY system, Colchester, USA) attached to their right index finger to record their movements. The virtual environment was presented on a 160 cm x 90 cm projector screen approximately 70 cm away from the participant using Vizard (WorldViz Inc, Santa Barbara, USA). The virtual environment depicted a female virtual character in the middle of the screen facing the participants. The virtual character's pictures were on the table in front of her and appeared on 25 cm x 25 cm placeholders. There were labels below the placeholders on the table with an 'A' or 'B' on a white tile below them. The participants' pictures were suspended to the left and right of the virtual character in 33 cm x 33 cm placeholders (see Figure 6-2).

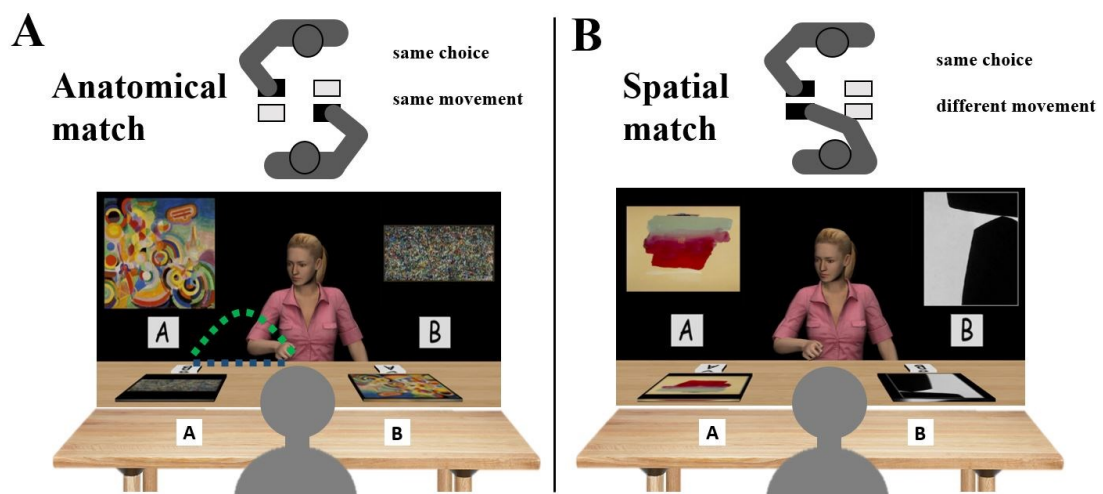


Figure 6-2 The social task setup.

Participants sat opposite the virtual character and she pointed to indicate her preference with either a low (blue) or high (green) movement trajectory. In each block there was either an anatomical (A) or spatial (B) match between the virtual character's pictures and those of the participant. Participants' movements were considered an anatomical match (A) if both moved contralaterally (as shown in A) or if both moved ipsilaterally. In the anatomical condition (A), pictures were arranged so that anatomically matching movements allowed both to point to the same picture. In the spatial condition, if participant made the same choice as the virtual character then they had to make a different movement – in this case the one makes an ipsilateral movement and the other a contralateral movement.

The table the participants sat at had three white markers: a resting pad labelled 'X' immediately in front of the participant, 20 cm in front of the participants and 40 cm to the left and right were white markers labelled 'A' and 'B.' If participants moved the magnetic marker on their right index finger onto either label on the table then the corresponding label under their pictures on the projector screen were highlighted with a yellow border.

The start of each trial was signalled by a beep with the virtual character's and participant's right index fingers in their respective resting positions. The virtual character's pictures pairs appeared on the table in front of the virtual character and the participant's pictures in the place holders either side of her. The pictures stayed on the screen for 6500 ms during which the participants were instructed to decide which picture they preferred but not to move their finger from the resting position. The virtual character also looked at the pictures as if she were deciding which picture she preferred. After 6500 ms the pictures disappeared and a "ding" sound occurred which acted as the virtual character's cue to move. The virtual character then pointed to either the 'A' or 'B' label on the table to indicate her preference. The label the virtual character pointed to was highlighted with a yellow border and she returned her finger to the resting position. 1500 ms after the "ding" sound, a "dong" sound occurred which acted as the participant's cue to indicate their preference by using their right index finger to point to either the 'A' or 'B' on the table in front of them. Once they had pointed, their A or B label on the screen was also highlighted with a yellow border to indicate their preference. The participant then returned their right index finger to the resting position. After the "dong" sound, participants had 3000 ms to respond before the beep signalled the start of the next trial and the next picture pair appeared.

The participants completed two blocks in the social setting - one anatomical block and one spatial. The order of these was counterbalanced across participants.

Participant were given 8 practice trials at the start of the experiment. This was always in the condition they encountered in the first block. At the start of the second block, the participants completed two or three practice trials in the new condition so that they were made aware of the difference in the layout of the virtual character's pictures. However, their task remained the same in both the anatomical and spatial condition - if they preferred picture A they pointed to the 'A' to their left on the table in front of them, whereas, if they preferred picture B they pointed to the B on their right (See Figure 6-2).

At the end of the experiment participants were asked to indicate how interested they were in art on a 7-point Likert scale and to indicate the number of times they had attended an art gallery or exhibition in the past 12 months.

6.3.2 Results

Excluded data

Failure to choose in the private task.

In the private setting, participants had 2 seconds to indicate which picture they preferred after having viewed the pictures for 5 seconds. However, on 5.0% (SD: 5.5%) of trials participants did not respond quickly enough so their preference could not be recorded (note we addressed this issue in Experiment 2). These trials were excluded from the analysis as it was not possible to establish whether participants later shifted their responses on these trials in the social setting. There were no significant differences in the number of these 'timed out' trials in the picture pairs which later appeared in the anatomical, 4.7% (4.9%), and spatial, 5.4% (6.8%), conditions.

Failure to choose in the social task.

On 2.5% (3.3%) of trials participants failed to indicate their choice in the social task. These trials were excluded from the analysis. These 'no choice' trials were

identified by plotting the kinematic data for each participant for each trial and identifying trials in which no clear pointing movement was made during the 3000 ms response period. There were no significant differences in the number of trials excluded for the anatomical, 2.9% (5.5%), and the spatial, 2.0% (2.9%), condition.

By combining both these exclusion criteria a total of 7.3% (6.8%) of trials were excluded. There were no significant differences in the total number of trials excluded for the anatomical, 7.5% (8.1%), and the spatial, 7.1% (7.3%), conditions.

Preference analysis

Agreement with the virtual character's pre-specified choices

The virtual character's choices were pre-specified. She made the same choice and movement for every participant for every picture pair. Thus, it was possible that in the private setting participants' choices may have coincidentally matched a large percentage of the virtual character's pre-specified choices. For example, if participants matched the pre-specified choices of the virtual character on 100% of trials in the private setting, then it would not have been possible for them to shift their preferences towards those of the virtual character in the social setting (as they already agreed with all of her choices). Similarly, if participants did not match any of the virtual character's pre-specified choices in the private setting, this would have given the participants more potential to shift their preferences towards those of the virtual character in the social setting.

However, this was not the case - participants matched the pre-specified choices of the virtual character between (min) 39.9% and (max) 61.1% in the private setting ($M = 49.3\%$, $SD = 5.38\%$) and this did not differ between the picture pairs which would later appear in the anatomical ($M = 49.5\%$, $SD = 7.22\%$) and spatial ($M = 49.2\%$, $SD = 7.17\%$) conditions. Thus, participants had the potential to shift their preferences on

approximately 40-60% of trials in the social setting. In the social setting participants matched the pre-specified choices of the virtual character between (min) 39.4% and (max) 66.4% ($M = 49.3\%$, $SD = 6.09\%$) ($t_{38} = -0.087$, $p = 0.931$, $d = -0.013$). Therefore, the overall extent to which participants matched the choices of the virtual character in the social setting did not change from the private setting (although differences were found between the different conditions, see below).

Shift in choice

Consistency.

The consistency of participants' choices for each picture pair were compared between the private and social setting. On average in the social setting participants stuck with their choice from the private setting on 78.1% ($SD = 11.2\%$) of trials. Greater consistency in participants' choices was significantly correlated with the number of times they reported visiting an art gallery in the past 12 months $r(37) = 0.400$, $p = 0.012$, but was not significantly correlated with self-reported interest in art, $r(37) = 0.285$, $p = 0.079$. Mean (SD) number of gallery visits in the last 12 months was 5.46 (3.54) and participants' mean (SD) self-reported interest in art (on a 1-7 point Likert scale) was 5.23 (1.35).

Preference shift.

On 21.9% of trials participants changed their picture choice from the private to the social setting. Next we investigated whether this preference shifting varied across conditions and if participants shifted their preferences towards or away from the preferences of the virtual character. If participants made the same choice in the private setting compared to the social setting, then this trial was assigned a 0. If participants changed their preference in the social setting so that they chose the same picture as the virtual character, the trial was assigned a +1. Finally, if participants changed their

choice in the social setting so that they choose the different picture to the virtual character, the trial was assigned a -1.

The scores in each condition (anatomical-high, anatomical-low, spatial-high, and spatial-low) were then summed, divided by the number of valid trials in that condition and then multiplied by 100 to give a shift score as a percentage for each participant. Each shift score could therefore range from -100% to 100% with negative scores indicating a shift away from the choices of the virtual character and a positive score indicating a shift towards the choices of the virtual character.

A 2 (configuration: anatomical vs. spatial) x 2 (height: high vs. low) within-subjects ANOVA was conducted on the shift scores. This revealed a main effect of configuration ($F_{1,38} = 4.27$, $p = 0.046$, $\eta_p^2 = 0.101$) with participants shifting towards the virtual character's preferences in the anatomical condition ($M = 1.79\%$, $SD = 8.27\%$) and away from the virtual character's preferences in the spatial condition ($M = -1.74\%$, $SD = 6.69\%$). The main effect of height was not significant ($F_{1,38} = 1.51$, $p = 0.226$, $\eta_p^2 = 0.038$). However, the interaction between configuration and height was significant ($F_{1,38} = 4.84$, $p = 0.034$, $\eta_p^2 = 0.113$).

Post-hoc paired samples t-test revealed that in the high condition, shift scores in the anatomical ($M = 2.70\%$, $SD = 11.7\%$) configuration were significantly greater than the shift scores in the spatial ($M = -4.79\%$, $SD = 8.26\%$) configuration ($t_{38} = 3.20$, $p = 0.003$, $d = 0.512$). However, there was no significant difference between shift scores in the anatomical ($M = 0.886\%$, $SD = 11.8\%$) and spatial ($M = 1.31\%$, $SD = 11.3\%$) configuration in the low condition ($t_{38} = -0.161$, $p = 0.873$, $d = -0.026$) (See Figure 6-3).

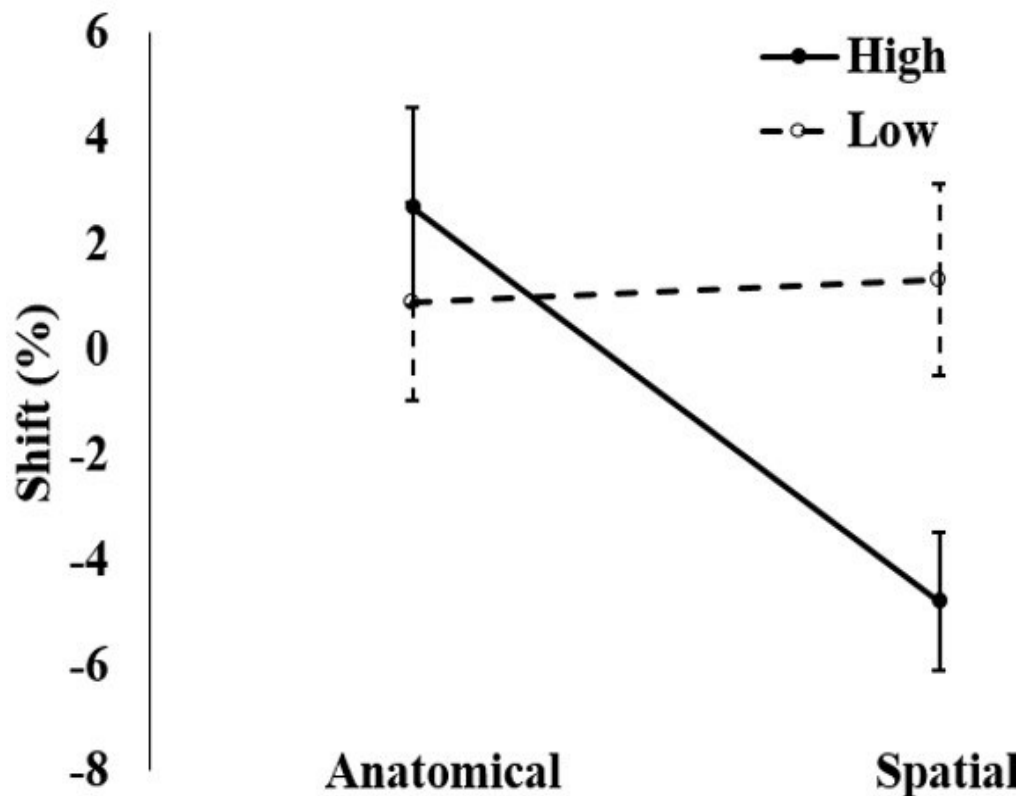


Figure 6-3 Mean shift scores. Errors bars indicate standard error.

Mean shift refers to the extent to the participants shifted their preferences towards (+) or away (-) from those of the virtual character in the social setting. Participants shifted when having observed the virtual character point with a high, but not a low, movement trajectory. In the anatomical condition participants shifted towards the preferences of the virtual character. Here, making the same topographical movement meant making the same choice. Whereas, in the spatial condition, participants shifted away from the preferences of the virtual character. Here, making the same topographical movement meant making a different choice.

6.3.3 Results summary and discussion

When given a choice of goals (e.g. picture A or picture B), do participants copy the choice of another agent (goal hypothesis) or do they copy the type of movement made by the other agent (movement hypothesis)? This was the primary question tested by Experiment 1. We found that participants' tendency to make the same (topographical) movement as a virtual character resulted in a change in the choices they had previously made in private thus supporting the movement hypothesis. In the anatomical condition, participants shifted their choices towards those of the virtual character as making the same movement as the virtual character meant making the same

choice as her. In the spatial condition, participants shifted their choices away from those of the virtual character as making the same movement as the virtual character meant making a different choice to her. This supports the movement hypothesis rather than the goal hypothesis.

Do the kinematic properties of another agent's movement, specifically the height of their point trajectory, influence people's tendency to copy their movements and choices? This was the second question tested in Experiment 1. We found that participants' tendency to imitate the type of movement made by the virtual character was driven by the observation of pointing movements with a high trajectory. Together these results suggest that our choices are not only influenced by other people's choices but also the types of movements others make to indicate those choices.

6.4 Experiment 2

6.4.1 Introduction

In Experiment 1 participants copied the movements of the virtual character and this changed the choices they had previously made in private. This tendency to imitate the virtual character's movements was modulated by the kinematic features of her movement - participants copied the movement of the virtual character more when she pointed with a high, but not a low, trajectory. People who receive a diagnosis of autism show differences in their everyday social behaviours (American Psychiatric Association, 2013). There has been a long debate whether autistic people show differences in their copying behaviours (Dapretto et al., 2006; Southgate & Hamilton, 2008). The aim of Experiment 2 was to replicate Experiment 1 with a sample of autistic participants and a matched neurotypical sample to explore these potential differences. First, we briefly review studies of imitation in autism to motivate our hypotheses.

Goal-directed imitation in autism

Studies investigating social influence suggest that the basic mechanisms of social influence are intact in autism, for example, autistic participants rate objects which are the goal of someone's action as more desirable than objects which are not the goal of their action (Forgeot D'Arc et al., 2016). This focus on other's goals in autism is supported by the imitation literature. Autistic people are more goal-focused when copying others but imitate the means with which a goal was achieved to a lesser extent than non-autistic people. For example, Hamilton, Brindley and Frith (2007) used the ear touching paradigm (Bekkering et al., 2000) to show that autistic children made the same types of errors and at the same frequency as their non-autistic peers suggesting intact goal-directed imitation in autism. Moreover, Hobson & Lee (1999) found that autistic participants were proficient in copying goal-directed actions, but tended not to copy the style with which the experimenter executed those actions. Similarly, Wild et al. (2012) showed that whilst non-autistic adults' own movements were sensitive to the movement speed of another agent's pointing movements, autistic adults' movements were not modulated by the agent's movement speed. Autistic participants also displayed more goal-directed eye-movements (Wild et al., 2012). These findings were in Chapter 3 which showed that autistic and neurotypical participants showed no differences in their ability to copy the goal of a virtual character's action, but autistic participants copied the kinematics of her action to a lesser extent. These results in adults are consistent with the developmental literature which show that autistic children do not overimitate (Marsh, Pearson, Ropar, & Hamilton, 2013). However, what happens to goal-directed imitation when autistic participants have a choice of goals as was the case in our current paradigm? If there is a focus on goals during imitation, rather than the types of movements made, then autistic participants should copy the goal of the virtual character's action. Thus, we predicted there would be comparable shifts in their

preferences (or lack thereof) in both the anatomical and spatial conditions. This was the first hypothesis tested in Experiment 2.

Social cues and imitation in autism

In Experiment 1 we found that participants copied the type of movement made by the virtual character more when she pointed with a high, compared to a low, movement trajectory. This maps on to a theory of mimicry, the social-top down response modulation (STORM) model, which states that people change their mimicry (i.e. their unconscious imitation) depending on social cues (Wang & Hamilton, 2012). For example, eye-contact (Wang, Newport, & Hamilton, 2011) and emotional facial expressions (Rauchbauer et al., 2015) have all been shown to enhance mimicry responses.

Movements with a high or exaggerated movement trajectory may also function as social cues (Forbes & Hamilton, 2017; Gergely & Csibra, 2003). They are produced in contexts where people intend to send a social signal of cooperation (Vesper, Schmitz, Safra, Sebanz, & Knoblich, 2016), and observation of high trajectories activates ‘mentalising’ areas of the brain (Marsh, Mullett, Ropar, & Hamilton, 2014). Similarly, caregivers often exaggerate components of an action sequence when interacting with an infant (Brand, Baldwin, & Ashburn, 2002) and it has been suggested that this “motionese” may help infants to establish what to imitate (Nagai & Rohlfing, 2007). Based on the results of Experiment 1, we suggest that the height of the movement performed by the virtual character acts as a social cue, in this case signalling ‘this one is important’. If neurotypical participants perceive and act on this social cue, this could drive their imitation of the virtual character.

Interpreting the results of Experiment 1 within the STORM model also leads to specific predictions for the performance of autistic participants. STORM predicts that

there is less modulation of imitation by social cues in participants with autism as was found in Chapter 2. For example, eye-gaze (Forbes et al., 2017; Vivanti & Dissanayake, 2014), prosocial priming (Cook & Bird, 2012), and emotional facial expressions (Grecucci et al., 2013) enhance imitative tendencies in non-autistic participants but not in autistic participants. Thus, according to STORM, autistic participants should not change their imitation behaviour based on the height of the virtual character's pointing movement as was found in Experiment 1. This was the second hypothesis we aimed to test in Experiment 2.

6.4.2 Method

Changes from Experiment 1

Methods for Experiment 1 were the same as Experiment 2 apart from the following changes:

Private task.

After the presentation of the pictures the question "Which picture do you prefer?" stayed on the screen until participants indicated their preference by pressing the appropriate key on the keyboard. This was done to prevent a loss of trials due to the participants not responding quickly enough as occurred in Experiment 1.

Copresence measures.

At the end of the task participants were asked to indicate the extent to which they agreed with seven copresence questions (Hale et al., 2018) on a 7-point Likert scale (e.g. *How much did you behave as if the virtual character was real? / How much did you feel that you and the virtual character were in the same environment?*).

Design.

A between-subject factor, group (neurotypical vs. autism), was added to the 2 (configuration: anatomical vs. spatial) x 2 (height: high vs. low) design.

Participants.

Table 6-1 A comparison of the autistic and neurotypical participants

	Neurotypical (<i>n</i> = 29)		Autistic (<i>n</i> = 27)		<i>t</i> test
	Mean (<i>SD</i>)	Range	Mean (<i>SD</i>)	Range	<i>p</i> value
Age (years)	31 (11)	19-61	32 (8)	20-53	0.59
Full IQ	117 (12)	87-138	117 (14)	86-152	0.75
Verbal IQ	117 (13)	88-147	119 (14)	91-155	0.46
Performance IQ	113 (15)	76-146	110 (15)	80-132	0.94
AQ	14 (7)	3-28	33 (9)	12-48	< .001
ADOS: total	-	-	9 (3)	4-17	-
ADOS: comm.	-	-	3 (2)	0-6	-
ADOS: RSI	-	-	6 (2)	2-11	-
Gender	20 M; 9 F	-	22 M; 5 F	-	-
Handedness	26 R; 3 L	-	24 R; 3 L	-	-

29 neurotypical and 27 autistic participants were recruited through the autism@icn participant database and came to the university as part of a research day during which they took part in multiple studies. Groups were matched on age, gender, handedness, and, verbal and performance IQ using either the Wechsler Adult Intelligence Scale (WAIS-III UK; Wechsler 1999a) or Wechsler Abbreviated Scale of Intelligence (WASI-II, Wechsler 1999b; Table 1). All autistic participants had a diagnosis of an autism spectrum disorder from an independent clinician: 20 participants had a diagnosis of Asperger's Syndrome and 7 participants had a diagnosis of autism

spectrum disorder. Autistic participants were also tested on module 4 of the Autism Diagnostic Observation Schedule (ADOS-G Lord et al. 2000) or ADOS-2 (Lord et al. 2012) by a trained researcher with research-reliability status: ten met the ADOS classification for autism, ten for autism spectrum, and, seven did not meet the classification of autism or autism spectrum. However, all seven who did not meet the cut off for an overall classification of autism or autism spectrum, reached the ADOS cut-off for autism spectrum on either the communication or reciprocal social interaction subscale. Five autistic participants had additional diagnoses: dyslexia (1), dyspraxia (1), or ADHD (2), and, one participant had additional diagnoses of both ADHD and dyspraxia. All participants were financially reimbursed for their time and gave written informed consent to participate.

6.4.3 Results

Excluded data

Failure to choose in the social task.

If participants failed to indicate their choice during the social task these trials were excluded from the analysis. This occurred on 1.38 % (2.07%) of trials for neurotypical participants and 2.36% (2.95%) for the autistic participants. There were no significant differences between the number of excluded trials between the groups ($t_{54} = -1.45, p = .16, d = 0.38$).

Shift in choice

Consistency.

In the social setting neurotypical participants stuck with their choice from the private setting on 76.72% (7.78%) of trials and autistic participants stuck with their choice on 58.81% (6.08%) of trials. An independent samples t-test revealed that

Table 6-2 A comparison of co-presence, interest in art and art gallery visits in the past 12 months between the two groups

	TD (<i>n</i> = 29)	ASC (<i>n</i> = 27)	<i>t</i> test		
	Mean (<i>SD</i>)	Mean (<i>SD</i>)	<i>t</i> ₅₄	<i>p</i>	<i>d</i>
Co-presence	2.95 (1.37)	3.04 (1.45)	-0.26	.80	.06
Art Interest	5.03 (1.30)	4.70 (1.68)	0.83	.41	.21
Art Visits*	4.70 (2.88)	2.96 (2.75)	2.29	.03	.62

neurotypical participants were more consistent in their choices than autistic participants, $t_{54} = -9.55, p < .001, d = 2.63$. Autistic participants reported having visited art galleries less often in the past 12 months (see Table 6-2). Experiment 1 found that gallery visits was significantly correlated with consistency. Thus, we conducted a multiple linear regression to explore whether consistency was better predicted by reduced art experience or an autism diagnosis. The model explained 62.9% of the variability in consistency, $R^2 = .63, F_{2,53} = 44.84, p < .001$. When holding the number of art visits in the past 12 months constant, group significantly predicted consistency, $\beta = .79, t_{53} = 8.96, p < .001$. When controlling for group, art visits did not significantly predict consistency, $\beta = -.02, t_{53} = -0.28, p = .78$.

Preference shift.

Shift was calculated as in Experiment 1. A one sample t-test ($t_{55} = 0.182, p = 0.856$) revealed that mean shift scores did not differ significantly from 0 showing that overall participants did not shift their choices towards or away from those of the virtual character from the private to the social setting. To explore differences across the conditions we conducted a 2 (configuration: anatomical vs. spatial) x 2 (height: high vs. low) within-subjects ANOVA on the shift scores. We first report the ANOVAs for each

group separately, before reporting the 2 x 2 x 2 ANOVA with group (neurotypical vs. autism) as a between-subject factor.

Neurotypical.

Neurotypical participants displayed a main effect of configuration ($F_{1,28} = 7.82, p = 0.009, \eta_p^2 = 0.218$) with mean shift scores greater in the anatomical condition, 1.75% ($SD = 6.33\%$), compared to the spatial condition, -2.89% ($SD = 7.32\%$) (see Figure 6-4). The main effect of height ($F_{1,28} = 1.76, p = 0.195, \eta_p^2 = 0.059$) and the interaction between configuration and height were not significant ($F_{1,28} = .371, p = 0.548, \eta_p^2 = 0.013$).

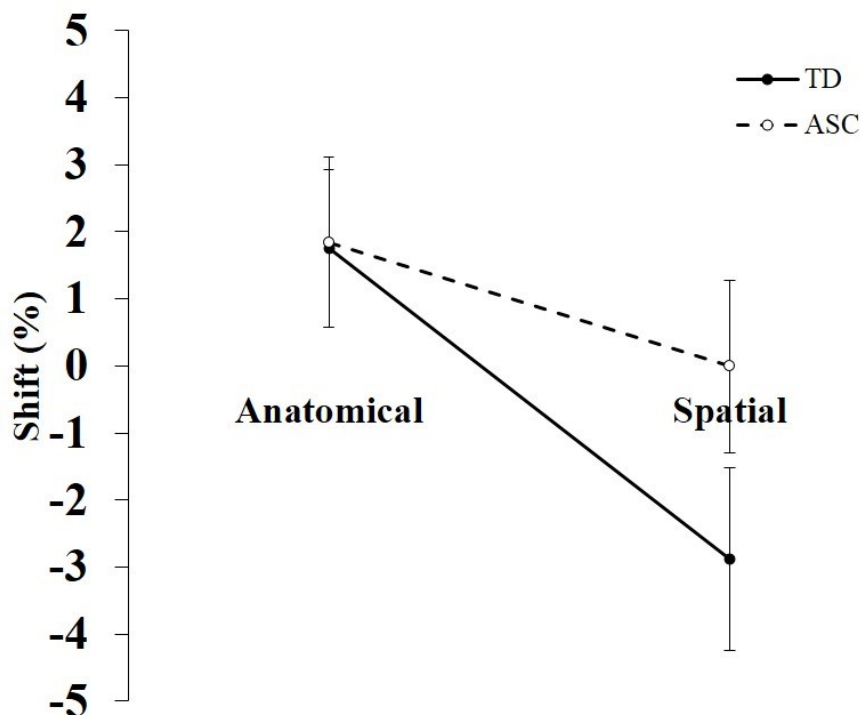


Figure 6-4 Mean shift scores for the autistic and neurotypical participants. Errors bars indicate standard error

Errors bars indicate standard error. For neurotypical participants, there was a shift towards the preferences of the virtual character in the anatomical condition, but a shift away from the virtual character's preferences in the spatial condition. Autistic participants did not show this same effect.

Autism.

Autistic participants did not display a main effect of configuration ($F_{1,26} = .957, p = .337, \eta_p^2 = .036$) or height ($F_{1,26} = .429, p = .518, \eta_p^2 = .016$) and there was no significant interaction between configuration and height ($F_{1,26} = .001, p = .976, \eta_p^2 < .001$).

Group comparison.

By including group as a between-subject factor, this revealed a main effect of configuration ($F_{1,54} = 6.69, p = .012, \eta_p^2 = .110$) with mean shift scores greater in the anatomical condition, 1.79% ($SD = 6.78\%$), compared to the spatial condition, -1.50% ($SD = 7.04\%$). No other main effects or interactions were significant (see Figure 6-4).

Table 6-3 The ANOVA table with and without copresence as a covariate

	Without covariate				With copresence as a covariate			
	<i>df</i>	<i>F</i>	<i>p</i>	Partial Eta Squared	<i>df</i>	<i>F</i>	<i>p</i>	Partial Eta Squared
Configuration	1,54	6.69	.012	.110	1,53	5.00	.030	.086
Height	1,54	.049	.826	.001	1,53	2.04	.159	.037
Group	1,54	1.20	.278	.022	1,53	1.25	.269	.023
Configuration * Height	1,54	.209	.649	.004	1,53	4.84	.032	.084
Configuration * Group	1,54	1.23	.272	.022	1,53	1.15	.289	.021
Height * Group	1,54	1.72	.196	.031	1,53	1.62	.209	.030
Configuration * Height * Group	1,54	.245	.623	.005	1,53	.377	.542	.007
Copresence					1,53	.497	.484	.009
Configuration * Copresence					1,53	1.59	.212	.029
Height * Copresence					1,53	2.16	.147	.039
Configuration * Height * Copresence					1,53	7.01	.011	.117

Post-hoc covariate analysis.

Previous studies investigating social interactions in virtual environments have included copresence as a covariate to account for differences in the extent to which participants felt immersed in the virtual social interaction (Hale & Hamilton, 2016a; Pan & Hamilton, 2015). There were no significant differences in copresence scores between the groups (neurotypical: $M = 2.95, SD = 1.37$; autism: $M = 3.04, SD = 1.45$; $t_{54} = -$

.258, $p = .797$) so we included copresence as a covariate in the 2 x 2 x 2 model. This revealed a main effect of configuration ($F_{1,53} = 5.00$, $p = .030$, $\eta_p^2 = .086$) and a significant interaction between configuration and height ($F_{1,53} = 4.84$, $p = .032$, $\eta_p^2 = .084$; see Table 6-3). There was also a significant three-way interaction between configuration, height and copresence ($F_{1,53} = 7.01$, $p = .011$, $\eta_p^2 = .117$). No other main effects or interactions were significant (see Table 6-3).

6.4.4 Results summary and discussion

Experiment 2 aimed to replicate the findings from Experiment 1 and explore any differences in autistic participants. Experiment 2 replicated Experiment 1 by demonstrating that participants' tendency to make the same (topographical) movement as a virtual character resulted in a change in the choices they had previously made in private. This suggests that when given a choice of goals participants are more likely to copy the type of movement made by another agent rather than the action goal. In the anatomical condition participants shifted their preferences towards those of the virtual character as making the same movement as the virtual character also meant making the same choice as her. In the spatial condition participants shifted their preferences away from those of the virtual character as making the same movement as the virtual character meant making a different choice to her. When we controlled for copresence - the extent to which participants felt immersed in the virtual social interaction - we replicated the second finding from Experiment 1 - the tendency to make the same movement as the virtual character was driven by the observation of pointing movements with a high trajectory. Finally, we found no evidence of any significant differences in the autism sample, except that autistic participants were less consistent in their choices between the private and social setting.

6.5 General Discussion

Across two experiments and 95 participants, we demonstrated that participants showed a consistent tendency to copy the (topographical) movements made by a virtual character rather than the goal of her action. This resulted in a change in the choices participants had previously made in private. In the anatomical condition, participants shifted their preferences towards those of the virtual character as making the same movement as the virtual character meant making the same choice as her. In the spatial condition, participants shifted their preferences away from those of the virtual character as making the same movement as the virtual character meant making a different choice to her. In Experiment 1, we showed that this tendency to copy the virtual character's movements was modulated by the kinematics of her pointing trajectory - participants copied her movements more when she pointed with a high, but not a low, trajectory. In Experiment 2, we replicated this effect when controlling for copresence – the extent to which participants felt immersed in the virtual interaction. However, we did not find any significant differences in the imitation behaviour of autistic participants.

The results suggest that when we have a choice of goals, as is common in many everyday social situations, imitation may sometimes be driven by others' movements rather than their action goals. More generally, these findings suggest that when we make choices in the presence of others, our choices are not only influenced by other people's choices but also the types of movement others make to indicate their choices. We discuss our findings in terms of theories of imitation.

Copying topographical movements rather than action goals

In contrast to many studies investigating imitation, the current study gave participants a choice of goal (e.g. picture A or picture B). Arguably, this is much more akin to how imitation operates in everyday social interactions. For example, at a

restaurant you are not obliged to copy the choice of your friend - you have a choice. Theories of imitation, such as GOADI (Wohlschläger et al., 2003), have mainly been tested under conditions where there is a clear, unambiguous goal or no goal at all (Bekkering et al., 2000; Wild et al., 2010, 2012). When the goal is clear, participants prioritise imitating the goal at the expense of the way in which the goal was achieved, such as the particular movement made to point to a target. Our findings suggest, however, that when the imitator has a choice of goal, the types of movements others make to indicate their choices plays a more important role in imitation.

We showed that participants show an imitative advantage when there is a topographical (i.e. anatomical) matching between the movement of a model and that of an imitator. Here, the participants can map the actions of another agent onto their own body (Tsakiris, 2010). This supports previous work comparing anatomical and spatial imitation (Pan & Hamilton, 2015; Ramenzoni et al., 2015). Both Pan and Hamilton (2015) and Ramenzoni et al. (2015) used reaction time measures of imitation - the time taken to tap the first drum in a sequence and tapping asynchrony, respectively. The present findings build on this work by showing that participants made the same anatomical movement as another agent with a greater frequency. This imitative advantage seen for anatomical movements can be explained by associative accounts of imitation, such as Heyes' associative sequence learning (ASL) account (Heyes, 2011).

According to Heyes, when we consistently observe an action and perform an action contingently, overtime, the connections between the visual representation and motor representation involved in observing and performing this action become strengthened. Thus, if we observe a particular action, we are primed to make a movement which has been associated with that action. In terms of the current paradigm, ASL rests on the assumption that we have greater experience of observing and executing anatomically matched pointing movements rather than those matched

spatially. Thus, following the observation of a pointing movement we are primed to make a pointing movement which matches this movement anatomically. Gillmeister et al. (2008) showed that through sensorimotor training it is possible to change these anatomically matched associations (Gillmeister et al., 2008). Thus, future studies using the current paradigm could train participants to observe and execute spatially matched, rather than anatomically matched, pointing movements to see if this alters participants' preference shifts.

In both experiments there was a shift towards the preferences of the virtual character in the anatomical condition, but a shift away from the virtual character's preferences in the spatial condition. In Experiment 1, for the high movements, the shift *away* from the virtual characters choices was larger in the spatial condition (-4.79%) compared to the shift *towards* the virtual characters choices in the anatomical condition (+2.70%). Similarly, for the neurotypical participants in Experiment 2, the shift away from the virtual character's preferences in spatial condition (-2.89%) was larger than the shift towards virtual character's preferences in the anatomical condition (+1.75%).

It is unclear why the tendency to copy the movement of the virtual character was stronger in the spatial condition, when disagreeing with her choice, compared to the anatomical condition, where copying her movement meant agreeing with her choice. If imitative tendencies are linked to affiliation (Lakin & Chartrand, 2003; Cheng & Chartrand, 2003), then one would expect the opposite pattern – with more copying of the movement in the anatomical condition (when agreeing with her choice) compared to the spatial conditions. Future studies which manipulate the affiliative motives of the participant will be needed to test this possibility.

Modulating imitation through actor kinematics

Experiment 1 showed that participants made the same movement as the virtual character if she pointed with a high, but not a low, trajectory. Thus, participants' propensity to imitate the virtual character was modulated by the kinematics of her pointing movement. This is in line with Wang and Hamilton's (2012) STORM model of mimicry, which predicted that all mimicry is subject to top-down modulation by a range of social cues (Wang & Hamilton, 2012). Our data shows that high or exaggerated movement trajectories, which have a communicative function (Cleret de Langavant et al., 2011; Peeters et al., 2013), appear to modulate imitative tendencies in a similar way to other social cues, such as eye-gaze (Forbes et al., 2017; Y. Wang et al., 2011), social priming (Cook & Bird, 2012) and emotional facial expressions (Grecucci et al., 2013). This is supported neuroimaging studies which show that high movement trajectories preferentially activate the brain's mentalising system, such as medial prefrontal cortex (Marsh, Mullett, Ropar, & Hamilton, 2014). This same region has been implicated in controlling the social modulation of mimicry by direct gaze (Wang, Ramsey, & Hamilton, 2011). Thus, high movement trajectories may modulate imitative tendencies via the same neurocognitive mechanism as other social cues, such as direct gaze. Future neuroimaging studies are needed to confirm this. Whilst the current study manipulated the height of the pointing movement, other kinematics features of pointing movements could modulate imitation in a similar way. For example, Patel et al. (2012) showed that when participants observed another agent make a movement more quickly then they rated their decision as more confident. Thus, future work should explore whether pointing movements with certain velocities are more readily imitated.

Imitation and autism

Experiment 2 had two hypotheses concerning the imitation behaviour of autistic participants. Firstly, previous work has suggested that autistic participants are more goal-focused during imitation (Marsh et al., 2013; Wild et al., 2012). We predicted therefore that there would be comparable shifts in preferences (or lack thereof) in both the anatomical and spatial conditions for autistic participants. Unlike the neurotypical participants, autistic participants did not display a significant effect of configuration. However, there were no significant differences in imitation behaviour between the groups (i.e. no significant configuration x group interaction). Thus, when given a choice of goals, we found no evidence for increased goal-directed imitation in autism. Secondly, we predicted that autistic participants would not change their imitation behaviour based on the height of the virtual character's pointing movement, as was found in Experiment 1. As, according to STORM, the modulation of imitative tendencies is different in autism (Wang and Hamilton, 2012). Again, we found no evidence to support this prediction, even when including copresence as a covariate in our post-hoc analysis. Thus, the implications of our findings for theories of imitation in autism remain equivocal. It is important to note, however, that most studies which have found differences in the social modulation of imitation and mimicry in autism have used reaction times measures of mimicry (Cook & Bird, 2012; Forbes et al., 2017; Grecucci et al., 2013). It has recently been demonstrated that different measures of imitation and mimicry are poorly related to one another (Genschow et al., 2017). So, when detecting differences in mimicry and imitation in autistic samples, the type of mimicry measure used may be critical.

One unexpected finding from Experiment 2 was that autistic participants were less consistent in their choices between the private and social setting. Neurotypical participants stuck with their choices from the private setting on 78% (Experiment 1) and

77% (Experiment 2) of trials in the social setting. Autistic participants stuck with their choices on 59% of trials and the analysis revealed that this reduced consistency could not be explained by the greater interest in art in the neurotypical group (as indexed by the number of gallery visits in the past 12 months). The finding that autistic participants changed their choices more from the private to the social setting seems at odds with one of the core features of autism - restricted and repetitive behaviours (American Psychiatric Association, 2013). Although an insistence on sameness has been widely reported in autistic individuals (American Psychiatric Association, 2013), the lack of consistency in the choices of autistic participants in our task may be due to differences in executive functioning and attentional processing (Happé, Booth, Charlton, & Hughes, 2006). Moreover, increasing evidence suggests that differences in experimental and neuropsychological measures of cognitive flexibility are poorly related to everyday restricted and repetitive behaviours (Geurts, Corbett, & Solomon, 2009; Teunisse et al., 2012).

Future directions

Although participants changed some of their choices from the private to the social setting, it is not clear whether this resulted in an actual shift in their art preferences. For example, if participants chose picture A in the private setting but then chose picture B in the social setting, did they actually prefer picture B? Or, alternatively, was this simply a transient change in choice driven by the observation of the virtual character's movements? For example, participants change their ratings of music when exposed to the opinions of others (Campbell-Meiklejohn et al., 2010) and Izuma and Adolphs (2013) found that participants preferences for t-shirt designs remained influenced by the opinions of others even after 4 months. Yet, Huang, Kendrick and Yu (2014) found that people's ratings of facial attractiveness were influenced by the ratings of others for up to three days but not longer than seven days.

Thus, future work using the current paradigm will need to establish whether any changes in participants' choices persist or are transient.

Participants changed their choice on approximately one in every four or five picture pairs and when participants did change their choices they were influenced by the virtual character's movements. However, the choices participants made in the current study did not have any significant consequences. Copying the movements of others has been shown to override strong financial incentives to avoid imitation during competitive games (Belot et al., 2013; Naber et al., 2013). So, had participants been incentivised to be consistent in their choices between the private and social setting, would the influence of virtual character's movements have had comparable effects on their choices? This remains to be tested in future studies.

Conclusion

Theories of imitation have stressed that we prioritise copying the goals of observed actions (Bekkering et al., 2000; Wohlschläger et al., 2003) and that social influences are driven by our observation of others' choices (Campbell-Meiklejohn et al., 2010). However, most experiments which have tested these theories have failed to include conditions in which participants have a choice of goal. Across two experiments we showed that when participants were given a choice of goal, they tended to imitate the topographical movement made by a virtual character rather than her choice.

In Experiment 1 we found that this tendency to copy the virtual character's movements was driven by the observation of the virtual character's high pointing movements, and we replicated this effect in Experiment 2 when we controlled for copresence. These findings support the STORM model by demonstrating that imitative tendencies are modulated by subtle social cues, such as the kinematics of an actor's

movements (Wang & Hamilton, 2012). More generally, we show that the way others move can influence what we choose.

Chapter 7 - Discussion

7.1 Summary of Experimental Chapters

The primary aim of this thesis was to explore whether mimicry is socially modulated and whether there are any differences in mimicry behaviour in autism. Using a range of mimicry methods, including reaction times measures, motion tracking and virtual reality, I found mixed support for STORM in both autistic and non-autistic participants. I briefly summarise each chapter before discussing the theoretical and methodological implications of the findings.

The experiment reported in Chapter 2 used a well-established stimulus response computability paradigm to demonstrate that direct gaze enhanced mimicry responses (i.e. automatic imitation) in non-autistic adults but did not do so in autistic participants. Instead, direct gaze enhanced all responses in autism rather than having a specifically social effect on mimicry. These findings support the STORM model which proposed that autistic people can and do mimic but do not modulate their mimicry in response to important social cues, such as gaze.

Chapter 3 aimed to move beyond traditional reaction times measures of mimicry and test the predictions of STORM in a more ecologically valid, virtual reality environment. Participants played an imitation game with a virtual character who was either socially engaged or socially disengaged whilst participants' hand movements were motion tracked. Both autistic and non-autistic participants mimicked the kinematics of the virtual character's movements, but autistic participants did so to a lesser extent. How socially engaged the avatar was did not modulate mimicry in either group. The experiment demonstrated the feasibility of using virtual reality to induce mimicry and explore mimicry differences in autism. However, the findings also

suggested that not all types of mimicry are socially modulated, challenging a key prediction arising from STORM.

Chapter 4 outlined two experiments in separate groups of (non-autistic) participants which investigated why mimicry was not socially modulated in Chapter 3. In the first experiment, video stimuli were used instead of virtual reality characters to test if the increased physical realism of the model would result in the social modulation of mimicry. However, mimicry responses were no different in the engaged and disengaged conditions. In the second experiment, the animacy of the model was manipulated so that participants interacted with either a moving ball or a virtual character. Again, this animacy manipulation has no effect and mimicry responses were comparable in both conditions.

In Chapter 5, I used the same paradigm as in Chapters 3 and 4 but manipulated the rationality of the model's movements rather than her social engagement. Participants mimicked the movements of the model even when these were rated as irrational. Moreover, participants coded the environment of the model into their own motor programs. For example, having observed the model move over an obstacle to reach a target, participants moved with a higher trajectory despite there being no obstacles in front of their own targets.

Finally, in Chapter 6, I explored whether people's tendency to mimic the movements of others could change the choices that participants had previously made in private. Across two experiments, I found that participants copied the movements made by the virtual character which resulted in a shift in people's preferences. Moreover, this tendency to mimic the movement of a virtual character was modulated by the kinematics of her pointing movements in line with the predictions of STORM. I first

deal with the theoretical implications of my findings before making methodological suggestions for how we can better study mimicry and related social behaviours.

7.2 Theoretical Implications

7.2.1 Not all mimicry is equal

This thesis aimed to test a key prediction arising from STORM: mimicry responses are socially modulated and this social modulation is different in autism. The results from Chapter 2 provided strong evidence for this prediction. In the presence of direct gaze, an important social cue, non-autistic participants showed an enhanced tendency to mimic. For the autistic participants, direct gaze had a general effect on all responses but did not specifically enhance mimicry. The result from Chapter 2 suggested that mimicry responses in autism are intact but that the social modulation of mimicry is absent in autism. These findings are in line with a several other studies which suggest that mimicry is not socially modulated in autism (Cook & Bird, 2012; Grecucci et al., 2013). Most of the studies in support of STORM have employed automatic imitation measures of mimicry. For example, Cook and Bird (2012) showed that neurotypical participants who had been prosocially primed showed enhanced mimicry responses compared to those who had not been prosocially primed. However, autistic participants did not show any differences in their mimicry responses following prosocial priming. Similarly, autistic children did not show enhanced mimicry responses following emotional facial expressions, unlike neurotypical children who showed larger congruency effects in the presence of emotional compared to neutral facial expressions (Grecucci et al., 2013).

Chapter 3 aimed to test STORM outside the constraints of a stimulus-response compatibility paradigm by measuring mimicry in a more ecologically valid, virtual environment. Automatic imitation studies have been criticised for being poorly related

to mimicry outside the lab (Cracco et al., 2018; Genschow et al., 2017). The task used in Chapter 3 was based on a paradigm devised by Wild and colleagues (Wild et al., 2010, 2012) which required participant to observe which targets the model pointed to and then point to the same targets in the same order on the table in front of them. The height of the model's trajectory between the targets was manipulated (i.e. high vs. low) and the extent to which participants copied the trajectory was taken as a measure of mimicry. Arguably, this type of mimicry is more akin to what happens in everyday social interactions. For example, we observe someone reach towards an object and then find ourselves mimicking the particular kinematics (or style) with which the agent moved towards that object. However, across three different experiments and nearly 100 participants (Chapter 3 and 4), I found no evidence that this type of mimicry is socially modulated. This was despite participants consistently mimicking the model across all experiments. This lack of social modulation raises the possibility that certain types of mimicry, such as the mimicry of a virtual character's movement trajectory, may be resistant to influence of social cues, such as eye gaze. If this is the case, why are certain types of mimicry more readily modulated by social cues?

The importance of timing

As highlighted in Chapter 3, the timing between the social cue and mimicry response might have accounted for the differences in social modulation between mimicry measures used in Chapter 2 and those used in Chapters 3 and 4. In Chapter 3 the delay between eye-gaze and then mimicry response was short, either 200 or 800 ms, and participants had to respond as soon as they saw the actor's hand move in the video. Similarly, Grecucci et al. (2013) found emotional facial expressions modulated automatic imitation in neurotypical but not autistic participants. Here, the facial expression was presented for 500 ms, participants then observed the moving hand for 1105 ms before making a response. Pan and Hamilton (2015; Experiment 2) asked

participants to tap a sequence of three drums having observed a virtual character or ball hit the same (congruent trials) or a different (incongruent trials) sequence. Congruency effects were enhanced for the virtual character compared to the ball but only for reaction times to tap the first, but not the last, drum in the sequence. This finding suggests that the social modulation of certain types of mimicry may be dependent on their being a short time period between the observation and performance of the action. In Chapters 3 and 4, however, there was a much longer delay between the social cue (i.e. whether the virtual character or actor looked at the participant) and the subsequent response. This long delay may have resulted in the social manipulation “wearing off” or diminishing. That is, participants realised they were not actually being observed and were just sitting in front of a projector screen. Such a timing explanation is supported by studies which have investigated the impact of artificial surveillance on social behaviours.

There has been a long debate over whether images of eyes (artificial surveillance) can impact social behaviours. For example, one study found that a poster containing eyes, as opposed to flowers, resulted in less littering in a university cafeteria (Ernest-Jones, Nettle, & Bateson, 2011). However, multiple laboratory and field studies have yielded mixed results for this so called “eyes effect” (Fathi, Bateson, & Nettle, 2014; Northover, Pedersen, Cohen, & Andrews, 2017). It has been suggested that the impact of eye images, rather than real eyes, is dependent on the length of exposure to the eyes (Sparks & Barclay, 2013). Sparks and Barclay (2013) found that brief exposure to artificial eyes resulted in increased sharing in the dictator game but this was not the case in a no eyes condition or when there was longer exposure to the eyes. Additionally, in a meta-analysis, Sparks and Barclay found that studies which showed increases in generosity involved a short exposure to artificial eye stimuli. This suggests, that under shorter time frames, images (and presumably videos) of eyes provoke an automatic and involuntary response which can impact behaviour, including sharing and mimicry

(Burnham & Hare, 2007). However, the effect of these eye stimuli may diminish over longer periods. To test this prediction future studies should systematically manipulate the time between the social cue and the mimicry response. The effect of social cues on mimicry should diminish as the gap between the social cue and response increases.

Another approach is to use the pointing paradigm used in Chapters 3 and 4 but use live human models. Here, participants would know they are being watched throughout the response period so the impact of the social manipulation should not diminish over time (Hamilton & Lind, 2016). For example, Vivanti and Dissanayake (2014) found increased imitation when a real world model gave children eye-contact compared to when they looked away. Moreover, Krishnan-Barman and Hamilton (in prep) have showed that participants copy the trajectory of their interaction partner with greater fidelity when they know are being watched compared to when their partner has their eyes closed.

This timing explanation for the impact of certain social cues on mimicry is also in line with the null effect of certain social cues on automatic imitation, such as animacy beliefs, status and power. For example, a recent meta-analysis found that animacy beliefs do not modulate automatic imitation (Cracco et al., 2018), and Farmer et al. (2016) conducted five experiments and concluded that power and status do not modulate automatic imitation. In these studies there is typically a long delay between the social manipulation and the subsequent response. This is consistent with the view that there needs to be a short time period between certain social cues and the response for automatic imitation to be socially modulated. In further support of this explanation, Butler, Ward and Ramsey (2016) compared the impact of emotional facial expressions, such as smiles and angry expressions, to trait based facial cues. Smiles resulted in greater automatic imitation of finger movements than angry or neutral faces, however, faces which signalled high or low agreeableness did not differentially impact automatic

imitation. Butler et al. concluded that only prosocial signals that indicate “in the moment” states impact automatic imitation. This could explain why cues such as some emotional facial expressions (Butler et al., 2016; Crescentini, Mengotti, Grecucci, & Rumiati, 2011; Rauchbauer et al., 2015) and eye gaze (Forbes, Wang, & Hamilton, 2017; Marsh, Bird, & Catmur, 2016; Wang, Newport, & Hamilton, 2011) have consistently modulated automatic imitations, whereas the findings from studies investigating other social modulators is more mixed (Cracco et al., 2018).

It is worth noting, however, that social priming has been shown to impact automatic imitation and in these studies the priming task usually takes place before a block of automatic imitation (Leighton et al., 2010; Wang & Hamilton, 2013). However, the mechanism by which social priming impacts mimicry may be different to other social cues. For example, Wang and Hamilton (Yin Wang & Hamilton, 2013a) suggested that prosocial primes “implicitly invoke one’s prosocial self-schema” whereas the impact of gaze is likely to operate via audience effects (Hamilton & Lind, 2016).

The importance of development

The associative sequence learning account (ASL) argues that mimicry develops by associating observed and executed motor actions to create sensorimotor contingencies (Heyes, 2011). During development we often observe and execute the same actions at the same time thereby developing imitative sensorimotor contingencies, for example, through self-observation of our own hands (Ray & Heyes, 2011) or parents often copy the facial expressions of their children (Jones, 2009), particularly their smiles (Messinger, Ruvolo, Ekas, & Fogel, 2010). These imitative sensorimotor contingencies are the basis of mimicry responses. ASL states that we learn about the consequences of imitative sensorimotor contingencies. For example, under certain

circumstances mimicry may result in a reward (e.g. food when interacting with a parent) whereas under other circumstances it may not. Thus, the likelihood and extent of mimicry may change depending on who we are interacting with. For example, 11 month old infants show facial mimicry towards linguistic in-groups but not linguistic out-groups (De Klerk, Bulgarelli, Hamilton, & Southgate, 2018). Thus, when considering how sensitive mimicry responses are to social cues, it is important to consider the environment in which a particular mimicry response developed.

To illustrate this point, I compare facial mimicry, which is likely to develop mainly within a social context, to the mimicry of movement trajectory, which, at least during infancy, is likely to develop mainly through self-observation. Farmer et al. (2018) have referred to the former as social sensorimotor contingencies and the latter as non-social sensorimotor contingencies. It is proposed that those mimicry responses which have developed through social sensorimotor contingencies are more readily socially modulated than those which develop via self-observation (Farmer et al., 2018). That is not to say that mimicry responses which develop primarily through self-observation are not socially modulated. For example, automatic imitation studies usually involve hand and finger movements, and, as outlined above, are susceptible to social modulation. However, due to the environment in which these mimicry responses develop it is likely that they are less susceptible to social modulation than other types of mimicry, such as facial mimicry.

Unless an infant has access to a mirror, they cannot look at their own face. Hence, facial mimicry is likely to develop largely within a social context (Farmer et al., 2018). There is conservable evidence that caregivers imitate infants' facial expressions (Jones, 2009) and social smiling may be particularly important for communication during development (Messinger et al., 2010). Given the social context within which facial mimicry develops it is unsurprising that facial mimicry is reliably socially

modulated. For example, adults are more likely to mimic the happy facial expressions of agents associated with positive (e.g. nice, likeable, kind) rather than negative (e.g. malicious, aggressive, deceitful) traits (Likowski, Mühlberger, Seibt, Pauli, & Weyers, 2008). Similarly, facial mimicry is enhanced in response to happy faces which have previously been associated with monetary rewards compared to those faces associated with monetary losses (Sims, Van Reekum, Johnstone, & Chakrabarti, 2012). Contextual information concerning a child's behaviour influences adults facial mimicry towards those children, for example, participants shown enhanced mimicry towards the angry facial expressions of children who behave negatively (Bos, Jap-Tjong, Spencer, & Hofman, 2016). Additionally, social cues, such as direct gaze (Rychlowska, Zinner, Musca, & Niedenthal, 2012) and in-group membership (Ardizzi et al., 2014) also enhance facial mimicry. Finally, that fact that facial expressions also carry an intrinsic meaning (e.g. smile = happy) means it is different to other types of mimicry. For example, a high movement trajectory is ambiguous in terms of its meaning whereas a parent copying her child's smile could signal "I am happy because you are happy" (Seibt, Mühlberger, Likowski, & Weyers, 2015). This intrinsic meaning associated with facial mimicry again makes it a much more likely candidate for social modulation compared to others types of mimicry. Thus, the rich social context within which facial mimicry develops (i.e. via social sensorimotor contingencies) ensures it is reliably socially modulated.

In contrast, mimicry responses to movement trajectories are more likely to develop through self-observation, for example, reaching for a toy or grasping a cup (Farmer et al., 2018). Ray and Heyes (Ray & Heyes, 2011) highlight how 4 month old infants spend up to 40% of their waking life looking at their own hands (White, Castle, & Held, 1964). Moreover, infants have a visual preference for hands so try and keep their moving hands within their visual field (van der Meer, 1997). For example, when

small forces are applied to an infants' wrists, they resist these forces to keep the arm moving normally but only when they can see the limb (van der Meer, van der Weel, & Lee, 1995). Finally, longitudinal studies show that reaching movements become smoother and straighter during the first year of life exposing infants to range of observed and executed kinematic profiles (Berthier & Keen, 2006).

The finding that certain types of mimicry are more readily socially modulated but others are not was recently demonstrated by de Klerk, Hamilton and Southgate (de Klerk et al., 2018). They found that gaze direction modulated facial mimicry in infants but did not modulate the mimicry of hand actions. This supports the prediction that those sensorimotor contingencies which develop largely within a social context are socially modulated whereas those which develop predominately through self-observation are less likely to be socially modulated. Whilst, most sensorimotor contingencies are likely to develop in similar contexts, some sensorimotor contingencies could develop within different contexts for different individuals. For example, a child who regularly eats their meals with a sibling is likely to develop strong sensorimotor contingencies between observing and performing mouth movements. This particular sensorimotor contingency may be less strong for a child how eats their meals alone. Exploring how experience modulates not only the development of mimicry responses (Heyes, 2018) but also the social modulation of these responses is an important aim for future work.

7.2.2 Is the social modulation of mimicry strategic?

If certain types of mimicry are socially modulated, is this social modulation strategic? STORM argues that mimicry is a Machiavellian tool which is implemented in a socially strategic manner to improve one's social standing; for example, to ensure people like us or to ensure a smooth interaction (Wang & Hamilton, 2012). Farmer et al.

(2018) argue that in order to show that mimicry has a particular function, it must be demonstrated that (1) mimicry causes an effect *and* that (2) mimicry is produced in order to cause that effect. Thus, to support STORM it must be demonstrated that (1) mimicry produces prosocial consequences and (2) it is deployed in situations in order to bring about those prosocial consequences. Farmer et al. argue that the key test is to demonstrate that mimicry is modulated by factors related to its function. As detailed above a range of social cues have been shown to modulate mimicry which would seem to lend support to STORM. For example, individuals scoring high in narcissism mimic individuals of high status more than those of low status (Ashton-James & Levordashka, 2013).

The ASL account, on the other hand, does not deny the role played by social cues in changing mimicry behaviour in different contexts but argues that these are the result of domain-general processes - input and output modulation (Heyes, 2011, 2017). Input modulation refers to changes in the processing of the action stimulus, for example, we may display increased attention towards an in-group member which means we mimic them more (De Klerk et al., 2018). Output modulation is the extent to which motor activation (and thus mimicry responses) is inhibited or enhanced. It has been suggested that the processes involved in the control of mimicry responses are related to social cognitive functioning, such as theory of mind and visual perspective taking (Heyes, 2011). For example, participants showed reduced automatic imitation when they were made to feel self-focused, either by observing their own body in a mirror or by making evaluative, self-referential judgments (Spengler, Brass, Kühn, & Schütz-Bosbach, 2010).

Heyes (2017) uses the example of group ostracism and its effect on mimicry to illustrate her domain general account. Infants, children and adults who are exposed to social exclusion tend to imitate or mimic more (De Klerk, Albiston, Bulgarelli,

Hamilton, & Southgate, 2018; Lakin, Chartrand, & Arkin, 2008; Over & Carpenter, 2009). Heyes (2017) argues that on the surface this finding seems to suggest that mimicry is a social strategy; when we feel socially excluded we mimic others more to strengthen social bonds with them and improve our social standing (Over & Carpenter, 2009; Yin Wang & Hamilton, 2012). Heyes (2017), however, states that social exclusion induces mild anxiety so that participants are more attentive to the movements of the model. This affects input modulation and thus results in more mimicry. Although a child may learn that mimicking others enhances social interactions, this does not mean mimicry evolved to function as a social strategy. Instead, Heyes argues that the prosocial consequences of mimicry develop through domain general associative processes. For example, Catmur and Heyes (2013) investigated whether it is the anatomical similarity of the movement between mimicker and mimickee (e.g. both touching their face) or the contingency between the movements (e.g. the mimicker's movements follow the mimickee's movements in a predictive manner) which accounts for the prosocial effects of mimicry. They found that the prosocial effects, such as increased enjoyment of the experiment, were mediated by contingency, rather than similarity, of the observed and executed movements. Thus, it is not mimicry *per se* which causes prosocial consequences but the predictability and temporal proximity of the movements between two interaction partners (see also Dignath, Lotze-Hermes, Farmer, & Pfister, 2018). Similarly, Marsh, Bird and Catmur (2016) have argued that the spatial component of automatic imitation is modulated by social cues, such as gaze and in-group membership, rather than its imitative component.

Thus, Heyes argues that mimicry develops and exerts its influence through domain general associative processes, whereas, STORM argues that mimicry is used strategically and rests upon specifically social processes (Wang & Hamilton, 2012). So how can we distinguish between these two accounts? Returning to the social exclusion

example, Heyes (2017) suggests that if the effect of increased mimicry is driven by anxiety we should expect to see similar effects with an asocial manipulation which induces similar anxiety (input modulation). Additionally, we should expect to see the effects of social exclusion impact other sensorimotor contingencies or overlearned responses, not just ones based on mimicry (output modulation). Yet, Heyes argues that “even with this result in hand, we should not jump to conclusions about how these processes became specialised” (Heyes, 2017; p. 6). Heyes states that during development we learn that copying others is often rewarding and promotes social interactions so may implement this when anxious or trying to influence others (Grusec & Abramovitch, 1982; Hsu, Sims, & Chakrabarti, 2018; Sims et al., 2012; Thelen, Miller, Fehrenbach, & Frautschi, 1980).

So, the ASL and STORM accounts can be, at least partially, reconciled if we separate the development or origin of mimicry from its function (Farmer et al., 2018). The view that mimicry develops through imitative sensorimotor contingencies via general associative mechanisms is compatible with the view that mimicry is deployed strategically in different social situations. As many mimicry behaviours develop in social interactions, children learn about the positive consequences of mimicry. Learning about the positive consequences of mimicry could develop via domain-general processes. However, this domain-general development of mimicry is consistent with the strategic deployment of mimicry in different social situations. A remaining point of contention between ASL and STORM, however, is the role of learning in the modulation of mimicry. ASL argues that the strategic deployment of mimicry is always result of learning, whereas, STORM argues that this can sometimes occur implicitly without learning. Carefully designed experiments are needed to resolve this controversy.

7.2.3 Multiple sources of mimicry differences in autism

STORM predicted that the social modulation of mimicry should be different in autism but the basic mechanisms responsible for mimicry are intact. I propose that there are two sources which can contribute to mimicry differences in autism: firstly, a reduced opportunity to establish sensorimotor contingencies during development, particularly those which develop through social interactions (Heyes, 2011); and, secondly, differences in autistic individuals' use of and response to mimicry (Wang & Hamilton, 2012). I deal with each in turn and emphasise the importance of distinguishing between mimicry responses which develop via social sensorimotor contingencies and those which develop through non-social sensorimotor contingencies (Farmer et al., 2018).

Reduced opportunities to develop sensorimotor contingencies

Ray and Heyes (2011) proposed their “wealth of stimulus” argument which states that “an infant’s interaction with the world, and especially with other agents, is the engine that drives cognitive development for imitation” (Ray & Heyes, 2011). There is considerable evidence to suggest that young infants later diagnosed with autism show differences in their interactions with others which may result in reduced opportunities to develop sensorimotor contingencies (for a review, see Jones, Gliga, Bedford, Charman, & Johnson, 2014). For example, within the first year of life these infants show less attention to faces and altered gaze towards them (Chawarska, Macari, & Shic, 2013; Ozonoff et al., 2010), display reduced instances of social smiling (Ozonoff et al., 2010) and use a smaller variety of gestures (Talbot, Nelson, & Tager-Flusberg, 2015). These differences in their interaction with other agents may limit the development of certain social sensorimotor contingencies, such as those responsible for facial mimicry. Studies also suggest differences in motor behaviour in infants later diagnosed with autism,

including limited motor control (Bryson et al., 2007) and lower activity levels (Zwaigenbaum et al., 2005). These differences in motor behaviour may also compromise the development of some non-social sensorimotor contingencies which develop through self-observation (Cook, Blakemore, & Press, 2013).

However, differences in motor behaviour in autism are common but not universal (Ansuini, Podda, Battaglia, Veneselli, & Becchio, 2018; Green et al., 2002), and, whether infants later diagnosed with autism show differences in the self-observation of their own limb movements remains to be systematically explored. Thus, although some sensorimotor contingencies may be slower or less likely to develop in autism, particularly those which develop through interactions with others, the basic mechanisms responsible for mimicry are intact in autism (Southgate & Hamilton, 2008). That is, the ability to form associations between contingent visual and motor representations is not affected in autism. This would help to explain the mixed results seen for studies investigating mimicry responses and motor resonance in autism - the extent to which our own motor systems are activated by the observation of other's actions. For example, Becchio and Castiello (2012) highlighted how autistic participants show intact automatic imitation responses (Bird et al., 2007; Forbes et al., 2017), motor interference to continuous incongruent arms movements (Gowen et al., 2008), and also similar neural responses to observed actions, such as mu wave suppression (Fan, Decety, Yang, Liu, & Cheng, 2010; Raymaekers, Wiersema, & Roeyers, 2009). Moreover, in Chapter 3 I showed that autistic participants mimicked the movement trajectory of a model even if this was reduced compared to neurotypical participants, and, in Chapter 6, I did not find any significant mimicry differences in autistic participants' responses to the pointing movements of an avatar.

Yet, for those sensorimotor contingencies which develop primarily through social interactions, such as facial mimicry, we would expect to see consistent

differences in autism. Indeed, there is strong evidence for differences in facial mimicry in autistic children and adolescence (McIntosh et al., 2006; Oberman, Winkielman, & Ramachandran, 2009; Rozga, King, Vuduc, & Robins, 2013), autistic adults (Mathersul, McDonald, & Rushby, 2013; Yoshimura et al., 2015) and non-clinical populations measuring high in autistic traits (Hermans et al., 2009; Neufeld, Ioannou, Korb, Schilbach, & Chakrabarti, 2016). An aim for future developmental work is to establish which sensorimotor contingencies develop largely through social interactions and those which do not. This will help to predict mimicry differences in autism. In terms of practical implications, activities which provide opportunities for the development of social sensorimotor contingencies, such as sport, dance and theatre, may be useful in overcoming differences in imitative behaviours in autism including mimicry (Koch, Mehl, Sobanski, Sieber, & Fuchs, 2015; Koehne, Behrends, Fairhurst, & Dziobek, 2016).

Differences in using and responding to mimicry

There is considerable evidence to suggest that autistic people show differences in their responses to and use of a range of social cues, such as gaze (Senju & Johnson, 2009), facial expression (McIntosh et al., 2006), gestures (Watson, Crais, Baranek, Dykstra, & Wilson, 2013), audience effects (Hamilton & Lind, 2016) and many others (Chevallier et al., 2012). STORM argues that these differences in the processing of social cues results in the altered top-down modulation of mimicry in autism. Or, in terms of ASL, one would predict differences in terms of input modulation, whereby social cues do not cause the same changes in the processing of the action stimulus. For example, autistic individuals may not display increased attention towards the actions of someone giving them eye-contact (Vivanti & Dissanayake, 2014). Research from automatic imitation studies have largely supported STORM, for example, Chapter 2 showed that eye-gaze does not socially modulate mimicry in autism, and similar effects

have been shown for emotional facial expressions (Grecucci et al., 2013) and pro-social priming (Cook & Bird, 2012). The next step will be to see whether these differences in the social modulation of mimicry in autism generalise to more naturalistic mimicry paradigms (see Methodological Implications below).

A further question is the extent to which autistic individuals are sensitive to relationship between rewards and mimicry (Kühn et al., 2010). Neuroimaging suggests that mimicry can result in activation in areas involved in processing reward, such as ventral striatum and orbitofrontal cortex (Hsu et al., 2018). Thus, one possibility is that some autistic individuals find mimicry less rewarding, as they do other types of social stimuli, such as smiling faces (Dubey, Ropar, & Hamilton, 2017). Furthermore, people tend to mimic agents more if they have been associated with rewards. For example, Sims et al. (2012) found that happy faces associated with high rewards resulted in greater facial mimicry than those associated with low rewards. This effect was related to autistic traits - participants high in autistic traits were less likely to show heightened mimicry responses to the faces associated with high rewards. Similar effects were shown for the mimicry of human, but not robot, hand movements (Haffey, Press, O'Connell, & Chakrabarti, 2013). In terms of the development of mimicry, this suggests that autistic people may be less likely to mimic agents which have been associated with rewards. For example, autistic children may be less likely to show enhanced mimicry towards a parent (e.g. who provides food) compared to a stranger. This question remains to be systematically explored in naturalistic settings (Haffey et al., 2013; Sims et al., 2012).

A final source of potential mimicry differences is how autistic individuals respond to being copied by others. Several studies have investigated the effect of autistic children being imitated by a parent or an experimenter and have found this has positive effects on social behaviours (Contaldo, Colombi, Narzisi, & Muratori, 2016).

For example, autistic children who are imitated show increased social attention towards the imitator (Nadel, 2002) including more eye gaze (Contaldo et al., 2016; Dawson & Galpert, 1990). Improvements in social responsiveness, such as increased smiling, verbalising and gesture, have also been reported following imitation in autistic children (Escalona, Field, Nadel, & Lundy, 2002; Katagiri, Inada, & Kamio, 2010). Moreover, therapeutic interventions based on imitation, such as reciprocal imitation training, have found improvements in social behaviours in autistic children (Ingersoll, 2010; Ingersoll, Walton, Carlsen, & Hamlin, 2013).

In many of these studies the control condition involves the child's interaction partner behaving contingently rather than imitatively. Sanefuji and Ohgami (2011) found that the positive social effects of imitation were dependent on mothers responding imitatively, rather than just contingently, towards their child. However, this was not the case for neurotypical children who responded the same in both the imitative and contingent conditions (Sanefuji and Ohgami, 2011). Thus, the finding that contingency alone, regardless of movement similarity, brings about the positive effects of copying behaviours may be specific to neurotypical development (Catmur & Heyes, 2013; Dignath et al., 2018). Contaldo et al. (2016) suggest that differences in predictive abilities in autism may mean that contingency, in the absence of movement similarity, is not enough to bring about the positive social effects of being copied (Palmer et al., 2017; Pellicano & Burr, 2012). A limitation of these studies is that they involve explicit imitation often by the child's parent. So the child is likely to be aware of the copying behaviour. What remains unclear therefore is whether autistic individuals benefit from the social effects of being mimicked by unfamiliar interactions partners even when this mimicry is not consciously detected. For example, do autistic individuals like interaction partners more if they mimic them? If so, do the prosocial effects of mimicry extend beyond the immediate interaction, such as increased helping behaviour (R. B.

van Baaren et al., 2003)? Finally, if there are differences in autistic individuals' responses to mimicry, are these related to their social abilities or more domain-general processes involved in prediction? These are all exciting questions for future research.

7.2.4 Summary

The primary aim of this thesis was to explore whether mimicry is socially modulated and whether there are any differences in mimicry behaviour in autism. The results from this thesis provided mixed support for STORM. Chapter 2 showed that mimicry is socially modulated in non-autistic participants but that this social modulation is absent in autism. The results presented in Chapter 3 and 4 were not consistent with STORM as the model's level of social engagement did not affect participants' mimicry responses. This inconsistency may be due to the timing between the social cue and the mimicry response. In the automatic imitation paradigm employed in Chapter 2 the timing between the social cue and the mimicry response was short, whereas, this period was much longer in Chapters 3 and 4. This may have diminished the impact of the social cues on mimicry. Future studies, which systematically manipulate the timing between the social cue and the mimicry response, are needed to test this interpretation. Moreover, studies involving live human actors using the pointing paradigm employed in Chapters 3 and 4 are likely to bring about social modulation as participants will be aware that they are being watched (e.g. Krishnan-Barman & Hamilton, in prep).

I also stress the need to distinguish between different types of mimicry, specifically those responses which develop via social interaction and those which develop through self-observation. For example, as facial mimicry develops also exclusively within a social setting one would expect this type of mimicry to be more readily socially modulated than those mimicry responses which are based on sensorimotor contingencies which have developed via self-observation. In terms of

theories of mimicry, the assumptions of STORM and of ASL are to some extent compatible. As the view that mimicry develops through imitative sensorimotor contingencies via general associative mechanisms is compatible with the view that mimicry may be deployed strategically in different social situations (Farmer et al., 2018). However, establishing whether the strategic modulation of mimicry can occur without learning will need to be tested in future experiments.

Finally, I propose that there are multiple sources of mimicry differences in autism. Firstly, although autistic people are able to form sensorimotor contingencies there may be some reduced opportunities to do so, particularly those which develop through social interactions, such as facial mimicry. Secondly, as proposed by STORM, autistic adults show differences in their responses to social cues, which may impact the modulation of mimicry. Findings from automatic imitation studies (e.g. Chapter 2) have supported STORM, however, whether these findings generalise to more naturalistic mimicry paradigms is an important question for future work. Thirdly, autistic people may be less sensitive to the relationship between mimicry and reward. Finally, developmental studies suggest that autistic children respond well to being explicitly imitated by their caregivers. However, whether autistic adults reap the prosocial benefits from mimicry has been relatively unexplored. Next, I consider methodological implications - how can we better measure and modulate mimicry?

7.3 Methodological Implications

One of the aims of this thesis was to try and investigate mimicry using novel methods with a particular focus on virtual reality. In the following section, I make some suggestions for how the field can better study mimicry. First, I emphasise the need to move away reaction time measures of mimicry and suggest alternative ways of studying

mimicry. Next, I argue that mimicry should be investigated in richer and more complex virtual paradigms.

7.3.1 Beyond automatic imitation

Heyes (2011) argued that reaction time measures of mimicry, such as automatic imitation, are related to mimicry “in the wild” as they share three characteristics. Firstly, automatic imitation is, to some extent (Marsh et al., 2016), based on a topographical matching between the observed and executed movement, rather than just spatial matching. Secondly, automatic imitation is independent of intention and attentional resources, and, finally, it is modulated by social cues in a similar manner to naturalistic mimicry. Heyes (2011) argued that the relationship between automatic imitation and mimicry “in the wild” is analogous to the relationship between reading aloud and silent reading. In the following section I question this analogy and hence the validity of automatic imitation as a measure of mimicry (Ramsey, 2018).

For nearly two decades (Brass et al., 2000; Stürmer et al., 2000) a vast number of studies, including the study reported in Chapter 2, have employed automatic imitation paradigms (Cracco et al., 2018). However, the validity of these automatic imitation measures has recently been questioned (Genschow et al., 2017; Ramsey, 2018). Firstly, Cracco et al.’s (2018) meta-analysis highlighted the inconsistency with which automatic imitation is modulated by social cues. For example, they found no consistent evidence for enhanced automatic imitation when participants believed the stimuli was human compared to nonhuman. Yet, when the participant’s gender matched that of the model (e.g. both the participant and the hand stimuli were male) larger automatic imitation effects were observed compared to when there was a discrepancy between the model’s gender and that of the participant. This highlights how certain social cues such as the similarity between the model and imitator enhance automatic

imitation, whilst, other factors, such as beliefs about animacy, have a less reliable impact on automatic imitation. This mirrors the studies described above which showed that some social cues, such as gaze, modulate automatic imitation consistently (e.g. Chapter 2; Wang et al. 2011), whereas other social modulators, such as power and status do not (Farmer et al., 2016). This is at odds with a number of studies using naturalistic mimicry paradigms which have found consistent modulation of mimicry by power and/or status (Ashton-James & Levordashka, 2013; Cheng & Chartrand, 2003). A similar case can be made for the effect of social anxiety which has been shown to impact naturalistic mimicry (Abbott, Kocovski, & Obhi, 2018; Vrijssen et al., 2010) but does not seem to modulate automatic imitation (Abbott, 2018). These inconsistencies in the extent to which social cues modulate automatic imitation brings into question the extent to which it is comparable to more naturalistic mimicry measures. Furthermore, automatic imitation does not seem related to any measures of social functioning, such as empathy, narcissism or autistic traits (Butler, Ward, & Ramsey, 2015; Cracco et al., 2018), whereas, other more naturalistic measures of mimicry are affected by these measures of social functioning (Genschow, Klomfar, Haene, & Brass, 2018).

Secondly, Marsh et al. (2016) have also argued that social modulators affect the spatial, not imitative, components of automatic imitation. Marsh et al. found that group membership and direct gaze modulated spatial compatibility but not imitative compatibility. Thus, they argued that social modulators of automatic imitation do not have a specific effect on imitation but rather operate via ‘domain general’ mechanisms, such as increased attention and response inhibition. So, the effect of these modulators is not imitation-specific but rather affect the extent to which any automatically cued behaviour is expressed (Marsh et al., 2016).

This proposal was recently supported by a neuroimaging study. Darda et al. (2018) found that the control of automatic imitation was supported by a domain-general

neural network, rather than brains areas specifically involved in social cognition (Brass et al., 2009). The domain-general regions controlling imitation were the same as those involved during a verbal working memory task (Duncan, 2010; Fedorenko, Duncan, & Kanwisher, 2013), rather than those involved during mentalising tasks, such as mPFC and TPJ (Van Overwalle & Baetens, 2009). Thus, Darda et al. concluded that the cognitive and neural mechanisms involved in controlling imitation during automatic imitation are not specifically related to social cognition.

Given these findings, Ramsey (2018) has questioned the validity of automatic imitation. Specifically, Ramsey assessed the construct, convergent and divergent validity of automatic imitation. Construct validity refers to the extent to which a measure measures what it claims to be measuring. Only one study has investigated the relationship between automatic imitation and naturalistic mimicry and found that these are not related (Genschow et al., 2017). Convergent validity refers to the extent to which measures which are theoretically related are actually related. It has been proposed that mimicry is related to social functioning and social processes generally (Chartrand & Lakin, 2013). However, there is no clear evidence that automatic imitation is related to social functioning (Butler et al., 2015; Cracco et al., 2018). Finally, divergent validity is the extent to which measures which are supposed to be unrelated to each other are unrelated. Ramsey argues that if automatic imitation measures the control of imitative responses then these should (to some extent) be distinct from those involved in the control of non-imitative and non-social processes. For example, studies which have aimed to separate the spatial from the imitative components of automatic imitation have shown that these are distinct, but the imitative component is approximately 3-4 times smaller than the spatial component (Marsh et al., 2016). Yet, the finding that social cues may impact the spatial rather than imitative component of automatic imitation (Marsh et al., 2016) makes this divergent validity hard to interpret (Ramsey, 2018).

In sum, Heyes (2011) has argued that the relationship between automatic imitation and mimicry “in the wild” is analogous to the relationship between reading aloud and silent reading. However, the evidence to support this analogy is unconvincing. Children who are better at silent reading tend to be better at reading aloud (Hale et al., 2011): there is no evidence that automatic imitation and naturalistic mimicry are related or related to the same social processes (Genschow et al., 2017). Factors which affect silent reading (e.g. text size, environmental distractions) are likely to have a similar impact on reading aloud: despite some rare exceptions (e.g. gaze), there is no consistent evidence to suggest that the same factors which modulate naturalistic mimicry also impact automatic imitation in the same way (Cracco et al., 2018). Thus, I feel the field should move beyond automatic imitation and study mimicry in richer and more complex, social environments. This is what I turn to in the next section.

7.3.2 Towards better virtual mimicry

The thesis aimed to create virtual mimicry paradigms which were both ecologically valid but also had a high level of experimental control. The results of this thesis have highlighted both the strengths and current limits of virtual reality when investigating social behaviours, such as mimicry. Chapters 3 and 6 both used virtual characters and managed to induce mimicry in participants. However, the studies presented in Chapter 4 and 5 showed that comparable mimicry effects could be induced using videos of human models or animations of a moving ball. If similar mimicry effects can be induced using these standard methods, why bother using virtual reality to study mimicry (Pan & Hamilton, 2018)? In this next section, I argue that virtual reality is a useful tool to study mimicry but only if a sense of immersion and interactivity is achieved between the participant and virtual character. I argue that this can be done by maximising the place illusion and plausibility illusion, respectively (Slater, 2009).

The place illusion ('presence') refers to the "feeling of being there" in the virtual environment, similarly, 'co-presence' refers to the extent of being there with another agent in the virtual environment (Slater, 2009). Overall, the participants who took part in the studies in this thesis self-reported low levels of co-presence. Low co-presence did not compromise the induction of mimicry but may have nullified the impact of certain social cues on mimicry. For example, in Chapter 6 (Experiment 2) the modulation of participants' mimicry by the height of the virtual character's trajectory only occurred when co-presence was controlled for. Similarly, the impact of social cues, such as eye-gaze, are dependent on the participants reacting as if they are being watched (Hamilton & Lind, 2016). However, if the place illusion is not working, these social cues are unlikely to impact mimicry. So how can we maximise co-presence when studying mimicry? As the level of immersion increases, the place illusion and feelings of co-presence tend to increase (Pan & Slater, 2011). Future virtual mimicry paradigms should use more immersive platforms if they aim to socially modulate mimicry. Slater (2018) has argued that the perceptual world should perceptually surround the participants and their perception should be a function of (at least) heading tracking. The virtual paradigms used in this thesis did not perceptually surround the participants nor was participants' perception a function of head tracking. Additional factors which can increase immersion include higher resolution graphics, real time motion capture, wide field of view, auditory feedback, and many factors (Slater, 2018). Thus, future virtual mimicry studies should try to implement some of these changes to increase feelings of co-presence and the impact of social cues. Here, the use of Cave systems may be particularly useful (Slater, Guger, et al., 2006). Unlike HMDs, participants are still able to see and move their own body when interacting with virtual characters. Moreover, Cave systems can be used in combination with some neuroimaging techniques, such as

functional near-infrared spectroscopy, which will allow the neural mechanisms responsible for mimicry to be investigated (Pinti et al., 2015).

The plausibility illusion is the extent to which participants believe that what is happening to them in the virtual environment is really happening, despite knowing explicitly that it is not happening (Slater, 2009). In terms of creating better virtual mimicry paradigms, one way to maximise the plausibility illusion is to create a greater sense of interactivity between the participant and the virtual character. The paradigms used in this thesis created a limited sense of interactivity. For example, in Chapter 6 the participants took turns to make choices with a virtual character about which art pictures they preferred and in Chapter 3 the engaged virtual character tried to give participants an illusion of eye-contact by orientating her head direction to that of the virtual character. However, for the most part, participants were sat in silence opposite a virtual character taking turns to make simple hand movements. To increase the plausibility illusion, the social interaction needs to be a better proxy of a real life social interactions. Although many studies have programmed virtual characters to mimic (or not mimic) participants, very few have tried to induce and then modulate mimicry in participants. To do this, virtual environments should be created in the sorts of contexts in which mimicry has been reported to take place “in the wild”, such as in restaurants (R. B. van Baaren et al., 2003), classrooms (LaFrance & Broadbent, 1976) and during business meetings (Maddux et al., 2008). This is what was attempted in Chapter 6 where mimicry was embedded within a virtual art gallery.

Moreover, interpersonal behaviours, including mimicry, change as our relationships with others develop (Ramseyer & Tschacher, 2014; Zajonc, Adelman, Murphy, & Niedenthal, 1987). Thus, virtual reality can be used to see how mimicry develops overtime between two individuals, such as a virtual therapist and patient or virtual teacher and student. Having participants establish these longer-term relationships

with virtual characters will hopefully result in increases in the plausibility illusion and may increase the chances of inducing and modulating mimicry. This may be particularly important if we aim to study the impact of social modulators which develop over longer periods (e.g. trust, friendship) and has clear implications for social robotics (Pennisi et al., 2016).

In sum, when studying mimicry, virtual reality has the potential to create ecologically valid social interactions with strong experimental control. I have argued that the place illusion and plausibility illusion should be maximised if we want virtual mimicry paradigms to offer something beyond the standard tools which have been used to study mimicry (e.g. video stimuli or the use of real life confederates). Maximising the place illusion can be achieved by creating more immersive virtual environments. Whilst maximising the plausibility illusion is dependent on the creation of interactive virtual characters in realistic social environments. Maximising these two illusions is not only a technical challenge but is also dependent on a better understanding of real life social interactions. This knowledge will allow us to create better virtual characters and more ecologically valid social environments.

7.4. Conclusion

This thesis investigated whether the mimicry is socially modulated and whether there are any differences in this social modulation in autism as predicted by STORM. Using a range of methods, I found mixed support for STORM. A study using a reaction time measure of mimicry suggested that mimicry responses are socially modulated by eye-gaze in neurotypical participants but that this social modulation may be absent in autism. Using virtual reality, I showed that certain types of mimicry may not be socially modulated, although autistic participants may mimic virtual characters to a lesser extent than neurotypical participants. In addition, I explored the impact of action rationality on

mimicry and found that participants mimicked the trajectory of a model even if this was rated as irrational. Finally, I found that people's tendency to mimic the movements of a virtual character could change the choices they had previously made in private. Overall, the results suggest that virtual reality can be used to induce and potentially modulate mimicry but highlight the need to ensure a sense of immersion and interactivity between the virtual character and participant.

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