Self-other processes in social cognition

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Self-Other Processes in Social Cognition

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

Abstract

This thesis aimed to investigate self-other processes in social cognition. Contrary to the traditional approach of focusing on self-other processes within the confines of a single domain, this thesis highlights the prominent role of these processes across different socio-cognitive domains. Three main empirical questions form the basis of the research reported here. The first is concerned with the extent to which self-other representations are shared across three different socio-cognitive abilities: the control of imitation, theory of mind, and visual perspective taking. The second relates to the neural underpinnings of self-other representations, in particular, the role of the temporoparietal junction (TPJ) during socio-cognitive processing. The third question examines the role of culture as a modulatory factor of self-other processes.

The findings from Experiment 1, 3 and 4 showed a relationship between the control of imitation and visual perspective taking. This relationship seems to rely on the online control of co-activated self-other representations, which at the neural level are mediated by the TPJ (bilaterally).

In Experiment 2 it was found that individuals with mirror-touch synaesthesia are impaired in the control of imitation but their performance on visual perspective taking and theory of mind is comparable with non-synaesthetes. It is hypothesised that atypical self-other processes in mirror-touch synaesthesia might be confined to situations in which representations of the 'other' should be inhibited, but not when they should be enhanced.

Experiment 5 showed that acculturation strategies adopted by migrants modulate their imitative behaviour towards a member of the heritage vs. a member of the host culture.

The diverse nature of the studies reported in this thesis shows the complexity of self-other processes in social cognition. Taken together, these findings demonstrate how adopting a wider approach to the investigation of self-other processes contributes towards a better understanding of the mechanisms underlying socio-cognitive abilities.

Table of Contents

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Publications Arising from this Thesis

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Santiesteban, I., Shah, P., White, S., & Bird, G. Is the Director Task a Valid Theory of Mind Measure? Evidence from Autism and Photographs. (*Under Review)*

Santiesteban, I., Bartl, G., Bird, G. Automatic Imitation is Modulated by Acculturation Strategies: Evidence from Polish Migrants in the UK. (*submitted)*

Santiesteban, I., Banissy, M. J., Catmur, C., & Bird, G. Social Cognition and (bilateral) TPJ – A tDCS Study (in preparation)

Santiesteban, I., Banissy, M. J., Tew, O., & Bird, G. When Self-Other Representations Go Awry: The Case of Mirror-Touch Synaesthesia. (in preparation)

List of Figures

List of Tables

Chapter 1: Introduction

This Chapter provides an overview of the research that has motivated the investigation of self-other processes in social cognition and outlines the three main objectives of this thesis. These include 1) to investigate if there is a relationship between the different socio-cognitive domains of imitation/ imitation-inhibition, visual perspective taking and theory of mind; and whether such a relationship, should it exist, relies on common self-other processes, 2) to explore the role of the temporoparietal junction – previously identified as a key brain region in socio-cognitive processing – in social abilities that rely on self-other representations, and 3) to examine the influence of culture – specifically acculturation strategies and self-construal styles – in social cognition.

1.1 Mental Representations of Self and Others

The question of how humans form mental representations of themselves and other individuals has long intrigued theorists and empirical researchers alike. From a philosophical stance, in order to become aware of the physical integrity of the self, the presence of another human being is required. The knowledge acquired through observation of the *other* can then be applied to the image of the *self* (Gasparyan 2014). For psychologists, the concepts of self and other are intrinsically linked and evoked either implicitly or explicitly in all forms of psychosocial processes. Most recently, a proliferating body of research within the emerging field of social cognitive neuroscience is beginning to shed light on the neural mechanisms underpinning self-other representations.

From a developmental perspective, the empirical concern has been mostly on representations of the self and the emergence of self-awareness. Parting from the view that knowledge of the self originates from perception rather than mental representations, (Neisser 1991) identifies two aspects of self perception, the ecological self and the interpersonal self. The former concerns the relationship of the self with the environment whereas the latter derives from information produced by social interactions. At around 18-20 months infants show the ability for self-recognition, as shown by experiments using the mark test {Amsterdam 1972). In these experiments a rouge mark is surreptitiously placed on the infant's face before they are placed facing a mirror. They successfully pass the task if they touch the mark on their face rather than their mirror reflection.

What about mental representations of others? Evidence from developmental studies supports the philosophical view that before an individual becomes aware of the physical integrity of the self, the presence of another individual is required. For example, (Pipp, Fischer, & Jennings, 1987) found that before the age of 18 months, infants' knowledge of physical features of the mother precedes equivalent knowledge of the self. Similarly, (Herold & Akhtar, 2014) tested featural self knowledge of 2 ½ year olds and found that infants were better able to identify body parts of a doll, of similar size to them, than their own body parts.

Over the last few decades research interest in mental representations of the self and other have been encompassed under the broader category of social cognition. Social cognition refers to the individual's cognitive processes in relation to their social world. Two principal aspects characterise social cognition research: the investigation of the individual's mental processes, including encoding and storage of social information, and the examination of how the individual mind is influenced by social interaction (Marsh & Onof, 2008). Self-other representations are at the core of both aspects. However, because mental representations of self and others are intrinsically linked to specific socio-cognitive processes (e.g., attribution of mental states, adopting the visual perspective of another or imitating the behaviour of others), there is a paucity of research on the mechanisms involved in self-other representations across different socio-cognitive domains.

1.2 Self-Other Overlap and Self-Other Distinction

Self-other overlap refers to a situation in which an observer adopts a state similar to that of another person via activation of the observer's representation of what it is like to experience that state (Preston & Hofelich, 2012). At the neural level, the observation of another's state can activate neural regions in the observer that are also activated when the observer experiences the state himself. The discovery of a population of neurons in the prefrontal cortex (area F5) in monkeys (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti et al., 1996), which fire during both action observation and execution – known as mirror neurons – have inspired a vast amount of cognitive neuroscience research investigating the presence of equivalent mirror neuron regions in humans. Evidence of neural regions involved in both action observation and execution in the human brain has been previously reported (e.g., Catmur, Walsh, & Heyes, 2007; Fadiga, Fogassi, Pavasi, & Rizzolatti, 1995; Gazzola & Keysers, 2009; Iacoboni 1999b)). Although both the existence and specialized function of a mirror neuron system in humans have been challenged (see Heyes, 2010) for a review), some researchers consider mirror neuron studies in humans as evidence of self-other overlap, specifically in the socio-cognitive domains of imitation and empathy (e.g., Iacoboni 2009; Singer et al., 2004; Wicker et al., 2003). In the context of imitation, self-other overlap has also been referred to as a 'direct matching' between action observation and execution (Buccino, Binkofski, & Riggio, 2004; Jackson & Decety, 2004). In neuroimaging studies this translates as activation of the same neural regions during action execution (self representation) and observation of the same action performed by another individual (representations of the other). These regions include the inferior frontal gyrus (IFG) and the rostral inferior parietal lobule (IPL) (e.g., Hamilton & Grafton, 2008; Iacoboni & Dapretto, 2006), for a meta-analysis of extended mirror neuron areas involved in imitation see (Caspers, Zilles, Laird, & Eickhoff, 2010)).

In the context of empathy (an individual's ability to share the feelings of others, e.g., Eisenberg 2000; Wispé 1986), self-other overlap occurs when the observation of an individual's affective state activates neural regions in the observer that are also activated when the observer directly experiences the same affective state. For example, studies of empathy for pain show consistent activation of the anterior cingulate cortex (ACC) and the anterior insula (AI) when participants experience painful stimuli (or are asked to imagine painful situations) and observe others experiencing the same painful events (e.g., Jackson, Meltzoff, & Decety, 2005; Singer et al., 2004 – see also meta-analysis by Lamm, Decety, & Singer, 2011).

Although robust evidence from social cognitive neuroscience research supports the view of overlapping self-other representations in the context of imitation and empathy, the relationship between mental representations of the self and others is not that simple or straightforward. Real life social interactions are richer and involve more complex processes than a mere self-other overlap. Indeed, human beings do not tend to go about their daily lives continuously imitating or experiencing the emotional feelings of others. Therefore, a certain degree of self-other distinction (the process of separating representations of the self and of the other) is essential for successful social interactions. This requirement is evident, for example, during the control of imitation[1]. In order to inhibit the tendency to imitate an interaction partner, an individual must enhance self-representations (i.e. representations of their own motor intention) while suppressing representations of the motor intentions of the other. Similarly, in the context of empathy, an absolute self-other overlap could lead to feelings of personal distress in the observer, which in turn could prevent an appropriate response to the person in need. Therefore, regulatory processes involving self-other distinction are necessary to prevent confusion between the emotional states of the self and the other. This process of self-other distinction is considered critical within a functional model of empathy (Decety & Jackson, 2006). Many factors have been identified as modulators of empathic responses ranging from situational: the intensity of the displayed emotion (Avenanti, Minio-Paluello, Minio Paluello, Bufalari, & Aglioti, 2006; Saarela et al., 2007), dispositional: individual differences in behavioural trait measures (Singer et al.,

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[1] The terms control of imitation and imitation inhibition are used interchangeably throughout this thesis.

2004), motivational: perceived fairness (by the empathiser) of the person suffering pain (Singer et al., 2006). Studies of imitation have also identified a number of motivational factors that modulate the extent to which individuals imitate their interaction partner. For example, participants are more likely to imitate an interaction partner if they share a common goal and cooperation is required, but not when they are competing against each other (LaFrance, 1985). Also, narcissists are more likely to imitate their interaction partner, particularly if they are judged to have a superior social status (Ashton-James & Levordashka, 2013) - see also (Carr et al., 2013). Furthermore, a recent neuroimaging study has reported differential neural activation when participants imitate a member of their own racial group compared to imitating someone from a different race (Losin, Iacoboni, Martin, Cross, & Dapretto, 2012). Therefore, the evidence suggests that self-other distinction processes are required for both imitation and empathy.

Social psychologists and, more recently, social cognitive neuroscientists have paid considerable attention to another important social domain with relevance to representation of the self and other, that of cognitive perspective taking or theory of mind (Premack & Woodruff, 1978). Theory of mind is an umbrella term referring to the ability to attribute mental states to self and others. Some social psychologists contend that this ability requires merging of self and others (e.g., Davis, Conklin, Smith, & Luce, 1996), which in turn can enhance the quality of social interactions by reducing stereotype, in-group favouritism (Galinsky & Moskowitz, 2000) and prejudice (Galinsky & Ku, 2004). Furthermore, self-other overlap has also been associated with fostering social bonds (Galinsky, Ku, & Wang, 2005) and promoting prosocial behaviour (Batson 2014). At the neural level, a network of regions have been consistently found to activate during the attribution of mental states to both self and others, mostly comprising the medial prefrontal cortex (MPFC), the temporoparietal junction (TPJ), posterior cingulate cortex and precuneus (e.g., Adolphs 2003a, 2009; Blakemore, Winston, & Frith, 2004; Frith & Frith, 2003).

Similarly to imitation and empathy, self-other distinction is also required in theory of mind. Although some researchers believe that when adopting another person's perspective, individuals tend to use their own perspective as a starting point (self-other overlap), and then gradually adapt their views and make the necessary adjustments to accommodate differences between their own and other's perspectives (Epley, Keysar, Van Boven, & Gilovich, 2004). Failing to do so can result in egocentric bias (Apperly et al., 2010; Epley et al., 2004), significantly affecting the quality of interactions.

Developmental studies of theory of mind have shown that the ability to represent the mental states of others and keep them separate from those of the self appears to require sophisticated faculties. Most 3-year-olds assume that others see the world the way they do, whereas from 4-5 years of age, children have little difficulty in correctly attributing a false belief to others (Wellman, Cross, & Watson, 2001; Ziv & Frye, 2003). The apprehension that the way the world is represented in another's mind may be different to the situations in the real world and to representations held by the self (Perner 1991) appears to be functionally related to the development of inhibitory control (Carlson & Moses, 2001; Frye, Zelazo, & Palfai, 1995). Yet, although even young children are able to understand that the content of other minds can be different from that of their own, it is well documented in the theory of mind literature that typically developing adults do not always make use of this ability and often exhibit an egocentric bias by attributing their own mental states to others (e.g., Apperly et al., 2010; Birch & Bloom, 2004; Epley et al., 2004; Mitchell, Robinson, Isaacs, & Nye, 1996). This suggests that beyond the ability to master inhibitory control, successful social exchanges are also influenced by the degree of interaction between self and other representations.

In summary, the literature discussed thus far implies that both self-other overlap and self-other distinction processes are required across different socio-cognitive domains. In order to successfully navigate their social environment, individuals must regulate the extent to which mental representations of themselves and others are kept separate or allowed to interact, depending on situational, dispositional, or motivational demands. Usually social cognition researchers are interested in a particular domain (e.g., imitation, theory of mind, empathy or perspective taking) and tend to consider self-other processes within the confines of that domain. However, the fact that regulatory processes are needed to control the extent to which self-other representations overlap or are kept separate suggests that common, underlying mechanisms of self-other processes may be shared by different socio-cognitive abilities. Contrary to the traditional approach of focusing on self-other processes within the confinement of a single domain, the aim of this thesis is to highlight the prominent role of self-other processes across different socio-cognitive domains. It will do so by: 1) investigating self-other representations across different social abilities, this in turn is expected to shed light on the interrelatedness of these different domains, 2) exploring the role of the TPJ – a neural region consistently found to activate during self-other processes – across the social abilities under investigation, and 3) examine the role of culture as a potential modulatory factor of self-other processes. The remainder of this chapter will present some of the most relevant findings and theories relating to the objectives of this thesis.

1.3 Interrelatedness of Socio-Cognitive Abilities: From Imitation to Theory of Mind

Because researchers tend to focus on a specific area within their chosen field, sometimes it is easy to overlook how the specific domain under investigation relates to findings from another domain. This has certainly been the case with social cognition research. However, there have been a few attempts to address the issue of interrelatedness of socio-cognitive abilities, which have led to the development of two contrasting theoretical accounts, as discussed below. The research described in Chapter 2 aims to investigate the relationship between different socio-cognitive domains (imitation/ imitation-inhibition, visual perspective taking and theory of mind) by adopting two different approaches. The first attempts to directly test the two contrasting theories described below (Experiment 1) and the second compares performance of individuals with mirror-touch synaesthesia, who are thought to have impaired self-other representations, and non-synaesthete controls (Experiment 2) in the three social domains under investigation.

1.3.1 Two Contrasting Theoretical Approaches

The discovery of the mirror neuron system (MNS) has led many researchers to speculate that the MNS forms the basis of social cognition, from action understanding to attribution of mental and affective states to others (Gallese & Goldman, 1998; Gallese, Keysers, & Rizzolatti, 2004; Rizzolatti & Craighero, 2004). Under the MNS theory, the observation of an action triggers motor representations in the observer, enabling the reproduction of the observed action (imitation). This in turn results in the attribution of mental states to the other associated with performance of that action (theory of mind). Therefore, the MNS acts as a bridge between the self and others (Gallese et al., 2004). Advocates of the MNS theory refer to findings from studies of imitation and empathy as evidence in support of this view. For example, they often cite neuroimaging studies showing that the rostral IPL, IFG and the adjacent parts of the premotor cortex activate during both action observation and execution (Caspers et al., 2010; Iacoboni 1999a; Rizzolatti, Fogassi, & Gallese, 2001) and that consistent activations of the AI and ACC are observed when participants experience pain and when they observe another individual experiencing pain (e.g., Lamm et al., 2011). Supporters of the MNS theory also link the MNS to the simulation hypothesis of theory of mind (e.g., Gallese & Goldman, 1998). According to this hypothesis (e.g., Gordon 1986), individuals use the content of their own minds as a simulation of other minds to understand and make inferences about the mental states of others[1]. However, as the evidence

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[1] The simulation account differs from the theory-theory approach (Gopnik 1993; Gopnik & Wellman, 1992), which states that theory of mind abilities rely on a set of concepts (beliefs, intentions, desires) and central principles about how these concepts interact (e.g., people

discussed above suggests, there is more to social cognition abilities than self-other overlap, or simulation of our own mental representations to understand and predict others' behaviour. Furthermore, although the MNS theory is based on the assumption of a relationship between different social abilities – imitation, empathy and theory of mind – as yet, evidence from studies directly comparing such a range of socio-cognitive abilities within the same experimental setup is lacking. A notable exception is the work carried out by Brass and colleagues (e.g., Brass, Ruby, & Spengler, 2009; Spengler, von Cramon, & Brass, 2009; Spengler, Yves von Cramon, & Brass, 2010). However, rather than supporting the MNS hypothesis, findings from these studies offer an alternative account to the MNS theory as a potential explanation of the mechanisms underlying processes involved in imitation and mental state attribution.

Contrary to the MNS account, (Brass et al., 2009) suggest that processes mediating self-other distinction, rather than self-other overlap, play a key role in supporting socio-cognitive abilities like theory of mind. A crucial consequence of this approach is that theory of mind is related to the inhibition of imitation, rather than to imitation per se. When inhibiting the tendency to imitate the behaviour of another person, the observer must distinguish their own action

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behave in accordance with certain principles that meet their beliefs). Therefore, the main assumption of this account is that behaviour is derived from a causal 'theory' of the interaction processes that occurs between these concepts and principles, which combined with appropriate initial information about the other, are used to infer and predict their behaviour. The debate between theory-theory vs. simulation theory dominated theory of mind research for a long time and although initially they have been viewed as mutually exclusive, recently there has been a shift in the debate. Some researchers who have considered the strong points of each account have argued for a hybrid approach to understanding mental state attribution (Carruthers & Smith, 1996; Nichols & Stich, 2003). Whereas, others argue that it is time for social cognition research to move away from this debate. As new findings emerge, mostly through neuroscience methods, it is likely that they would motivate the development of new approaches comprising a better understanding of cognitive and neural processes involved in socio-cognitive abilities, thus making the theory-theory vs. simulation theory debate redundant(Apperly 2008).

intentions from those of the observed person (Brass, Derrfuss, & Cramon, 2005), thereby enhancing self-representations while inhibiting representations of the other. Similarly, self-other distinction is also required when making inferences about the mental states of another person, although this time, self-representations must be inhibited while representations of the other must be enhanced in order to avoid egocentric bias (Apperly et al., 2010; Epley et al., 2004). Therefore, this theory suggests that the control of shared representations of self and other is at the core of socio-cognitive processes such as theory of mind and the inhibition of imitation. Evidence in support of the 'self-other control[1]' theory comes from neuroimaging and neuropsychology studies.

The neural mechanisms involved in imitation inhibition have been investigated with fMRI (e.g., Bien, Roebroeck, Goebel, & Sack, 2009; Brass, Derrfuss, & von Cramon, 2005; Spengler et al., 2009). Although different versions of imitation-inhibition tasks have been used, the paradigms usually require participants to perform a predefined finger movement (e.g., lifting or tapping the index finger) while observing the same (congruent) or a different (incongruent) finger movement (e.g., lifting or tapping) being performed on a computer screen. These studies have found stronger activation in the MPFC and the TPJ during incongruent trials – in which the inhibition of imitation is required – compared to congruent trials. These two brain areas are part of a wider network of regions thought to be involved in theory of mind (e.g., Adolphs 2003a, 2009; Frith & Frith, 2003).

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[1] Brass et al., (2009) referred to the control of shared representations to describe their proposed theory. Throughout this thesis the term 'self-other control' will be used as it seems to capture the essence of Brass and colleagues' theory.

In support of the self-other control theory, which suggests a functional and anatomical overlap between the inhibition of imitation and theory of mind, (Brass et al., 2009) draw from extant literature and evidence from two recent studies (Spengler et al., 2009; Spengler et al., 2010). Brass et al., (2009) compared the results of two previous fMRI studies of imitation-inhibition (Brass et al., 2005; Brass, Zysset, & von Cramon, 2001) with two meta-analyses, each focusing on neural regions involved in social cognition (MPFC and TPJ). The results revealed an overlap of activation between imitation inhibition, theory of mind and agency processing in MPFC and TPJ. Aware of the limitations of cross-sectional comparisons inherent in meta-analyses, (Spengler et al., 2009) carried out a within-subjects study with healthy, young adults who performed a range of tasks including imitation-inhibition, theory of mind, self-referential judgements, and agency. They found common activation during imitation-inhibition, theory of mind and self-referential processing in the MPFC and overlapping activation in the TPJ during imitation-inhibition, theory of mind and agency processing. A second study (Spengler et al., 2010) investigated whether imitation-inhibition deficits were correlated with impairments in perspective taking, empathy scores and theory of mind in patients with either frontal or TPJ lesions. The results revealed a significant correlation between imitation-inhibition and theory of mind in the frontal lesion group and controls, although in controls the correlation was smaller than in the patient group. The data from the TPJ lesion group on these two measures did not reveal any significant correlation. However, in the latter group, a significant correlation was found between performance on the imitation-inhibition task and visual perspective taking, whereas no such correlations were found in the frontal lesion group or controls. Finally, patients with lesions in the TPJ showing a higher interference effect in the imitation-inhibition task also achieved low scores on the empathy scale; whereas no significant correlation between these measures were found for either the frontal lesion patients or the control group. Spengler and colleagues interpreted these findings as further supporting evidence in favour of the ‘self-other control’ theory.

Put together, the above empirical findings provide evidence of a correlation between imitation inhibition and socio-cognitive abilities such as perspective taking and theory of mind. However, causation cannot be inferred from these findings. A more direct testing of the ‘self-other control’ hypothesis advanced by Brass et al., (2009) would require the manipulation of imitation-inhibition to measure its effect on perspective taking and theory of mind performance. Given the relevance of this hypothesis for advancing current knowledge and understanding of the functional mechanisms involved in theory of mind reasoning, it is reasonable to argue that more empirical evidence is needed to disentangle the relationship between imitation-inhibition and the range of social cognitive abilities that are often included within the theory of mind domain. Experiment 1 from Chapter 2 aimed to directly test the MNS theory vs. the self-other control hypothesis by employing a training paradigm to enhance either self-other overlap (imitation training) or self-other distinction (imitation-inhibition training) and then testing participants’ theory of mind and perspective-taking abilities. If the MNS theory is correct and there is a direct link between imitation and theory of mind, then imitation training is expected to result in better performance in the theory of mind and perspective taking tasks compared to imitation-inhibition training (and an additional control condition in which participants received domain-general inhibition training). Conversely, if imitation-inhibition training leads to improved theory of mind and perspective taking performance (compared to the other types of training), then this would provide evidence in favour of the self-other control hypothesis. Finally, a lack of an effect on tests of perspective taking and theory of mind by either type of imitative training would suggest that imitation, perspective taking and theory of mind are distinct socio-cognitive processes.

A different approach to investigating the interrelatedness of socio-cognitive abilities is adopted in Experiment 2 (Chapter 2), by assessing the performance of a group of individuals with mirror-touch synaesthesia, a condition in which self-other processes are thought to be impaired, on a range of social cognition tasks. The section below describes the relevance of this approach for addressing the first aim of this thesis.

1.3.2 When Self-Other Representations Go Awry: The Case of Mirror-Touch Synaesthesia

Synaesthesia (derived from the Greek *syn* meaning ‘together’ and *aisthesis* meaning ‘of the senses’) is a rare condition in which an otherwise normal person experiences sensations in one modality when a second modality is stimulated[1]. For example, some synaesthetes might see colours when they listen to music (known as music-colour synaesthesia; (Ward & Mattingley, 2006), while in others, the experiences of colour could be elicited by numbers, letters or words, in either their written (grapheme-colour synaesthesia) or their spoken form (phoneme-colour synaesthesia) (e.g., Simner, Glover, & Mowat, 2006). Recently, a different form of synaesthesia has been documented and is referred to as vision-touch or mirror-touch synaesthesia (e.g., Banissy & Ward, 2007, 2013; Blakemore, Bristow, Bird, Frith, & Ward, 2005; Holle, Banissy, Wright, Bowling, & Ward, 2011). For individuals with this form of synaesthesia, observing touch to another person elicits tactile sensations on the equivalent part of their own body. This condition has only recently been documented, but since the first single case study was reported (Blakemore et al., 2005), researchers have become increasingly interested in this condition (e.g., Aimola Davies & White, 2013; Banissy & Ward, 2007, 2013; Banissy, Cohen Kadosh, Maus, Walsh, & Ward, 2009; Goller, Richards, Novak, & Ward, 2013; Holle et al., 2011; Maister, Banissy, & Tsakiris, 2013). The prevalence rate of mirror-touch synaesthesia is 1.6%, making it one of the most common forms of synaesthesia (Banissy et al., 2009). A neurocognitive model of mirror-touch synaesthesia has been proposed in which the 'who' mechanism, responsible for self-other distinction during visual encoding of the perceived touch, appears to be impaired (Banissy et al., 2009). Such impairment is likely to manifest by a

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[1] This description of synaesthesia is only useful as a shorthand definition. Describing synaesthesia in purely sensory-perceptual terms does not fully capture the nature of this condition. There is growing evidence that synaesthetic experiences appear to be triggered by high-order cognitive constructs such as those involved in language comprehension and production (Simner 2012).

tendency to over-incorporate mental representations of the other into the self, thereby blurring self-other boundaries (Banissy & Ward, 2013; Banissy, Walsh, & Muggleton, 2011). This characterisation of mirror-touch synaesthesia makes a compelling case for studying the interrelatedness of socio-cognitive abilities relying on the control of self-other representations in individuals who experience this form of synaesthesia.

Three defining features have been identified when characterising Synaesthesia. First, the experiences are elicited by perceptual or conceptual stimuli that would not normally evoke such experiences in most members of the population. Second, experiences occur automatically. Third, the experience resembles that of a conscious event (Ward & Mattingley, 2006). Therefore, in order to establish the authenticity of mirror-touch synaesthesia, these defining features should be taken into account. Simply put, mirror-touch synaesthesia requires the conscious experience of a tactile sensation, occurring automatically following observation of touch to another person (Banissy et al., 2009).

Different methods have been used to validate the authenticity of mirror-touch synaesthesia[1]. The most common one involves participants watching videos of human and objects being touched and then asked to report about their synaesthetic experience of touch including ratings of the intensity (e.g., Blakemore et al., 2005) and location of such experience (e.g., Banissy & Ward, 2007; Banissy et al., 2009). Banissy and Ward (2007) developed a visuo-tactile

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[1] Although not discussed here, Aimola Davies & White, (2013) used the rubber hand illusion paradigm (Botvinick & Cohen, 1998) with mirror-touch synaesthesia and found the usual rubber hand illusion effect (touch sensation elicited by observing the prosthetic hand being touched) in the absence of actual touch. Therefore, the authors consider this paradigm as an appropriate method of validating the authenticity of mirror-touch synaesthesia.

congruity paradigm to explore the automaticity of the synaesthetic experience – see Figure 1.1. Participants were presented with videos of either another person being touched on the cheeks/ hands, or an object (a lamp) being touched, while the experimenter delivers touch (or no touch in the control condition) to the participant's cheeks or hands (either left, right, both or no touch). Participants were asked to report the location of the actual touch while ignoring the observed touch. For synaesthetes, the observed touch to another person (but not the object) elicited the expected tactile sensation, which was either in the same spatial location as the actual touch (congruent) or in a different spatial location (incongruent). Furthermore, responses of the mirror-touch synaesthetes were faster than controls when the spatial location of the observed touch (right/left) was congruent with the actual touch relative to the incongruent spatial location. They also made more errors than controls. For example, if the actual touch was on the left cheek but the observed (synaesthetic) touch was on the right cheek, synaesthetes would report both cheeks or right cheek as the location of touch (see Figure 1). The difference in the reported location was dependent on the synaesthesia subtype. For some synaesthetes observing touch on the left cheek evoked the synaesthetic sensation on their left cheek (anatomical correspondence subtype), however for others the synaesthetic sensation was reported on the right cheek (as if looking at a mirror, a specular correspondence subtype) (Banissy & Ward, 2007).

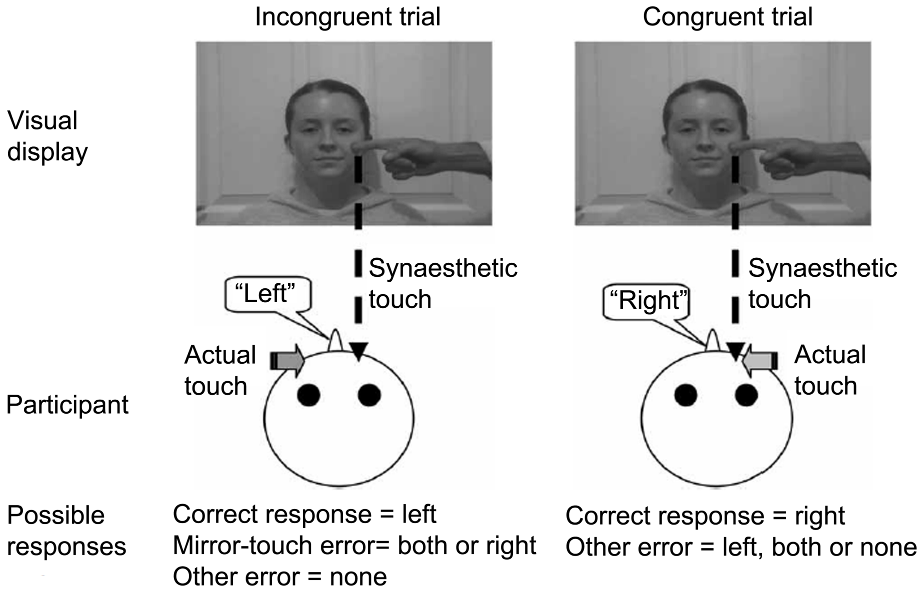

Figure 1.1 Illustration of the paradigm used by (Banissy & Ward 2007). Reprinted by permission from Macmillan Publishers Ltd: Nature Neuroscience, Copyright © 2007

Due to the recency of research interest in this type of synaesthesia, there are only a handful of studies investigating the impact of mirror-touch synaesthesia on social cognition. However, mirror-touch synaesthetes have been found to show enhanced emotion recognition (Banissy et al., 2011; Banissy et al., (2011) and score higher than controls on measures of empathy (Banissy & Ward, 2007). Both of these findings lend support to the inclusion of the other into representations of the self account (Banissy et al., 2009). Furthermore, a recent study (Maister et al., 2013) found that observing touch to others not only elicits the expected tactile sensations in individuals with mirror-touch synaesthesia, but it also induces changes in mental representations of the self. Meister and colleagues found that mirror-touch synaesthetes' ratings of a morphed photograph containing varying degrees of the participant's own face and an unfamiliar face, was modified after viewing videos of another person been touched. Specifically, synaesthetes rated the morphed faces as more similar to the self than they did before they watched the videos, which elicited a mirror-touch experience. In order to extend these findings, Experiment 2 (Chapter 2) aims to further investigate if self-other representations are impaired in individuals with mirror-touch synaesthesia by comparing their performance to non-synaesthete controls on a range of social cognition tasks requiring the control of self-other representations (control of imitation, visual perspective taking, theory of mind). It is expected that the findings from this experiment will contribute not only to a further characterisation of this condition, but also to a better understanding of the interrelatedness of these three different socio-cognitive domains.

1.4 The Role of the Temporoparietal Junction in Social Cognition

The second main empirical question of this thesis relates to the neural underpinnings of self-other representations, in particular, the role of the temporoparietal junction (TPJ) during socio-cognitive processing. This brain area was targeted because of the overwhelming amount of neuroimaging literature reporting TPJ involvement in social processing.

The label TPJ is commonly used to describe the region of the cerebral cortex lying at the boundary of the posterior superior temporal sulcus, the inferior parietal lobule and the lateral occipital cortex (Corbetta, Patel, & Shulman, 2008) – see Figure 1.2. Although it is an abstract label, which does not represent any specific anatomical structure, the TPJ has increasingly become the object of attention in the cognitive and social neuroscience literature. Neuroimaging studies have reported activation of TPJ in a variety of experimental paradigms ranging from attention (see review by Corbetta & Shulman, 2002), memory (Anticevic, Repovs, Shulman, & Barch, 2010; Todd, Fougnie, & Marois, 2005; Vilberg & Rugg, 2008), language (Kobayashi, Glover, & Temple, 2008; Price 2012) and social cognition (Frith & Frith, 2012; Gallagher & Frith, 2003; Van Overwalle & Baetens, 2009). To date, however, there is no consensus on the functional role of the TPJ. For example, a search in Google Scholar using the term 'function of temporoparietal junction' generates more than 7000 entries. This illustrates the popularity and diversity of studies – and ensuing myriad of interpretations of functional accounts – of this brain region.

The two most frequent accounts of TPJ function are found within the domains of attention and social cognition. Although previous work questioned the specificity of function within each of these domains (Kubit & Jack, 2013; Mitchell 2008; Saxe 2006; Scholz, Triantafyllou, Whitfield-Gabrieli, Brown, & Saxe, 2009), recently, new theoretical approaches have emerged attempting to reconcile these seemingly contradictory findings (Carter & Huettel, 2013; Corbetta et al., 2008). It is beyond the scope of this thesis to discuss the entirety of functional accounts of TPJ in the cognitive domain. Instead, the experiments presented in Chapter 4 aim to provide further supporting evidence for the role of this brain structure in social cognition.

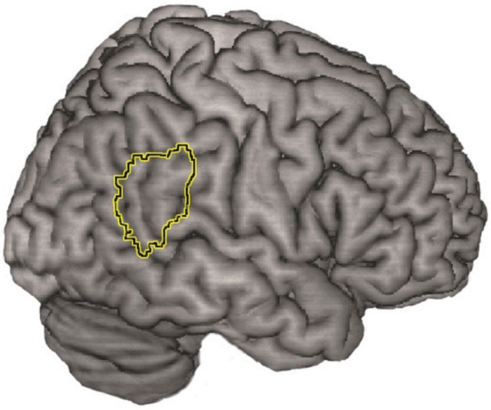

Figure 1.2. The TPJ is represented with a black and yellow outline and includes portions of the angular gyrus, supramarginal gyrus, and superior temporal gyrus and/or sulcus. This outline has been adapted from Carter & Huettel, (2013), who used reverse inference maps from http://neurosynth.org.

1.4.1 The TPJ and its role in social cognition

The TPJ is considered a key node within the 'social brain'[1] (Frith & Frith, 2010). Several lines of research suggest a socio-cognitive role for the TPJ centred on the processing of representations of the self or another individual. With respect to self-other processing, TPJ activation has been reported during low-level tasks such as agency discrimination (David et al., 2006; Farrer & Frith, 2002), visual perspective taking (Aichhorn, Perner, Kronbichler, Staffen, & Ladurner, 2006) and the control of imitative responses (Spengler et al., 2009), and in high level socio-cognitive processes such as mental state attribution (Kestemont et al., 2014; Saxe & Kanwisher, 2003), empathy (Völlm et al., 2006),

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[1] The term social brain has been extensively used to refer to a network of brain regions that have been found to consistently activate during attribution of mental states to either the self or another individual. These include medial prefrontal cortex, posterior cingulate cortex, precuneus and TPJ, and perhaps less commonly identified, superior temporal sulcus, inferior frontal gyrus, and amygdala (e.g., Adolphs 2003a, 2009; Blakemore et al., 2004; Frith & Frith, 2003).

and moral reasoning (Young, Cushman, Hauser, & Saxe, 2007). The range of tasks producing reliable TPJ activation suggests that activity in this area is in response to a basic function, shared by all of the above processes. Candidate processes include the distinction between self and other representations (Decety & Sommerville, 2003), the control of self-other representations (i.e. biasing processing towards the self or other, Spengler et al., 2009), and the representation of transient mental states of others (e.g., beliefs, perspectives, and goals, Van Overwalle & Baetens, 2009).

Most of what is known to date about TPJ involvement in social cognition comes from neuroimaging (PET and fMRI) studies. A handful of studies of patients with TPJ lesion are also consistent with neuroimaging data and provide support for the role of TPJ in the attribution of false belief to others (Samson, Apperly, Chiavarino, & Humphreys, 2004), the control of imitation, visual and cognitive perspective taking abilities (Spengler et al., 2010). Non-invasive brain stimulation methods provide an important addition to neuroimaging as they allow the modulation of cortical excitability in focal areas of the brain. Transcranial magnetic stimulation (TMS) of TPJ has been shown to impair performance on measures of false belief and faux pas (Costa, Torriero, Oliveri, & Caltagirone, 2008), moral judgements (Jeurissen, Sack, Roebroeck, Russ, & Pascual-Leone, 2014; Young, Camprodon, Hauser, Pascual-Leone, & Saxe, 2010), attribution of intentionality (Giardina, Caltagirone, & Oliveri, 2011) and the control of imitation (Sowden & Catmur, 2013). Transcranial direct current stimulation (tDCS) is another non-invasive brain stimulation method that although frequently and effectively used to investigate motor and cognitive functions (see Jacobson, Koslowsky, & Lavidor (2012) for a recent review), it has rarely been used in the social cognition domain (a few exceptions include a study of deception (Karim et al., 2010) and another of unfairness (Knoch et al., 2008). TDCS was employed in Experiments 4 and 5 to investigate the functional role of TPJ in self-other representations in the control of imitation, visual perspective taking and theory of mind. The methodological principles of tDCS will be further described in Chapter 3.

1.5 The Role of Culture in Social Cognition

The third aim of this thesis concerns culture as a modulatory factor in socio-cognitive processes. The term culture is an abstract label that is used in many different ways in everyday language to describe and explain a broad range of activities and behaviour adopted by a group of people. There is not one accepted definition of culture, although there are probably as many definitions as there are major influential scholars in the fields of social psychology, philosophy and anthropology. However, most, if not all, of these definitions have one aspect in common that encompasses the essence of culture. It is inherently a social phenomenon that relies on shared information between individuals. According to Matsumoto & Juang, (2012), as an adaptive response to the environment, culture helps to select behaviours, attitudes, values and opinions that help individuals maximise resources to meet their survival needs. These two aspects characterising culture, namely the sharing of information between individuals and the adaptation of attitudes, values and behaviour underlie the third empirical question this thesis aims to address.

Two different lines of research from cultural psychology are relevant to mechanisms of self-other representations. The first one refers to the set of cultural attitudes migrants may hold towards their native and host culture: integration, assimilation, separation and marginalization (Berry, Kim, Power, Young, & Bujaki, 1989), see also (Hutnik 1991)[1]. According to Berry's model of acculturation (Berry 2005), integration is achieved when individuals value both maintenance of the heritage culture and identity but also seek contact with, and take part in, the larger society within the host culture. Assimilation refers to a preference for the host culture at the expense of the heritage culture. Separation is associated with a preference for the heritage compared to the host culture. Finally, marginalization occurs in the presence of little or no interest in either the heritage or the host culture. Experiment 5 (Chapter 5) will explore if adopting different cultural attitudes modulate the imitative behaviour of migrants towards a member of the host or the heritage culture. By investigating cultural attitudes, a well-established concept from cultural psychology, in the context of empirical social cognition research, this study will bring together two separate fields of inquiry that have not been previously linked.

The second line of research from cultural psychology, relevant to self-other processes in social cognition, relates to how individuals see themselves in relation to others – also known as self-construal styles (SCS). Those with

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[1] Hutnik (1991) refers to the four acculturation attitudes as assimilation, dissociation, acculturation and marginality.

'independent' self-construals have a sense of the self as autonomous beings, separate from interpersonal context. They tend to value uniqueness, self-promotion and assertiveness. A contrasting view of the self is present in individuals with 'interdependent' self-construals, who tend to value cooperation and group cohesiveness. They have a sense of self as intertwined with the other, particularly close others, to such extent that meeting another's goals and desires are a requirement to achieving their own goals and desires (Markus & Kitayama, 1991). Since the publication of Markus and Kitayama's influential paper, there has been a surge in cross-cultural studies exploring the influences of self-construal in various areas of research across social, cognitive, and developmental psychology. Moreover, recent years have seen the emergence of the field of cultural neuroscience (Chiao 2009; Han & Northoff, 2008; Kitayama & Park, 2010), which takes an interdisciplinary approach by combining theories of social and cognitive psychology with neuroimaging.

One of the earliest cultural neuroscience studies used fMRI to compare Chinese and Western participants while performing a self-referential task (Zhu, Zhang, Fan, & Han, 2007). Participants were required to make trait judgements about themselves, their mother, or a famous person. The authors found differential brain activation for the self vs. unrelated other contrast in the MPFC and ACC for both Chinese and Westerners. However, Chinese participants (and not Westerners) showed overlapping activation of the MPFC during self and mother judgements. The authors did not use a self-construal measure in this study; instead they used culture as a proxy for this measure and attributed their findings to the interdependent self-construal style often found among Chinese individuals, claiming that the concept of the self in this typically interdependent culture expands to include the mother.

Social psychologists have also investigated the effect of self-construal on automatic imitation (also known as nonconscious mimicry). In a set of experiments, van Baaren, Maddux, Chartrand, de Bouter, & van Knippenberg, (2003) found that participants who were primed with words eliciting interdependent self-construal (e.g., together, group, cooperate) imitated the gestures of a confederate more than participants who were either primed with words eliciting independent self-construal (e.g., unique, alone, individual) or a control group who received no priming. When the experimenters tested Japanese (typically interdependent) and American (typically independent) participants, their previous results were confirmed as Japanese participants imitated more than their American counterparts. For similar findings see (Hogeveen & Obhi, 2010). The researchers claim that interdependent self-construal affords assimilation of the other to the self. In van Baaren and colleagues' study, Japanese participants imitated the Japanese confederate just as much as they imitated the American confederate, suggesting no in-group bias to the degree of overlap of self-other representations. However, this pattern of results does not seem to replicate across other domains in social cognition. (Markus & Kitayama, 1991, pp. 229) point out " … interdependent selves do not attend to the needs, desires, and goals of all others. Attention to others is not indiscriminate; it is highly selective and will be most characteristic of relationships with 'in-group' members." In support of this premise, (Xu, Zuo, Wang, & Han, 2009) reported an in-group racial bias in empathy for pain for both Chinese and American participants. Importantly, such bias was not evident during self-report ratings of empathy but was only noticeable at the neural level, with increased BOLD signals in the ACC when subjects viewed facial stimuli representative of in-group members experiencing pain compared to out-group faces. In sum, the data from the above studies reveal the complexity of the processes underlying self-other representations in social cognition. Self-construal styles appear to modulate social interactions to adapt human behaviour in a socially effective manner. In the context of empathy, it appears that self-other distinction is modulated according to the significance of the relationship with the other, then cognitive processes intervene to adjust this distinction and respond in a more socially appropriate manner as suggested by the lack of in-group bias in the self-reported measures. The effects of self-construals on social cognition will be explored in Experiments 5 and 6 (Chapter 5).

1.6 Summary

Three main empirical questions are addressed in this thesis. The first aims to explore the interrelatedness of socio-cognitive abilities by investigating if common self–other processes are shared between different social domains (imitation/ imitation-inhibition, visual perspective taking and theory of mind). Two different approaches will address this question in Chapter 2. The first one (Experiment 1) employs a behavioural training paradigm to test, a) if there is a relationship between imitation/ imitation-inhibition, visual perspective taking and theory of mind, and b) whether such relationship, if it exists, is based upon self-other overlap (as advocated by the MNS theory) or self-other distinction (as advanced by the self-other control hypothesis). The second approach will compare the performance of individuals with mirror-touch synaesthesia and non-synaesthete controls (Experiment 2) on the same socio-cognitive domains mentioned above. The second question addressed in this thesis concerns the function of the TPJ, a key node in the 'social brain' (Frith & Frith, 2010), in self-other processes that underlie the socio-cognitive abilities under investigation. To this aim, Experiments 3 and 4 will employ a tDCS paradigm to modulate cortical excitability of the right TPJ (Experiment 3) on healthy adults prior to testing their performance in the three relevant domains. Experiment 4 is informed by the findings from Experiment 3, to explore if the effects found are localised to the right hemisphere or not, by delivering anodal tDCS to both right and left TPJ and a control occipital area to a new group of participants prior to assessing their performance on social cognition tests. To address the third empirical question, Chapter 5 will explore whether culture plays a modulatory role in social cognition. Two specific aspects of culture are particularly relevant to self-other processes. These includes cultural attitudes that migrants choose to adopt when living in a different culture (Experiment 5) and how individuals from different cultures perceive themselves in relation to others, known as self-construal style (Experiments 5 and 6).

Chapter 2: Self – Other Representations: From Imitation to Theory of mind

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The experiments described in this chapter aimed to investigate the relationship between three different socio-cognitive skills: imitation/imitation-inhibition, visual perspective taking and theory of mind. They do so by employing two different approaches. Experiment 1 contrasted the MNS and the self-other control theories (described in Chapter 1) using a behavioural training paradigm to manipulate the control of self-other representations in a between-subjects design. Following the training, participants' performance on the control of imitation, visual perspective taking and theory of mind is assessed on the basis of the type of training they received. A different approach was adopted in Experiment 2, which sought to investigate if individuals with mirror-touch synaesthesia show atypical behaviour (compared to non-synaesthetes) on measures of social cognition requiring the control of self-other representations. The findings from both experiments are discussed in relation to the self-other control theory. Additionally, the findings from Experiment 2 are also discussed in terms of their contribution towards a better understanding and characterisation of mirror-touch synaesthesia.

2.1 Experiment 1: Training Social Cognition

The role of automatic, unconscious imitation (also known as mimicry; (e.g., Chartrand & Bargh, 1999; Lakin, Jefferis, Cheng, & Chartrand, 2003) in social interactions has been the subject of extensive research in social psychology. For example, it has been demonstrated that imitative behaviour increases rapport (Chartrand & Bargh, 1999), trust (Bailenson & Yee, 2005), altruistic behaviour (Van baaren, Holland, Kawakami, & Knippenberg, 2004), and feelings of closeness (Stel & Vonk, 2010). Such positive impact of imitative behaviour has led some researchers to consider imitation as a 'social glue' that facilitates positive social interactions (Lakin et al., 2003). Interestingly, some of the early attempts to conceptualize imitation linked it to our ability to understand other people's minds. For example, Adam Smith (1759) (Smith 2010) claimed that *"reflexive"* imitation occurs after one takes the perspective of others and realizes what they must feel. But is this a correct assumption - does the act of imitating make the imitator better at taking the perspective of others? Social interactions can be very complex and while in some circumstances, imitating others can have beneficial effects, as a general rule, persistent imitation is not socially appropriate and, at times, the intention to imitate an interacting partner has to be suppressed. But what effect does the inhibition of imitation have on our ability to understand the mental states of others?

2.1.1 Two Contrasting Theories

Two theoretical approaches suggest contrasting answers to the above questions. The first, advanced by various researchers (e.g., Gallese & Goldman, 1998; Rizzolatti & Craighero, 2004), suggests that imitation, and its neural substrate the mirror neuron system (MNS; Catmur et al., 2007; Heiser, Iacoboni, Maeda, Marcus, & Mazziotta, 2003), is at the core of higher-order socio-cognitive functions. Under this hypothesis, action observation triggers motor representations that enable the reproduction of the observed action (imitation). This in turn results in the attribution – to the other – of mental states associated with performance of that action (theory of mind). On this account, it would be expected that a training paradigm promoting the activation of corresponding motor representations by observing another person's action (imitation training) would enhance the ability to represent the mental states of others.

A recent, alternative theoretical framework suggests that theory of mind is related not to imitation, but to the inhibition of imitation (Brass et al., 2009). When inhibiting the tendency to imitate another person's behaviour, the observer must distinguish between their own action intentions and those of the observed person (Brass et al., 2005), and perform the action they intended rather than the action performed by the other. Similarly, the process of distinguishing mental states pertaining to the self from those of another individual is argued to be necessary for theory of mind, even though frequently the 'control problem' in theory of mind is the opposite of that encountered in imitation inhibition; self-representations must be inhibited and representations of the other must be enhanced. Thus, Brass and colleagues' *self-other control* account suggests that both theory of mind and imitation inhibition share common underlying processes pertaining to the control of self-other representations. Crucially, in contrast to the *MNS* theory of social cognition, this theory predicts that training in imitation inhibition (rather than imitation) will result in an improvement in theory of mind ability.

Experiment 1 aims to test whether imitation or imitation-inhibition training results in improved theory of mind and / or perspective taking ability. If the *MNS* hypothesis is correct and there is a direct link between imitation and theory of mind, then the imitation training group is expected to perform better in the theory of mind and perspective-taking tasks than the other groups. Conversely, if the imitation-inhibition training group outperforms the other groups, then this study would provide evidence in favour of *the self-other control* hypothesis, suggesting that the control of shared representations might be the 'missing link' between the functions of the MNS and theory of mind abilities. Finally, a lack of an effect on tests of perspective taking and theory of mind by either type of imitative training would suggest that imitation, perspective taking and theory of mind are distinct socio-cognitive processes.

2.1.2 Method

Participants

Fifty-three adults (29 females, age range 19-50 years, *M* = 26.7, *SD* = 6.6), recruited from the local psychology department subject pool, participated in this study for a small monetary reward. Prior to conducting this experiment, ethical approval was sought and granted by Birkbeck's Ethics Committee. All participants were healthy individuals with no history of medical or developmental conditions. They were randomly assigned to the imitation (*N* =19), imitation-inhibition (*N* = 17), or inhibitory control (*N* = 17) groups. Groups did not differ in terms of age (*F*(2,52) = .221, *p* =.80), gender (χ^2 (2, *N* = 53)= 2.72; *p* = .26), or handedness (*F*(2,52) = .228, *p* =.80).

Procedure

All participants attended two sessions on consecutive days. On the first day they received training, and on the second day they completed the imitation-inhibition, Strange Stories, and Director tasks.

Imitation and Imitation-inhibition training

Participants in these two groups performed a task based on that developed by (Brass, Bekkering, Wohlschläger, & Prinz, 2000). The stimuli consisted of short videos showing either an index or middle finger performing a lifting movement (Figure 2.1). The imitation group was asked to perform the action they observed on the screen. When the index finger of the stimulus hand lifted, participants were required to lift their own index finger. Similarly, when the middle finger lifted, participants were required to lift their middle finger. The imitation-inhibition group were instructed that when they saw an index finger lift they should lift their middle finger, and when they saw a middle finger lift they should lift their index finger. The stimulus hand was rotated around the sagittal and transverse planes with respect to the participant's hand (Figure 2.1), which rested on the computer keyboard. As response movements were spatially orthogonal to stimulus movements, imitation could be isolated from spatial compatibility.

Inhibitory control training

A third group received training in a Stroop-like task, the temporal and spatial features of which were matched with those of the imitation and imitation-inhibition training procedures (Figure 2.1c). A red and a green sticker were placed on the knuckle (where the finger joins the hand) of the participant's right index and middle fingers. Placement of the red and green stickers on the participant's fingers was counterbalanced on each block on a within-subjects basis. On each trial, the stimulus fingers remained static and either a red or green circle appeared between the fingers. Participants were instructed to lift their 'red finger' (the finger with a red sticker) when a green circle appeared, and to lift their 'green finger' when a red circle appeared. For all training conditions (and the imitation-inhibition task – see below) the interstimulus interval varied randomly from 800ms to 2400ms. Training consisted of 6 blocks of 72 trials and lasted approximately 40 minutes.

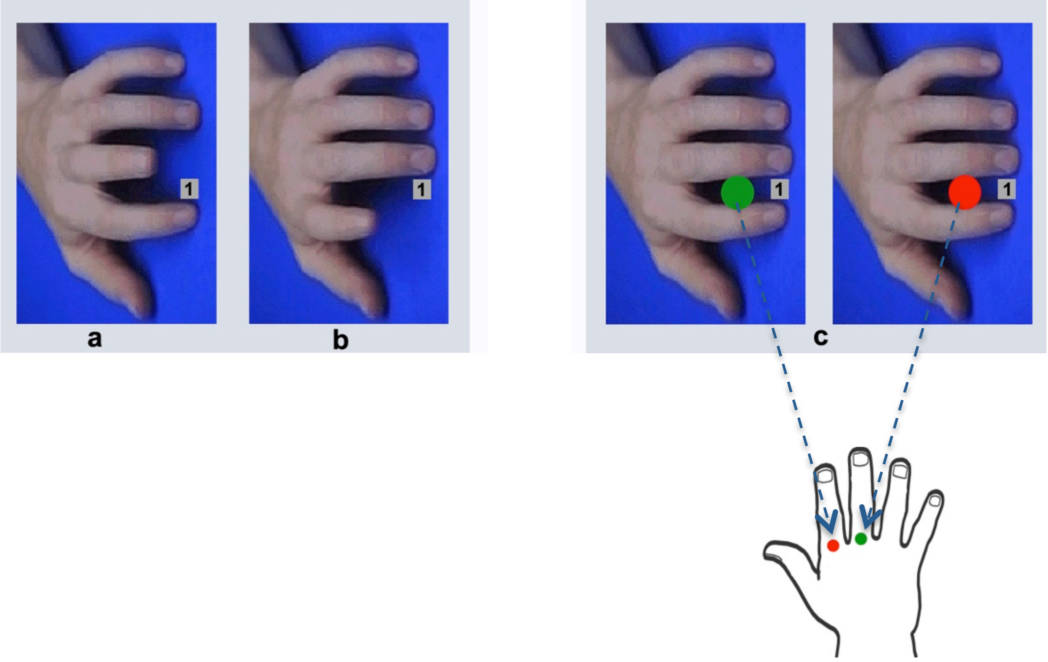


Figure 2.1. *Panels* ***a*** *and* ***b*** *are examples of the stimuli used for imitation, imitation-inhibition training, and for the imitation-inhibition task. The numbers are irrelevant in the training conditions and participants are instructed to ignore them. However, in the imitation-inhibition task participants were instructed to follow the number on the screen and lift their index finger upon appearance of a 1, and their middle finger upon appearance of a 2. Thus, panel* ***a*** *shows an example of an incongruent trial and panel* ***b*** *illustrates a congruent trial.*

Both images on panel ***c*** *are examples of the stimuli used for inhibitory control training. The bottom part of panel* ***c*** *shows the placement of the colour stickers in the participant's hands, which was counterbalanced on each block on a within-subjects basis. The dashed arrows indicate the correct finger movement upon appearance of either the green or red circles on the screen.*

Tests of Social Cognition

Control of imitation task

All participants were presented with the same finger movement videos used for imitation and imitation-inhibition training, but this time participants were asked to lift their index finger upon appearance of a 1, and their middle finger upon appearance of a 2. At the same time as the appearance of the number cue, there was a lifting movement of the index or middle finger of the stimulus hand. Although the observed movements were formally task-irrelevant, the relationship between the observed movement and the movement required by the number defined two trial types. On congruent trials, the required finger movement was the same as the observed movement (Figure 2.1b); whereas on incongruent trials, the required finger movement was different from the observed movement (Figure 2.1a). Thus, on incongruent trials participants were required to inhibit an imitative response and perform the pre-instructed movement. Twenty trials in each of the four combinations of observed and executed finger movements were presented in a random order. The interstimulus interval varied randomly from 800ms to 2400ms. The main objective of this task was to validate the training paradigm. Therefore, it was expected that participants in the imitation-inhibition group (and those in the inhibitory control condition) would perform significantly better than the imitation group in this task, both in terms of faster RTs during incongruent trials and smaller imitation effect – see Results section.

Visual Perspective Taking (Director task)

Modelled on Keysar, Barr, Balin, & Brauner, (2000), this task required participants to take into account the point of view of a character, introduced as 'the director'. The visual stimuli consisted of a 4x4 grid ('shelves') as depicted in Figure 2.2. Five slots were occluded from the view of the director, who stood on the other side of the shelves. Participants listened to auditory instructions from the director who asked them to move specified objects in a particular direction. On experimental trials, there was a conflict between the participant's and the director's perspective. For example, if the participant was presented with the array shown in Figure 2.2a, and was asked to "move the small apple left", they should ignore the smallest apple they can see, the 'competitor object', (because the director cannot see this apple), and instead move the next smallest apple, which is visible to the director. There were two control conditions: C1 and C2. In C1, the director instructed participants to move an object placed in one of the clear slots (e.g., "move the chocolate down". In C2, an irrelevant object replaced the 'competitor' item from the experimental condition but the instruction remained the same (see Figure 2b). Accuracy of the selection and movement of the target object and RTs were recorded. Eye movement data were also recorded using an Eyegaze Edge™ System eye tracker (sampling rate 60 Hz). The eye tracking measure consisted of the number of 100ms fixations on the 'competitor' object (the object the director could not see) in the experimental condition, relative to the irrelevant object placed on the same slot in the C2 condition. This measurement is thought to be an index of the extent to which participants considered (incorrectly) the 'competitor' as the appropriate object to move (Wu & Keysar, 2007).

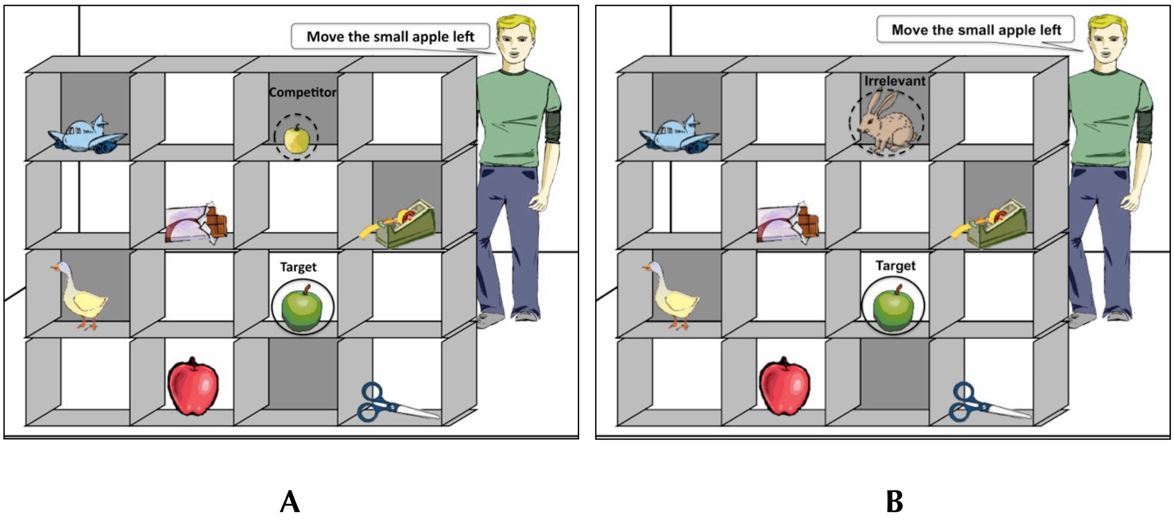


Figure 2.2. *Visual Perspective-taking Task. Panel* ***A*** *shows an example of an experimental trial and Panel* ***B*** *shows an example of one of the control conditions (C2).*

Theory of Mind (Strange Stories task)

Participants were presented with a total of 32 stories of four different types (mental, physical, animal and natural) based on those developed by (Happé 1994). There were 8 stories of each type, matched for the number of words across story type. After reading each story, participants were presented with a comprehension question, followed by 3 possible answers. RT and accuracy were recorded. Only the mental stories required the correct attribution of mental states for successful performance on this task – see Table 2.1.

Table 2.1. Example of the story types from the Strange Stories task. Correct answers are highlighted in bold.

Mental	Helen waited all year for Christmas because she knew at Christmas she could ask her parents for a rabbit. Helen wanted a rabbit more than anything in the world. At last Christmas Day arrived, and Helen ran to unwrap the big box her parents had given her. She felt sure it would contain a little rabbit in a cage. But when she opened it, with all the family standing round, she found her present was just a boring old set of encyclopaedias, which Helen did not want at all! Still, when Helen's parents asked her how she liked her Christmas present, she said, "It's lovely, thank you. It's just what I wanted". Q: Why did she say this? 1. Because she didn’t want to be told off by her parents 2. Because she wanted to trick her parent© **3. Because she didn’t want to be rude to her parents**
Physical	A burglar is about to break into a jewellers' shop. He skilfully picks the lock on the shop door. Carefully, he steps over the electronic detector beam. If he breaks this beam it will set off the alarm. Quietly he opens the door of the store-room and sees the gems glittering. As he reaches out, however, he steps on something soft. He hears a screech and something small and furry runs out past him, towards the shop door. Immediately the alarm sounds. Q: Why did the alarm go off? 1. Because he disturbed a mouse and it set the alarm off **2. Because he trod on a mouse and it ran through the alarm beam** 3. Because the mouse made him step into the beam by mistake
Natural	The little village of Littlehurst is close to the river Worrow. A year ago, a wall was built all the way round the edge of the village. The river floods its banks in April every year and, in the past, water would flow into many houses and cause lots of damage. For three weeks now the rain has been pouring down. However, this year, all the houses in Littlehurst are perfectly dry inside. Q: Why were all the houses dry? 1. Because the water from the river can’t get into the houses **2. Because the wall stopped the water getting into the village** 3. Because there was a new wall around the village
Animal	Some types of birds, like geese and swallows, only like very warm weather. When it is winter in England, it is still very warm in other countries that are further south. Last autumn, flocks of swallows could be seen flying in huge groups in the same direction away from England. At the beginning of summer, these swallows flew back to England. Q: What were the swallows doing? **1. They were always flying to the place that was warm** 2. They were flying south 3. They were flying away from England

2.1.3 Results and Discussion

Where sphericity assumptions were not met, Greenhouse-Geisser corrected values are reported. Bonferroni corrections were used for post hoc multiple comparisons.

Training

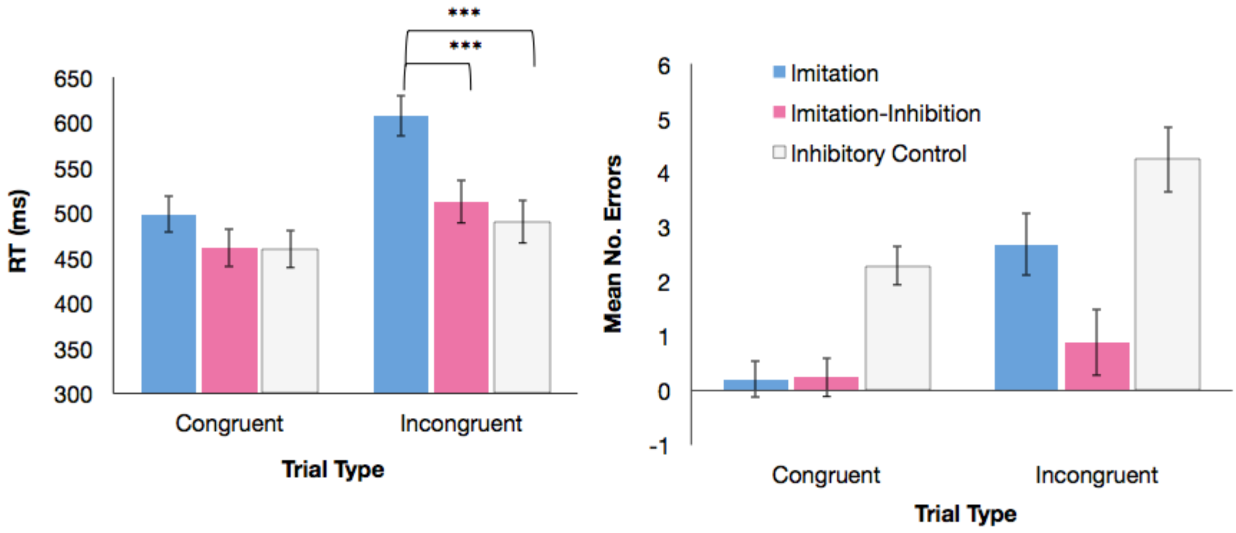
Response times were faster in the imitation training group (*M* = 461; *S.E.M.* = 13.73) than the imitation-inhibition (*M* = 640; *S.E.M.* = 46.97; *p*= .003) and the inhibitory control (*M* = 637; *S.E.M.* = 41.93; *p* = .003) groups; *F*(2,52) = 8.39; *p* < .001. In terms of accuracy, the imitation group made significantly fewer errors (*M* = 15.74; *S.E.M.* = 2.57) than the inhibitory control group (*M*= 39.35, *S.E.M.* = 9.8; *p*=. 033); *F*(2,52) = 3.51; *p* < .037, but no other contrasts were significant (*ps* > .38*)*.

Control of imitation task

Prior to the statistical analysis, extreme RT scores identified by the 1.5 x inter-quartile range rule (IQR, Tukey, 1977) were removed from each participant's dataset. The RT and accuracy data were analysed using ANOVA with Group as the between-subjects factor (imitation vs. imitation-inhibition vs. inhibitory control) and Trial Type as the within-subjects factor (congruent vs. incongruent).

RTs. Figure 2.3a shows RTs from the control of imitation task. Responses on congruent trials were executed faster than those on incongruent trials, *F*(1,50) = 114.59; $p < .001$; η^2_p= .70. The main effect of group was also significant, *F*(2,50) = 4.04; $p = .024$; η^2_p= .14. Pairwise comparisons showed that this effect was driven by the overall difference in performance between the imitation and the inhibitory control group ($p = .035$). The Group × Trial Type interaction was significant, *F*(2,50) = 16.62; $p < .001$; η^2_p= .40, indicating a larger RT difference between congruent and incongruent trials in the imitation group (*M* = 109 ms, *S.E.M.* = 13.36) than in the imitation-inhibition (*M* = 51 ms, *S.E.M.* = 7.04; $p = .005$) and inhibitory control (*M* = 30 ms, *S.E.M.* = 8.09; $p = .001$). The interaction effect could be due to a) stronger imitation inhibition, or b) a weaker tendency to imitate in the two inhibition groups than in the imitation training group. To distinguish these possibilities, RTs on incongruent trials were analysed including congruent trials as a covariate (and thereby accounting for the variance due to the tendency to imitate). This analysis revealed a significant effect of group *F*(2,49) = 15.43; $p <.001$; η^2_p= .39. Pairwise comparisons showed that the imitation group took longer to inhibit an imitative response than both the imitation-inhibition ($p = .001$) and the inhibitory control groups ($p < .001$), suggesting that RT differences in congruent and incongruent trials were caused by an increased ability to inhibit the tendency to imitate in the imitation-inhibition and the inhibitory control groups. Supporting this interpretation, when congruent and incongruent trials were analysed separately, a significant main effect of group was only observed on incongruent trials (*F*(2,50) = 7.54; $p =.001$; η^2_p= .23), Pairwise comparisons: imitation vs. imitation-inhibition, $p = .015$; imitation vs. inhibitory control, $p = .002$; imitation-inhibition vs. inhibitory control *n.s.*

Accuracy. Error data are displayed in Figure 2.3b. Overall, participants made more errors in the incongruent (*M* = 2.60, *S.E.M.* = .38) than in the congruent trials (M = .89, *S.E.M.* = .24), *F*(1,50) = 21.16, *p* < .001; $\eta^2 p$= .29. The inhibitory control group made significantly more errors than the imitation (*p* < .001) and the imitation-inhibition (*p* = .001) groups, *F*(2,50) = 13.24; *p* < .001; $\eta^2 p$= .34. A correlation analysis revealed that there was no speed-accuracy trade-off during incongruent trials in the inhibitory control group (*r (17)* = -.224, *p* = .39) – see also Figure 2.3C. The Group × Trial Type interaction was not significant (*p* = .12), indicating that training type did not affect accuracy on this task.



A **B**

Figure 2.3. *Mean RT (A) and number of errors (B) on the control of imitation task for each group. The error bars represent standard error of the mean.* **** (p ≤ .001).*

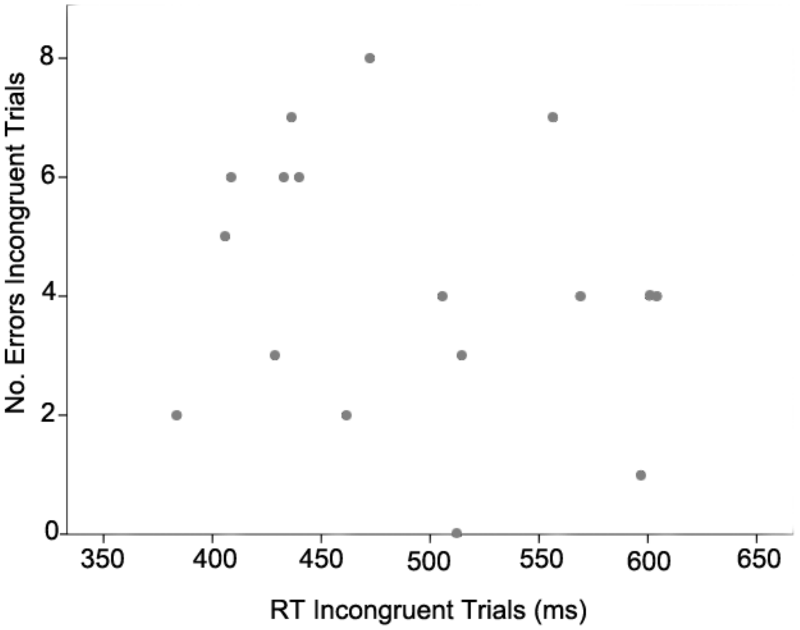


Figure 2.3 C. *Scatterplot of RT and number of errors during incongruent trials in the Inhibitory Control group showing that there was no speed-accuracy trade off.*

The observed pattern of performance on the RT measure of this task confirms the efficacy of the training paradigm in the control of self-other representations. Imitation training resulted in enhanced self-other overlap, therefore, participants in this group found it harder to inhibit the tendency to imitate. On the other hand, imitation-inhibition training led to increased self-other distinction, which in turn facilitated performance on this task as shown by a reduced tendency to imitate. Similar effects were also found after inhibitory control training, suggesting that perhaps the effects in the imitation-inhibition training group might not be specific to imitation but that they are closely linked to domain-general inhibitory processes. The inhibitory control condition was carefully designed in order to match as closely as possible the imitation-inhibition training condition. The only difference between the two types of training was the absence of a finger lifting action during the inhibitory control condition, which was replaced by the appearance of a red or a green dot. It is possible that the similarity in performance between the two groups could be related to the closely matched design. This could be further investigated by replacing the inhibitory control condition with another more conventional inhibition task such as the Stroop or a go-no-go task. A second, and perhaps more likely explanation could be that the inhibitory control training afforded participants in this group, the level of inhibition required for self-other distinction in the control of imitation task.

Director Task

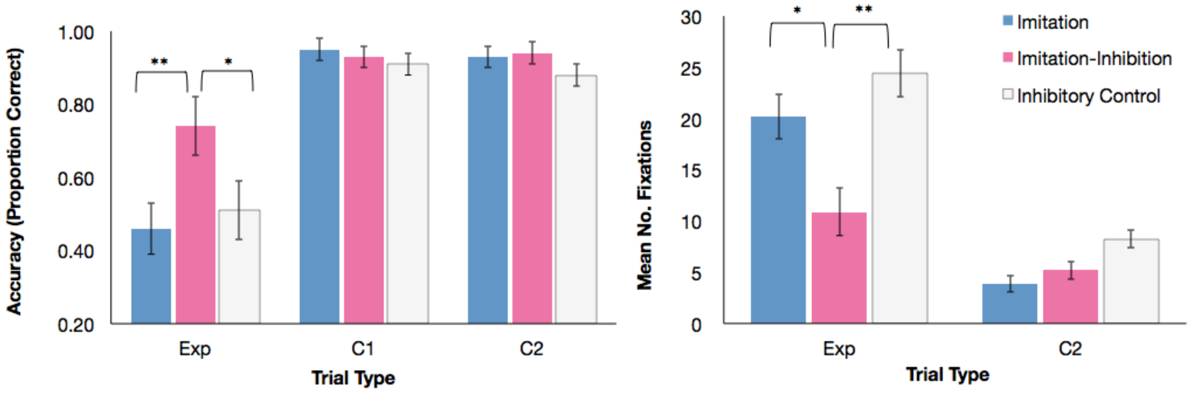
The accuracy and RT data were analysed using ANOVA with Group as a between-subject factor and Trial Type (exp vs. C1 vs. C2) as the within-subjects factor.

RTs. Participants responded faster to the C1 trials than to the experimental (p <.001) or the C2 trials (p <.001), $F(1.72, 86.36) = 35.70$; $p < .001$; $\eta^2_p = .42$. No other main effects or interactions were significant (all *p*s > .10).

Accuracy. The accuracy data are shown in Figure 2.4A. Overall, performance was worse on experimental trials ($M = .56$, *S.E.M.* = .04) than on control trials: C1 ($M = .92$, *S.E.M.* = .01), C2 ($M = .90$, *S.E.M* = .01), $F(1.02,51.43) = 66.61$; $p = .014$; $\eta^2_p = .11$; confirming the previously reported difficulty in taking the director's perspective observed using this task (e.g., Dumontheil, Apperly, & Blakemore, 2010). The Group × Trial Type interaction was significant, $F(2.05, 51.43) = 3.45$; $p = .03$; $\eta^2_p = .12$, indicating that the pattern of performance across experimental and control trials differed between the groups. Post-hoc analysis showed that on experimental trials the imitation-inhibition group performed significantly better than the imitation (*p* = .01) and the inhibitory control (*p* = .03) groups. Thus, participants in the imitation-inhibition group were better able to separate their perspective from the director's perspective.

Eye-tracking data. Figure 2.4B shows the eye-tracking data for the Director task. These data were analysed using ANOVA with group as the between-subject factor and trial type: (exp vs. C2) as a within-subject factor. The analysis revealed a significant main effect of trial type, $F(1,50) = 93.95$; $p < .001$; $\eta^2_p = .65$. Overall, participants fixated more on the competitor object in the experimental trials (*M* =18.5*, S.E.M.* = 1.49) than on the irrelevant object (*M* = 5.7, *S.E.M.* = .53) placed in the same slot in Control trials, again suggesting a difficulty in adopting the director's perspective. The main effect of group was also significant, $F\ (2,50) = 10.23$; $p < .001$; $\eta^2_p = .29$). Post-hoc pairwise comparisons revealed that this effect was driven by the fact that the imitation-inhibition group (*M* =8.02, *S.E.M.* = 1.3) had fewer fixations than the inhibitory control group (*M* =16.32, *S.E.M.* = 1.3); $p < .001$.

The Group × Trial Type interaction was also significant, $F(2,50) = 7.02$; $p = .02$; $\eta^2_p = .22$. Simple effects analysis revealed that the imitation-inhibition group (*M* = 10.88, *S.E.M* = 2.30) were better able to separate their perspective from the director's perspective than either the imitation (*M* = 20.16, *S.E.M* = 2.18; *p* = .016) or the inhibitory control (*M* = 24.41, *S.E.M* = 2.30; $p < .001$) groups, again indicating that imitation-inhibition training resulted in an improved ability to take the perspective of the director.



A **B**

Figure 2.4*. Accuracy and eye-tracking data from each training group on the Perspective-taking task. The eye-tracking measure consisted of the number of 100ms fixations on the competitor object (the object the director could not see) in the experimental condition and the irrelevant object replacing the competitor in the control (C2) condition. The error bars represent standard error of the mean. ** (p ≤ .01), * (p < .05)*

Strange Stories

A preliminary analysis of the three types of control stories revealed no significant differences; therefore the data were combined and compared to the mental stories. Accuracy and RT data were analysed using ANOVA with Group as the between subject factor and Story Type (mental vs. control) as the within-subject factor.

RTs. Across groups, RTs were faster in the mental stories (*M* = 7.54 s, *S.E.M.* = .04) than in the control stories (*M* = 8.39 s, *S.E.M.* = .04), *F*(1,50) = 6.43; *p* = .014; η^2_p= .11. The main effect of Group and the Group × Story Type interaction were not significant (*p* > .30).

Accuracy. Overall, the proportion of correct responses on the mental stories ($M = .84$; *S.E.M.* = .02) was higher than on the control stories ($M = .71$; *S.E.M.* = .02), $F(1,50) = 47.20$; $p < .001$; $\eta^2_p = .49$. Neither the main effect of Group nor the Group × Story Type interaction were significant (*ps* >.20). The lack of a significant interaction in both the RT and accuracy analyses shows that there was no significant effect of training on this theory of mind task.

These results indicate that training to control self-other representations in one socio-cognitive domain, inhibition of the tendency to imitate the actions of others, enhances the control of self-other representations within a different socio-cognitive domain, the ability to adopt the perspective of others. This improvement in perspective-taking ability was specific to imitation-inhibition training; it was not seen after either imitation training or training in general inhibitory control.

MNS VS. SELF-OTHER CONTROL

No evidence was found in support of the MNS hypothesis that suggests a direct relationship between imitation and theory of mind. Participants who had been trained to imitate were no better than the imitation-inhibition or inhibitory control training groups on either the Strange Stories or Director tasks. In contrast, this study provides some support for the *self-other control* hypothesis, which proposes that both imitation inhibition and theory of mind depend on processes that distinguish self from other (Brass et al., 2009). Although imitation-inhibition training did not result in improved performance in the Strange Stories task, which measures theory of mind abilities, an improvement was observed in the Director task, which requires third-person perspective taking. The role of self-other distinction in the control of imitative responses (Brass et al., 2005) and the association of imitation-inhibition with socio-cognitive abilities such as perspective taking (Spengler et al., 2009; Spengler et al., 2010) has been suggested by previous studies on the basis of correlational evidence. However, this is the first study to provide experimental evidence by showing that imitation-inhibition training improves perspective-taking ability.

The lack of a transfer effect from imitation-inhibition training to the Strange Stories task appears at first, to contradict the *self-other control* theory. However, a crucial difference between the theory of mind and the perspective-taking tasks used in this study is that, although the former requires mental state attribution to the protagonist, successful performance is not dependent on the ability to distinguish self from other; whereas self-other distinction is crucial for the latter. For example, to understand a story from the Strange Stories task, participants must separate the facts presented to them from the relevant mental states they attribute to the character. This self vs. other distinction process takes place '*online*'. However, when subsequently presented with a question about the protagonist's mental state (i.e. '*offline*'), participants can answer correctly by 'stepping into the mental shoes' of the character; they do not need to represent simultaneously their own mental states and those of the character. On the other hand, in the Director task, participants need to take into account what they can see vs. what the Director can see on a trial-by-trial basis (*online*) in order to choose the correct object (and move it to the correct location). This difference between the '*online*' processing required in the perspective- taking task and the '*offline*' measure used in the theory of mind task could explain why participants in the imitation-inhibition training group outperformed the other groups in the Director task, but not in the Strange Stories task. However, it remains a possibility that the theory of mind task used in this study is not sensitive enough to ascertain differential effects of training. Accuracy on mentalising trials in the Strange Stories task was very high; on average participants made approximately only one error. It is possible that a ceiling effect impeded a differential effect of training being observed on this task. Further experiments with alternative theory of mind tasks will be essential to determine if processes pertaining to self-other representations are shared within the control of imitation, perspective taking and theory of mind.

2.2 Experiment 2: When Self-Other Representations Go Awry: The Case of Mirror-Touch Synaesthesia

Adopting a different approach, Experiment 2 also sought to investigate the relationship between imitation/ imitation-inhibition, perspective taking and theory of mind in a group of individuals with mirror-touch synaesthesia – a condition that has been related to atypical self-other representations – (Banissy & Ward, 2013; Banissy et al., 2009).

For mirror-touch synaesthetes, observing touch to another person elicits tactile sensations on the equivalent part of their own body. In the original study by (Blakemore et al., 2005), the authors describe the case of synaesthete C. Apart from her synaesthetic experiences, C is a healthy female adult leading a normal everyday life. She reports experiencing touch on her own body when observing another person being touched, but not when observing inanimate objects being touched. Blakemore and colleagues used fMRI to investigate the neural systems underlying C's synaesthetic experience compared to 12 non-synaesthetic control subjects. They found that compared to controls, C showed hyperactivity within a number of regions including primary somatosensory cortex, left premotor cortex and the anterior insula bilaterally when watching videos of humans being touched. Based on this evidence, the authors suggest that mirror-touch synaesthesia can be explained by increased activity in the tactile mirror system, which activates above a threshold for conscious perception of touch. However, although Blakemore et al.'s study shows correlational evidence of hyperactivity of somatosensory mirroring mechanisms in mirror-touch synaesthesia, the cause of such hyperactivity is not yet known.

One recent account (Banissy & Ward, 2013; Banissy et al., 2009) suggests that impaired self-other representations, specifically self-other monitoring, could contribute to a disinhibition of normal somatosensory mirroring mechanisms in individuals with mirror-touch synaesthesia. Relevant to this view, a study of non-synaesthetic individuals (Serino, Giovagnoli, & Làdavas, 2009) shows that observing another person being touched enhances the perception of touch on the self, when the other is perceived as similar or belonging to the observer's ethnic or political group. Furthermore, a recent study (Maister et al., 2013) found that observing touch to others not only elicits overt tactile sensations in individuals with mirror-touch synaesthesia, but it also induces changes in mental representations of the self. Maister and colleagues used an experimental paradigm based on the 'enfacement illusion', in which participants are shown a series of morphed images made up of varying proportions of an unfamiliar face and the participant's face. Participants are then required to report the extent to which the morphed stimulus face looks like the self. Following this, they are presented with videos of another person being touched, which occurs in synchrony and location-congruent with the touch delivered to the participant's face. The synchrony between observed and felt touch results in participants rating the morphed face as more similar to the self than prior to observing the touch video. In mirror-touch synaesthetes, such blurring of self and other identity was seen in the absence of felt touch. In particular, the images that participants had initially rated as containing equal quantities of self and other became more likely to be recognised as the self after viewing the other being touched, thus implying that merely observing touch to others elicits a change in mental representations, whereby the boundaries between self and other become blurred. This study represents a change of direction in mirror-touch synaesthesia research by shifting the emphasis from increased activation in somatosensory mirroring mechanism to potential causes leading to such pattern of activation, such as impaired self-other representations. However, further research is needed in support of this claim.

Experiment 2 aimed to expand on the findings from Experiment 1 by using the same measures of the control of imitation and visual perspective taking employed in the first experiment – plus a different theory of mind task–, but this time participants were individuals with mirror-touch synaesthesia and non-synaesthetic controls. Examining self-other processing in individuals with atypical representation of the self and others provides an insight into the ways in which the control of these representations typically functions. The findings are discussed in relation to a) the self-other control theory and b) their contribution to our understanding of this condition.

Findings of a comparable performance on the control of imitation and visual perspective taking within each group would support the view of a link between these two socio-cognitive abilities, as suggested by the results from Experiment 1. Findings of differential group performance would provide further evidence in support for the hypothesis of atypical self-other representations in mirror-touch synaesthesia (Banissy & Ward, 2013; Banissy et al., 2009). Finally, Experiment 2 also addresses the issue of task sensitivity arising from Experiment 1 by employing a different measure of theory of mind, designed as an ecologically valid assessment of mental state attributions approximating real-life social interactions.

2.2.1 Method

Participants

Sixteen mirror-touch synaesthetes (10 female, 6 male; age *M* = 32, *SD* = 12.2 years) and 16 non-synaesthetic control participants (12 female, 4 male; age *M* = 32.6, *SD* = 11.2 years) participated in this study for a small monetary reward. Thirteen mirror-touch synaesthetes were recruited from an existing database (held by Dr Michael Banissy at Goldsmiths College, University of London) and had previously been screened in order to authenticate their synaesthetic experience. The remaining 3 mirror-touch synaesthetes were first selected through self-report via a web-based questionnaire investigating different types of synaesthesia. Those who answered 'agree' or 'strongly agree' to the statement 'I sometimes feel touch when I see other people being touched' on a 5-point Likert scale (*N* = 30), were subsequently contacted to complete two further screening tests. The first was a web-based paradigm devised by (Holle et al., 2011). For this part of the screening, participants watched a series of videos showing people and objects being either touched or approached by a finger. Then participants were asked to report their experiences of touch for each video. Those who reported feelings of touch in two or more of the 68 videos were then invited to a second screening test consisting of a visual-tactile congruity paradigm designed to provide further evidence for mirror-touch synaesthesia (Banissy & Ward, 2007) – also described in the Introduction Chapter. Only those reporting synaesthetic tactile experiences (*N*=3, 10% of the original self-report questionnaire) in the second screening test were invited to take part in the study. The study received full ethical approval from Birkbeck's Ethics Committee.

Non-synaesthetic control participants were recruited from the self-report web-based screening questionnaire. Only those respondents answering negatively to the statement 'I sometimes feel touch when I see other people being touched' were invited to participate in the experiment. The groups did not differ in terms of age ($F(1,30) <1$, $p = .94$), gender (χ^2 (1, $N = 32$= .58, $p = .45$) or IQ (measured with the Ravens Progressive Matrices; $F(1,30) <1$, $p = .73$). Except one participant from the mirror-touch synaesthesia group, all participants were right-handed. In order to exclude handedness as a confounding variable in the control of inhibition task, the data from the left-handed participant were not included in the analysis of this task.

Procedure

Participants completed the control of imitation and visual perspective-taking tasks described in Experiment 1. The stimuli in the visual perspective-taking task were modified in order to make the objects and the figure of the director more lifelike (see Figure 2.5 below).

Figure 2.5. *Modified (more realistic) stimuli for the perspective-taking task. Panel* ***A*** *shows an example of the stimuli used for an experimental trial (e.g., the director instructs participants to move the 'large candle up') and a C1 trial (e.g., 'move the camera up'). Panel* ***B*** *shows an example the second control condition (C2) where the largest candle (i.e. the competitor) is replaced by an irrelevant object (a chair) but the director's instruction is the same as in the experimental condition (i.e. 'move the large candle up').*

Another variation from the design of Experiment 1 was the introduction of a different theory of mind task, the movie for the assessment of social cognition (MASC; Dziobek et al., 2006). Dziobek et al. (2006) showed that the MASC is a reliable and highly sensitive instrument for the evaluation of complex mental state recognition in both normal participants and individuals with autism spectrum disorders. The MASC is a computer-based task designed as an ecologically valid assessment of theory of mind ability. Participants are required to watch a 15-minute film and to make inferences about the mental states of the characters. The film shows four people interacting as they get together on a Saturday evening. The video is paused at various points and participants answer a multiple-choice question about the last scene. There are two types of questions: theory of mind (e.g., "what is Betty thinking?" or "why is Cliff saying this?") and control questions (e.g., "what was the weather like that evening?" or "what kind of pasta sauce are the characters preparing?"). To answer the theory of mind questions correctly, participants are required to make mental inferences through visual and auditory input approximating real-life social interactions. The MASC also allows the distinction of three different types of errors (complete lack of, insufficient, or excessive/over-interpretative mental state reasoning) – See Figure 2.6 below.

The order of the three tasks was counterbalanced across participants. After completion of the three tasks, participants were administered the Ravens Progressive Matrices (standard version). The testing session lasted approximately 90 minutes.

Figure 2.6. *Example of a theory of mind (ToM) question from a scene in the MASC.*

Betty (second from right) enters the room and joins the other three characters. She sees fresh flowers on the table and assumes that Cliff (left) brought them for Sandra, but it was in fact Michael who did. Betty complements Cliff on his choice of flowers for Sandra and Cliff replies: "not me, chocolates are more my thing." Then participants are asked: "why is Cliff saying this?"

a) he wants them to know that he would bring chocolates (insufficient ToM)
b) he is too modest to take credit for something he did not do (excessive ToM)
c) he did not bring anything for Sandra (lack of ToM)
d) he wants to diffuse the awkwardness of the situation (correct)

2.3.2 Results and Discussion

Control of imitation task

Additional to the excluded data from the left-handed mirror-touch synaesthete – as mentioned above –, the data from another participant from the same group were excluded due to extremely long overall RTs falling outside 1.5 x IQR (Tukey 1977). The RT and accuracy data from the remaining participants (mirror-touch synaesthetes $N = 14$, controls $N = 16$) were analysed using ANOVA with Group as the between-subjects factor (mirror-touch synaesthetes vs. controls) and Trial Type as the within-subject factor (congruent vs. incongruent).

RTs. Figure 2.7a shows RTs from the control of imitation task. There was a main effect of Trial Type $F(1,28) = 109.12$; $p < .001$; $\eta^2_p = .80$; indicating that overall, participants responded faster on congruent than on incongruent trials. The main effect of Group was also significance $F(1,28) = 6.77$; $p = .015$; $\eta^2_p = .20$. Overall, the mirror-touch synaesthetes (M=551.03 ms, *S.E.M.* = 15) were slower at responding to both types of trials than controls (M=497.60 ms, *S.E.M.* = 14). The Group × Trial Type interaction was also significant, $F(1,28) = 4.26$; $p = .048$; $\eta^2_p = .13$. Simple effects analysis shows that this interaction was driven by the mirror-touch synaesthetes taking longer when responding to incongruent trials (M=587.28 ms, *S.E.M.* = 14.67) than the controls (M=521.89 ms, *S.E.M.* = 13.92); $F(1,28) = 10.59$; $p = .003$; $\eta^2_p = .27$; whereas the group comparison for congruent trials was not significant ($p = .08$). A further post hoc analysis was performed to confirm if the poorer performance of mirror-touch synaesthesia during incongruent trials was due to a greater difficulty to inhibit imitation by analysing the incongruent trials and entering the RT of congruent trials as a covariate. This analysis revealed that the group difference remained significant (*F*(1,27) = 9.11; p = .005; η^2_p = .25), thus indicating that mirror-touch synaesthetes found it harder to inhibit the tendency to imitate than did the participants from the control group.

Accuracy. Error data are displayed in Figure 2.7b. Overall, participants made more errors in the incongruent (*M* = 6.1%, *S.E.M.* = 1%) than in the congruent trials (*M* = 1.5%, *S.E.M.* = .3%), *F*(1,28) = 19.48, $p < .001$; η^2_p = .41. The mirror-touch synaesthetes made significantly more errors than the controls, *F*(1,28) = 6.10; *p* =.020; η^2_p = .18. The Group × Trial Type interaction was also significant *F*(1,28) = 4.44; *p* =.044; η^2_p = .14. Simple effects analysis revealed that again, the mirror-touch synaesthetes made significantly more errors in the incongruent trials (*M*=8.4%, *S.E.M.* = 1.4%) than controls (*M*=3.8%, *S.E.M.* = 1.4%); *F*(1,28) = 5.59, *p* = .025, η^2_p = .17. Furthermore, this effect remains significant even after controlling for covariance in the congruent trials, *F*(1,27) = 5.39; *p* =.028; η^2_p = .17. These results confirm the greater difficulty experienced by the mirror-touch synaesthetes when required to control self-other representations. Taken together, the RT and accuracy data from the imitation-inhibition task provide further support for the faulty self-other representations account in mirror-touch synaesthesia (Banissy & Ward, 2013).

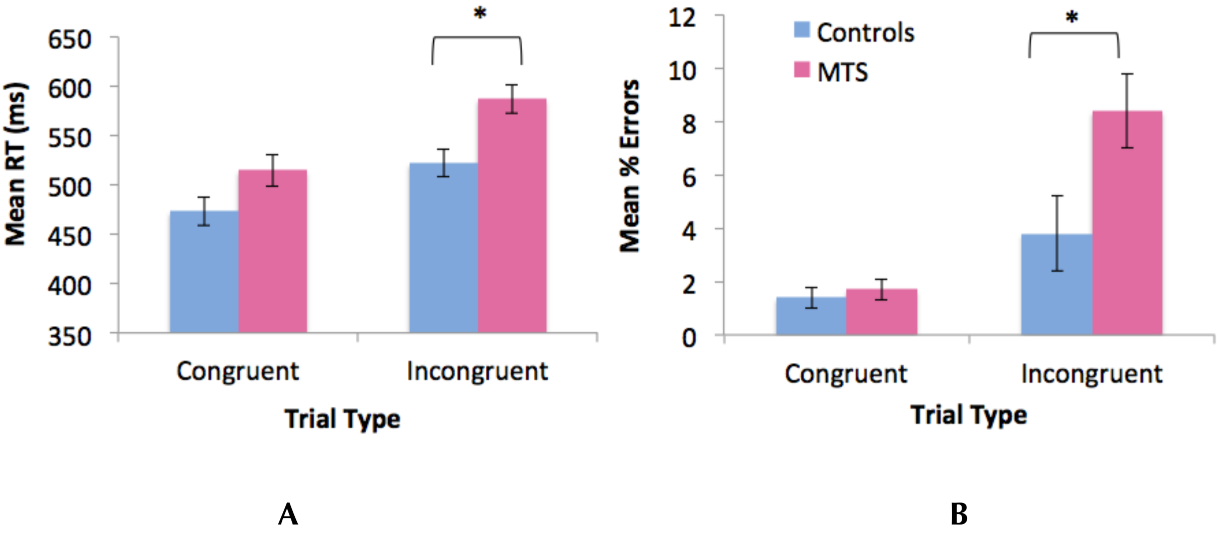


Figure 2.7. *Mean RT (A) and percentage of errors (B) on the control of imitation task for each group. The error bars represent standard error of the mean. MTS = mirror-touch synaesthesia. * (p < .05)*

Director task

Due to faulty equipment the data from 4 participants in the mirror-touch synaesthesia group were not recorded. The accuracy and RT data from the remaining participants (mirror-touch synaesthetes N = 12; controls N = 16) are reported here. Since no significant differences were found between the C1 and C2 control trials, the data were collapsed and analysed as a single control trial. An ANOVA was performed with Group as a between-subject factor and Trial Type (Exp vs. Control) as the within-subjects factor.

RTs. Participants responded faster to the control trials (M=2.9 s, $S.E.M.$ = .08 s) than to the experimental trials (M=3.1s, $S.E.M.$ = .12 s), $F(1, 26)$ =11.04; $p < .003$; $\eta^2_p = .30$. No other main effects or interactions were significant (all ps > .74).

Accuracy. There was a significant main effect of Trial Type *F*(1,26) = 36.37; $p < .001$; $\eta^2_p = .58$. Overall, performance was poorer on experimental trials (*M* = 52%, *S.E.M.* = 7.6%) than on control trials in which participants performed at ceiling: (*M* = 96%, *S.E.M.* = 1.3%). No other main effects or interactions were significant (all *p*s > .70). Notably, performance on experimental trials by the synaesthetes (*M* = 52%, *S.E.M.* = 11.5%) was the same as controls (*M* = 52%, *S.E.M.* = 10%), suggesting that perspective-taking abilities are not impaired in individuals with mirror-touch synaesthesia. However, since the performance by both groups was not particularly high, these findings require future replications.

The MASC

Two separate analyses were performed on the MASC data. The first analysis included the accuracy rate for theory of mind and control questions and the second sought to investigate if there were group differences in the type of errors participants made. The first analysis revealed that overall, participants' accuracy was higher for control questions (*M* = 87.7%, *S.E.M.* = 1.1%) than for questions requiring mental state attribution (*M* = 80.1%, *S.E.M.* = 1.5%), *F*(1,30) = 34.06; $p < .001$; $\eta^2 p = .53$. Neither the main effect of Group, nor the Group × Question Type interaction were significant, (*ps* > .66).

The analysis of error data revealed a significant main effect of Error Type, *F*(2,60) = 29.37; $p < .001$; $\eta^2 p = .49$, pairwise comparisons showed that overall, participants made more excessive theory of mind errors (*M* = 4.66, *S.E.M.* = .37) than errors reflecting either insufficient theory of mind (*M* = 2.84, *S.E.M.* = .38;

p = .003) or lack of theory of mind ability (M = 1.44, *S.E.M.* = .21; p < .001). No other main effects or interactions were significant (all *p*s > .21). Since performance on the crucial experimental condition (theory of mind questions) was high on both groups, these results imply that mirror-touch synaesthetes' ability to attribute mental states to other individuals is not impaired.

Are self-other representations atypical in mirror-touch synaesthesia?

The results from the control of imitation task in Experiment 2 suggest that the ability to control self-other representations in mirror-touch synaesthetes is impaired, as implied by the longer reaction times and larger number of errors in incongruent trials compared to controls. In order to succeed in this task, participants must supress the tendency to imitate the observed action from the stimulus hand on the screen (i.e. inhibit 'other' representations) and instead perform their intended actions as per task instruction, (i.e. enhance 'self' representations). Although interference from representing the other was observed during incongruent trials in both groups, the mirror-touch synaesthetes were significantly more affected and therefore, less able to inhibit mental representations of the other than non-syneasthete controls. This finding is in line with those recently reported by (Maister et al., 2013), discussed earlier, and provide further support for the hypothesis of atypical self-other representations in mirror-touch synaesthesia (Banissy & Ward, 2013; Banissy et al., 2009). An alternative interpretation to this finding would suggest that the finger tapping movement of the stimulus hand elicits a tactile experience on the synaesthete group, thereby interfering with their performance on this task. However, it should be noted that participants are required to respond to the finger lifting movement, not to the tapping, and when the stimulus finger is tapping, or in the down position, it rests on a blue background devoid of any objects. Therefore, there is no tactile experience during lifting or tapping by the stimulus finger. Furthermore, previous studies have shown that while the mirror-touch synaesthesia experience is elicited by touch to a real face, observing touch to a photo of a face, objects or even a dummy face fail to elicit the same tactile experience (Holle et al, 2011). Therefore, it is unlikely that the magnitude of the effects observed in the control of imitation task (RT: $p = .003$; accuracy: $p = .025$) is caused by the stimulus evoking a synaesthesia experience. Nevertheless, future studies could verify this by taking self-report measures of tactile experiences in synaesthetes when performing this task.

The control of self-other representations is also required in the visual perspective-taking task used in this study. However, in contrast with the control of imitation task, successful performance in the Director task requires participants to inhibit self-representations (by ignoring the objects visible to themselves) and enhance representations of the 'other' (by only choosing the objects visible to the director). Perhaps this difference in self-other control demands between the two tasks could explain the absence of a group effect in the Director task. Performance of the mirror-touch synaesthetes was identical (52%) to that of the non-synaesthete controls on the experimental trials, where the two perspectives were in conflict. It is possible that impairment of self-other processes in mirror-touch synaesthesia is specific to situations in which representations of the other should be inhibited (e.g., the control of imitation task) but not when they should be enhanced (e.g., perspective taking). This interpretation provides an interesting avenue for future research.

Nevertheless, a null finding in the Director task should be interpreted with caution as performance of both groups was not very high. Unlike previous studies using this task (e.g., Apperly et al., 2010; Dumontheil et al., 2010), the experimental design employed here has the additional complexity of a left/ right switch from the participant's point of view when moving the object to the correct location (from the director's perspective). It is possible, that this change to the design could have resulted in a processing cost to participants, by (unintentionally) encouraging the allocation of more attentional resources to the left/right switches than to choosing the correct object during the experimental trials. The current data provide partial support for this: overall, participants make more object-selection mistakes, by choosing the 'competitor' object (the one the director could not see), significantly more often during left/right trials (47%) than during up/down trials (42%; *p* <.001)[1]. However, since 42% of errors were made during up/down trials, devoid of directional conflict between the director and participant's perspective, the processing cost from left/right switches does not fully account for the overall poor performance on this task.

In sum, the current results suggest that visual perspective taking abilities of mirror-touch synaesthetes are not impaired, however, future replications are needed to support this interpretation. In light of the overall low performance on this task by both synaesthetes and controls, replicating these findings with

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[1] The remaining errors in Experimental trials were due to participants choosing irrelevant objects, other than the competitor. Neither the main effect of Group, nor the Group × Movement Instructions (left/right vs. up/down) interaction were significant, *ps* > .38.

different measures of perspective taking would contribute towards a better understanding of self-other processes in this condition.

Theory of mind in mirror-touch synaesthesia

Although no differential effects between the synaesthetes and controls were found in the theory of mind task either, the pattern of results for the MASC was the opposite of that seen for the Director task. While in the latter performance was relatively poor for both groups, in the former accuracy performance was high, but not at ceiling, in both groups (mirror-touch synaesthetes: *M* = 80%, *S.E.M.* = 2.1%; controls: *M* = 81%, *S.E.M.* = 2.1%), suggesting that the ability to attribute mental states to others is not impaired in individuals with mirror-touch synaesthesia. This finding is of interest to mirror-touch synaesthesia researchers as it provides another piece of the puzzle that contributes to the understanding and characterisation of this rare condition. In the context of the current set of experiments, this finding has further implications, specifically in relation to the *self-other control* theory proposed by (Brass et al., 2009). Experiment 2 addressed the potential lack of sensitivity of the Strange Stories task by using a different measure, designed to elicit mental state inferences in a setting approximating real-life social interactions, and yet again no evidence of a relationship between the control of imitation and theory of mind was found.

2.3 General Discussion

The experiments reported here intended to investigate whether socio-cognitive abilities such as the control of imitation, perspective taking and theory of mind share common underlying mechanisms for the control of self-other representations as advanced by Brass et al. (2009). Experiment 1 specifically addressed this experimental question by contrasting the *MNS* theory vs. the *self-other control* hypothesis using a behavioural training paradigm to manipulate the control of self-other representations.

The results from this experiment suggest a link between the control of imitation and perspective taking. However, these two socio-cognitive abilities do not appear to be related to the attribution of mental states to others, as also shown by the results from Experiment 2. Such discrepancy could lie in the requirement for the control of *online* self-other representations, common to both the control of imitation and to perspective taking but not to the attribution of mental states to others.

While these findings provide some support for the *self-other control* theory, it should be noted that neither the imitation nor imitation inhibition theories are likely to be sufficient to account for theory of mind in its entirety. Indeed, the *self-other control* theory explicitly states that imitation inhibition is related only to a sub-process within a wider theory of mind ability, the control of shared representations relating to self and the other. In contrast, it is often implied that the imitation / *MNS* theory provides a sufficient account of theory of mind competence. For example, it has been claimed that the MNS provides a mechanism by which humans may "directly understand the meaning of the actions and emotions of others by internally replicating ('simulating') them without any explicit reflective mediation" (Gallese et al., 2004, pp. 396), and may explain how "we assign goals, intentions, or beliefs to the inhabitants of our social world" (Gallese & Goldman, 1998, pp. 493). However, many authors have provided theoretical and empirical objections to this view based both on empirical work with typical individuals (e.g., Saxe 2005; Van Overwalle & Baetens, 2009), and with individuals with autism spectrum disorders (Bird, Leighton, Press, & Heyes, 2007; Southgate, Gergely, & Csibra, 2009; Spengler, Bird, & Brass, 2010).

A different approach to the experimental question concerning a relationship between the control of imitation, perspective taking and theory of mind was adopted in Experiment 2, which sought to investigate if individuals with mirror-touch synaesthesia display impairment in the control of self-other representations during performance of these three socio-cognitive abilities. The poor performance observed in the mirror-touch synaesthetes in the control of imitation task provides further evidence for the hypothesis of atypical self-other representations in individuals with this condition (Banissy & Ward, 2013; Banissy et al., 2009). However, no difference in performance was observed between the synaesthetes and controls in the visual perspective-taking task. Although both tasks require the control of self-other representations, the control demands are different for each task. The control of imitation requires enhancing 'self' and inhibiting 'other', whereas perspective taking requires enhancing 'other' and inhibiting 'self'. Could the similar performance between synaesthetes and controls in perspective taking indicate that self-other representation impairments of mirror-touch synaesthetes are limited to inhibition of the other? Future research could explore the answer to this question, perhaps by using different measures of perspective taking.

No differential effects between mirror-touch synaesthetes and controls were found on the theory of mind task. Performance of both groups was very high in this measure. Such good performance of the synaesthetes in this task suggests that their ability to attribute mental states to others is not impaired. Furthermore, the contrasting performance between theory of mind and the control of imitation provide further support for the view that they are distinct socio-cognitive abilities. The relatively poor performance by both groups on the perspective taking measure calls for future research in this social cognition domain before any firm conclusions could be drawn about the relationship between perspective taking and theory of mind.

Chapter 3: Transcranial Direct Current Stimulation (tDCS): A Methodological Overview

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This chapter provides an introduction to the methodological principles of transcranial direct current stimulation. The first section briefly summarises the origins of this method. This is followed by a discussion of the physiological mechanisms thought to underlie the aftereffects observed with tDCS and the parameters that could affect its efficacy. Finally, due to increasing research interest in this non-invasive technique, the safety considerations within experimental settings are discussed.

3.1 Introduction

Transcranial direct current stimulation (tDCS) is a non-invasive method that is increasingly being used to modulate cortical excitability and behaviour in a range of experimental conditions and clinical settings. Although it is only in the last few decades that researchers have started to employ tDCS to modulate human cerebral cortical functioning by inducing focal changes of cortical excitability (Nitsche & Paulus, 2001a, 2000; Priori 2003), the idea of electrical stimulation goes as far back as the first century AD.

3.1.1 The Origins of Direct Current Stimulation

In 43 to 48 AD, Scribonius Largus, the physician of Roman emperor Claudius, observed that placing a live torpedo fish (electric eel) – delivering a strong direct electric current – over the scalp of a patient suffering with headache, elicited a sudden transient stupor with pain relief (Kellaway 1946; Priori 2003). The systematic study of the torpedo electric fish by John Walsh between 1772 and 1775 (Piccolino & Bresadola, 2002) stimulated the work of the Italian scientists Galvani and Volta who established the existence of bioelectric potential (Geddes & Hoff, 1971; Priori, 2003). The discovery of galvanic currents (Direct Current, DC) led to its prompt application in clinical medicine, in particular mental disorders. In 1804, Giovanni Aldini, Galvani's nephew, reported the successful treatment of melancholia by applying galvanic currents over the patient's head. Aldini tested galvanic currents on himself before doing so with his patients. He reported side effects such as prolonged insomnia and unpleasant sensation lasting few days. Nevertheless, he still believed in the efficacy of galvanic scalp current to treat mental disorders (Priori, 2003). For the following two centuries many more researchers continued to use galvanic current for the treatment of mental disorders with mixed results. The inconsistent findings and sometimes failure to see any positive effects resulted in a gradual abandonment of DC stimulation, particularly after the discovery of electroconvulsive therapy (ECT, Cerletti & Bini, 1940) and the development of drugs to treat mental disorders. ECT signified a breakthrough in the treatment of mental illness due to the marked improvements observed in these patients (Mukherjee, Sackeim, & Schnur, 1994). However, there are fundamental differences between ECT and DC. ECT induces convulsive activity, whereas, DC stimulation does not induce seizures, instead, more subtle physiological changes take place by modulation of spontaneous neuronal activity (Terzuolo & Bullock, 1956). Unlike DC stimulation, ECT requires the use of anaesthesia. Furthermore, ECT causes memory disturbance or loss of consciousness (e.g., Rose, Fleischmann, Wykes, Leese, & Bindman, 2003), whereas no such effects have been found with DC stimulation. In the 1950s and 1960s most DC stimulation experiments were carried out in animals, and the results from these studies have contributed to current knowledge of the impact of DC stimulation in humans. A resurgence of DC stimulation (now better know as tDCS) has taken place over the last decade or so as researchers are beginning to understand the physiological basis and safety aspects of this brain stimulation method.

3.2 Physiological Basis of tDCS

Unlike transcranial electric stimulation (TES) or transcranial magnetic stimulation (TMS), tDCS does not induce neuronal action potentials because the static fields in this range do not yield the rapid depolarization needed to generate them (Nitsche et al., 2008). The application of tDCS involves delivering a weak electric current to the brain by placing two surface electrodes, one positively charged (anodal) and one negatively charged (cathodal) – See Figure 1 –, polarising the cortical area directly beneath and, therefore, modifying spontaneous neuronal excitability by depolarisation or hyperpolarisation of the resting membrane potential (Nitsche, Boggio, Fregni, & Pascual-Leone, 2009; Purpura & McMurtry, 1965). The current flows from the anodal to the cathodal electrode. It is widely assumed that the anodal electrode causes depolarization, increasing the probability of an action potential (excitatory effect), whereas the cathodal electrode causes hyperpolarization, thereby reducing the chances of action potentials (inhibitory effect). This effect is usually referred to as anodal excitatory, cathodal inhibitory (AeCi) – (Fregni et al., 2006; Nitsche & Paulus, 2000, 2011; Stagg et al., 2009). The evidence in support of this assumption comes mostly from studies investigating the effects of motor function. However, other motor studies (e.g., Priori, Berardelli, Rona, Accornero, & Manfredi, 1998a), but particularly studies in the cognitive domain have failed to replicate these polarity (AiCe) effects - (see Jacobson et al., 2012 for a review). In their meta-analytical review, Jacobson and colleagues found homogeneity of the generally assumed polarity effects (AeCi) among motor studies but heterogeneity in cognitive studies. The conclusion of this meta-analysis based upon the behavioural effects of stimulation suggest that during cognitive tasks the anodal electrode elicits excitation, while it is often the case that the cathodal electrode fails to produce inhibitory effects, at least as observable measures of task performance.

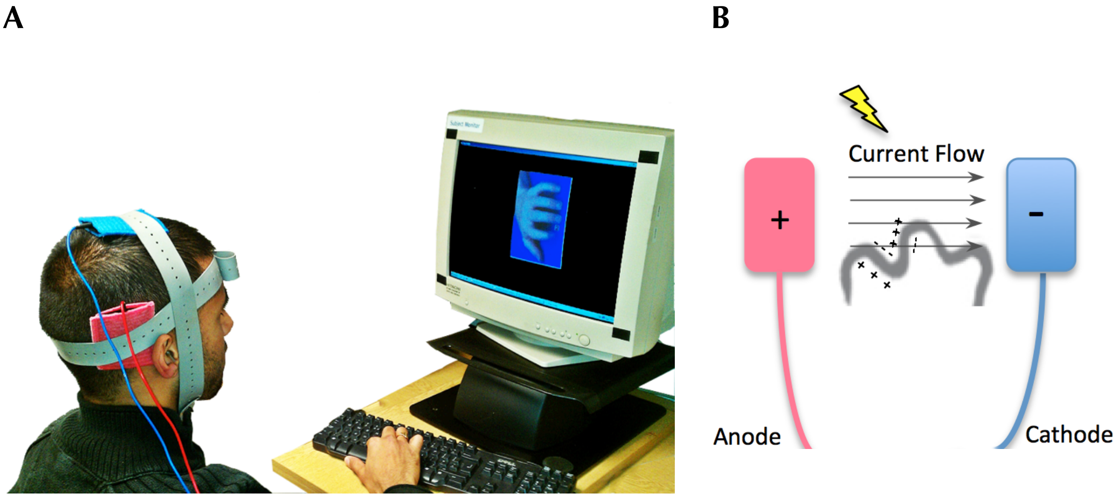

Figure 3.1. *Example of electrode placement in an experimental setting (A) and schematic representation of tDCS (B). Two 35* cm^2 *saline-soaked sponge electrodes are fixed to the participant's scalp. A weak (1mA – 2mA) constant electrical current generated by the tDCS stimulator (not shown) is applied over a few minutes (either online, i.e. while participants perform the experimental task as shown in panel A; or offline, i.e. prior to task performance). The electrical current flows from the anodal (+) to the cathodal (-) electrode through the superficial cortical areas leading to polarization.*

It is worth pointing out that Jacobson and colleagues' conclusions are based on performance data and do not necessarily reveal a lack of polarity effects on cortical excitability; as they suggest (see also (Antal et al., 2004), cathodal tDCS might enhance performance in a certain cognitive task by decreasing neuronal competition.

In their meta-analytical review, Jacobson and colleagues offer several potential interpretations of the lack of cathodal tDCS effects in cognitive studies. Parting from the premise that effects of brain stimulation are determined by the initial state of neuronal activation (Silvanto, Muggleton, & Walsh, 2008), Jacobson and colleagues posit that the initial state of cognitive regions is not passive prior to tDCS, these areas are likely to be activated by several situational and motivational factors. Therefore, tDCS is applied over an already activated region and as a result, anodal stimulation increases further neuronal firing, which contributes to the enhancement or facilitation of the cognitive performance. Conversely, the cathodal electrode is unable to generate measurable inhibitory effects when the initial state of neuronal activation is already high. In contrast, the initial state of the motor cortex is less active than cognitive regions. Therefore, stimulation effects (both anodal and cathodal) operate under less competition and are fully expressed. Another explanation proposed by Jacobson et al. (2012) to the lack of cathodal (inhibitory) effects in cognitive studies, is the differences in the dependent variables used. For example, most tDCS studies of the motor cortex use changes in motor evoked potentials (MEP), which is a passive measure involving only the stimulated motor region, whereas cognitive effects of tDCS use a variety of measures such as RT, accuracy, and sometimes fMRI data. All of these measures can generate external 'noise', which could affect the stimulation effects.

Furthermore, while cortical motor projections are almost always contralateral, bilateral activity is commonly found in cognitive functions. Therefore, it is possible that cathodal tDCS fails to induce inhibition of the cognitive function under investigation due to contralateral compensation effects (Jacobson et al., 2012). Although these observations seem plausible, future research could provide empirical support for these assumptions. For example, the level of activation of the cognitive regions under investigation could be assessed by using fMRI, both before and during tDCS, and changes in BOLD signals during the two conditions could verify the validity of the 'initial state activation' account.

Animal studies using tDCS have also reported contradictory findings with respect to the AeCi polarity effects. For example, (Creutzfeldt, Fromm, & Kapp, 1962) found that in the cat motor cortex, neurons in deep cortical layers were de-activated by anodal and activated by cathodal stimulation. The researchers attributed this finding to the spatial orientation of these neurons, which could have caused a reversed direction of the current flow compared to the dominant type of neurons in which the AeCi effects were found. Furthermore, the type of neurons modulated by tDCS seems to be related to the strength of stimulation, weaker stimulation (e.g., 30-80 $\mu A/mm^2$) modulates predominantly non-pyramidal cells, whereas stronger levels of stimulation (e.g., 100-400 $\mu A/mm^2$) seem to be required to modulate excitability of pyramidal neurons (Purpura & McMurtry, 1965).

This non-invasive brain stimulation technique has received considerable attention since its successful re-introduction in the study of the human motor functions (Nitsche & Paulus, 2000; Priori, Berardelli, Rona, Accornero, & Manfredi, 1998b) and cognitive functions such as working memory (e.g.,Fregni et al., 2005); executive functions (e.g., Boggio et al., 2007) and language (e.g., Monti et al., 2013). It is also increasingly been used in clinical settings for the treatment of depression (e.g., Boggio et al., 2008; Dell'osso et al., 2013; Nitsche et al., 2009) and other neurological conditions (see review by Fregni & Pascual-Leone, 2007). The behavioural effects of single tDCS sessions are relatively short-lived. Previous studies have shown that, for humans, 13 minutes of offline anodal tDCS at 1 mA results in a sustained increase in cortical excitability for up to 90 minutes after stimulation, followed by a linear decrease to baseline levels (Nitsche & Paulus, 2001a). However, there is recent evidence that the duration of these behavioural effects could last several weeks following repeated sessions both in healthy individuals (Reis et al., 2009) and in patients (Boggio et al., 2008).

Although the mechanisms underlying these changes are not fully understood, early tDCS studies with animals have revealed that the duration of aftereffects are dependent on protein synthesis (Gartside 1968) and accompanied by changes in intracellular cAMP and calcium (Ca^{2+}) levels (Hattori 1990; Islam 1995). Therefore, the aftereffects elicited by tDCS have been associated with the phenomena of long-term potentiation (LTP) and long-term depression (LTD) (e.g., Nitsche et al., 2008). The phenomenon of LTP (Anderson & Lomo, 1966; Bliss & Gardner-Medwin, 1973) has its foundation on the Hebbian principle that "neurons that fire together, wire together" and is considered one of the underlying mechanisms of synaptic plasticity. LTP is a long-lasting synaptic enhancement resulting from strong NMDA (N-methyl-D-aspartate) receptors and requiring postsynaptic Ca^{2+} entry and activation of glutamate receptors (Bear & Malenka, 1994). LTP has been considered the likely candidate for memory formation in the brain as it allows for modulation of synaptic strength that stabilizes for long periods of time (Anderson & Lomo, 1966; Bliss & Gardner-Medwin, 1973). LTD is the antithesis of LTP (Linden & Connor, 1993). "Neurons that fire out of sync lose their link" – synapses whose activity fails to correlate with that of the postsynaptic cell are weakened and then eliminated (Bear, Connors, & Paradiso, 2007, pp. 718).

Human studies using pharmacological intervention support the evidence from animal studies showing that modulation of cortical excitability elicited by tDCS depends on membrane polarisation, thus modulating the conductance of sodium and calcium channels. For example, (Nitsche et al., 2003) found that sodium channel blocker carbamazepine and calcium channel antagonist Flunarizine selectively eliminate the excitability enhancement associated with anodal tDCS during and after stimulation. Furthermore, the NMDA receptor antagonist dextrometorphan have been found to block aftereffects for both anodal and cathodal stimulation (Liebetanz, Nitsche, Tergau, & Paulus, 2002; Nitsche et al., 2003), but the partial NMDA receptor-agonist D-cycloserine lengthens the aftereffects (Nitsche et al., 2004).

3.3 Parameters Affecting the Efficacy of tDCS

A number of factors can determine the efficacy of tDCS. For example recent studies have identified current density, length of stimulation, electrode positioning, electrode size and experimental setup (offline vs. online) among the factors to consider for achieving optimal efficacy.

3.3.1 Current Density

The current density is the quotient of current strength and electrode size. Studies with animals have shown that current density determines the efficacy of tDCS for inducing acute modifications of membrane polarity (Bindman, Lippold, Redfearn, 1964; Purpura & McMurtry, 1965). Studies with humans have also found that larger current densities result in stronger tDCS effects. For example, (Nitsche & Paulus, 2000) applied tDCS over the motor cortex using a range of current density (0.2 mA, 0.4 mA, 0.6 mA, 0.8mA, 1mA) and stimulation duration (1-5 minutes), MEP measures showed increased stimulation aftereffects with increases of both current density and length of stimulation. Similarly, in a tDCS study of cognitive function, Iyer et al. (2005) used current densities of 0.4mA and 0.8 mA to stimulate the prefrontal cortex and found no significant stimulation effects on any of the measures (attention, self-emotion recognition, verbal fluency) in the 0.4mA condition; however, an improvement in verbal fluency was detected with the higher current density of 0.8mA.

3.3.2 Length of Stimulation

In line with the findings from (Nitsche & Paulus, 2000) that longer stimulation times increase the duration of aftereffects, Nitsche & Paulus (2001) found significant increases of MEP amplitudes after applying tDCS of the motor cortex at intervals ranging from 5 to 13 minutes. Whereas 5 to 7 minutes of tDCS resulted in aftereffects of less than 5 minutes, increasing stimulation to 13 minutes led to elevations of MEP amplitudes for up to 90 minutes. The relationship between length of stimulation and duration of aftereffects has also been replicated by Nitsche et al. (2003a). In a more recent study, Monte-Silva et al. (2009), reported that 9 to 18 minutes of cathodal tDCS induces a slight prolongation of inhibition. However, repeated tDCS during the aftereffects of the first stimulation with the same total stimulation was more efficient. These results suggest an interesting avenue for future tDCS studies looking to increase the efficacy of stimulation.

3.3.3 Electrode Positioning

In order to achieve the intended stimulation effects, another important factor to consider is orientation of the electric field, which is generally determined by the electrode position and polarity (Nitsche et al., 2008). Most of what is known about tDCS effects in humans and its methodological principles comes from studies stimulating the motor cortex. The first tDCS studies of the motor cortex in humans found contrasting polarity effects. Nitsche & Paulus, (2000) found the commonly assumed AeCi effects, whereas Priori et al. (1998b) found that anodal stimulation elicited inhibitory effects. A reason for this discrepancy has been attributed to differences in electrode positioning (Jacobson et al., 2012; Nitsche et al., 2008). (Nitsche & Paulus, 2000) placed the reference electrode over the contralateral orbit, but (Priori et al., 1998b) placed it on the chin. Similarly, two studies stimulating the primary visual cortex (Oz) found contrasting polarity effects. Antal et al., (2004) placed the reference electrode over the vertex and found that cathodal stimulation increased the amplitude of visually evoked potentials (VEP) of the P100 component, but anodal stimulation did not affect it. In a separate study, (Accornero, Li Voti, La Riccia, & Gregori, 2007) placed the reference electrode on the neck and found that, although cathodal stimulation increased the VEP-P100 amplitude – in line with the findings from Antal et al. (2004) – anodal stimulation reduced it.

Concerning the placement of the reference electrode, a more recent study by (Moliadze, Antal, & Paulus, 2010) found that when increasing the interelectrode distance[1], higher current intensity is required for achieving similar aftereffects.

3.3.4 Electrode size

One of the limitations of tDCS is its low spatial resolution. In a typical tDCS setting, the size of electrodes used is 5 cm x 7 cm (35 cm^2). It has been estimated that approximately 40-45% of the total current applied to the scalp passes through the cranial cavity, therefore the peak current density is found in

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[1] In their study, Moliadze et al., (2010) measured the intensity and aftereffects of anodal tDCS of M1 using four different electrode montages, with the reference electrode placed on the: contralateral forehead, contralateral upper arm, ipsilateral upper arm and ipsilateral forearm.

the cortices directly under the electrode with a rapid decrease for distal areas (Lang et al., 2005a; Rush & Driscoll, 1968). Therefore, changing the size of the electrodes should contribute to higher spatial resolution. For example, (Nitsche et al., 2007) demonstrated two ways of achieving higher focality of cortical excitability in the area beneath the stimulation electrode. The first method was reducing the size of the stimulation electrode, from the conventional 35 cm^2 to 3.5 cm^2, while holding current density constant (~ 0.03mA/cm^2). The second method consisted of increasing the size of the reference electrode from 35 cm^2 to 100 cm^2, resulting in a reduction of current density from 0.03mA/cm^2 to 0.01mA/cm^2 under this electrode – while the stimulation electrode was kept at 35 cm^2 and the current density at 0.03mA/cm^2. The reduction in size of the reference electrode was based on findings from an earlier study (Nitsche & Paulus, 2000) showing that in humans a minimum current density of 0.017A/cm^2 was necessary to modify cortical excitability, therefore, the reduced current density under the large reference electrode of 0.01mA/cm^2 makes it functionally inefficient. Making the reference electrode inefficient while maintaining the current density at the same level as with a larger active electrode, results in higher concentration of the current density under the stimulated region, thereby facilitating the tDCS effects.

A new approach to tDCS has recently been developed to increase focality of stimulation that uses a montage of 4 x 1 small ring electrodes (<12 mm diameter), called high-definition tDCS (HD-tDCS) (e.g., Borckardt et al., 2012; Datta et al., 2009; Datta, Elwassif, & Bikson, 2009; Minhas et al., 2010; Villamar et al., 2012). In this setup, a central (stimulation) electrode is surrounded by 4 reference electrodes placed within a radius of approximately 7 cm. It has been reported that in 4x1 HD-tDCS the area of cortical excitability modulation is confined to the ring boundary and the peak of electrical field is under the centre electrode, in contrast to conventional tDCS, in which stimulation can spread to unintended cortical regions (Datta et al., 2009; Datta, Truong, Minhas, Parra, & Bikson, 2012). Furthermore, a direct comparison of conventional and HD tDCS (10 minutes of stimulation at 2mA) showed a delayed peak in the intensity of stimulation (at 30 minutes) and aftereffects of more than 2 hours after HD-tDCS compared to conventional tDCS (Kuo et al., 2013). However, further comparative studies are required to provide a better understanding of the advantages and potential safety concerns of HD-tDCS compared to the conventional method.

3.3.5 Online vs. Offline tDCS

Another parameter that researchers usually consider in order to achieve the intended effects is the timing of the stimulation. During online tDCS, participants receive stimulation while executing an experimental task, whereas in an offline setting, stimulation precedes performance of the experimental measures. In a previous study, (Nitsche et al., 2003b) found that applying anodal tDCS during the execution of a motor learning task improved the rate of learning. However, in an offline setting consisting of 10 minutes tDCS prior to performance of the same task, (Kuo, Paulus, & Nitsche, 2006) found no effect on the rate of learning. In line with these findings, Stagg et al. (2009) compared the results of 10 tDCS studies stimulating M1 (8 used online and 2 used offline tDCS) and found stronger effects in the online condition. However, the limited number of studies overall and, particularly the low number of studies utilising offline stimulation suggest that further research is needed – including studies from outside the motor domain – in order to objectively assess the effect of stimulation timing. A recent study (Pirulli, Fertonani, & Miniussi, 2013) aimed to do precisely that. The researchers compared performance on a visual attention task during online vs. offline tDCS (of V1). They found greater facilitation of task performance for the offline condition. Further studies, particularly those investigating cognitive function, would contribute to determining the optimal timing protocol for eliciting the desired stimulation effects.

3.4 Safety of tDCS

The health and safety of participants is of paramount importance in the application of tDCS both in basic science experimental conditions and in clinical settings. As discussed in the previous sections of this chapter, the re-introduction of tDCS in humans (Nitsche & Paulus, 2000; Priori et al., 1998a), has led to a surge of published research using this technique. The majority of these studies show that tDCS is a relatively safe, non-invasive, brain stimulation method. The most severe adverse effects are limited to a few isolated reports of skin lesions under the electrodes (Loo et al., 2011; Frank et al., 2010; Palm et al., 2008). These lesions have occurred in the context of multiple tDCS sessions at the upper range of stimulation parameters (2mA). Two reviews (Brunoni et al., 2011; Poreisz, Boros, Antal, & Paulus, 2007) have identified itching or tingly sensation under the electrode during and after tDCS as the most commonly reported side effect, followed by infrequent reporting of moderate fatigue, headache, and in rare cases, nausea and insomnia. In addition, (Poreisz et al., 2007) found that healthy participants report more incidences of itching sensation whereas patients treated with tDCS reported headaches as the most common adverse effect.

A recent study used different concentrations of NaCl to determine the perceived comfort for participants (Dundas, Thickbroom, & Mastaglia, 2007). Three concentrations of NaCl were determined relative to biological levels of sodium in the human body as follows: low NaCl concentration was equivalent to the intracellular sodium concentration of most cells (15 mM); medium NaCl concentration was equivalent to the sodium concentration in blood plasma (140 mM); and, high NaCl concentration was equivalent to sodium levels expelled from the kidneys (220 mM) (Dundas et al., 2007). The researchers found that as the NaCl concentration increased, participant's comfort ratings decreased. Thus, Dundas and colleagues recommend that in order to reduce discomfort, NaCl concentrations should be kept between 15 and 140 mM. Regardless of the choice of electrolyte, it is recommended that impedance levels should be monitored during stimulation in order to achieve the target current and for safety reasons, many devices provide an indication of impedance during the stimulated period. In some cases, the tDCS device automatically terminates stimulation or reduces stimulation intensity if resistance increases beyond a certain threshold.

Overall tDCS is considered a safe method (e.g., Iyer et al., 2005; Merrill, Bikson, & Jefferys, 2005; Nitsche & Paulus, 2001b), despite the rare reports of undesirable side effects. However, some researchers (e.g., Bikson et al., 2009) have drawn attention to potential brain tissue damage that could lead to cognitive impairment. Bikson and colleagues' concern originated from a previous report by Liebetanz et al. (2009) of brain lesions in rats following tDCS exposure with a current density of 142 A/m^2 for 10 minutes or longer. Liebetanz and colleagues related the lesions to tissue burning. However, as Nitsche & Paulus (2011) point out, the current density used by Liebetanz et al. (2009) is about two orders of magnitude higher than the commonly applied in human studies.

The recent introduction of HD-tDCS comes with warnings regarding the establishment of safety parameters. Although the relatively small number of studies using this approach highlight safety (additionally to focality), compared to conventional tDCS, as the motivations for its development (e.g., Minhas et al., 2011; Datta et al., 2009; Datta et al., 2009; Datta et al., 2012; Kuo et al., 2013; Minhas et al., 2010), it is expected that increased popularity of this approach will contribute to the establishment of safety guidelines for future HD-tDCS research.

To summarise, tDCS is a non-invasive brain stimulation method that is increasingly being employed in the study of motor, visual and cognitive functions in healthy humans (Nitsche & Paulus, 2011; Nitsche et al., 2008) and as a therapeutic tool with clinical populations (e.g., Brunoni et al., 2012). As a suitable methodology for research purposes, tDCS has witnessed a revolutionary transformation since its historical beginnings and as the development of HD-tDCS shows, that transformation is far from complete. TDCS is inexpensive (compared to other brain stimulation methods such as TMS), highly portable (a small battery-driven electric stimulator, sponge electrodes, connecting wires and an electrolyte fluid are all that is needed) and easy to use, all this make it a very appealing experimental tool. As new tDCS research emerges, experimental procedures can be supported by a better understanding of the parameters affecting its efficacy and the safety protocols to which experimenters should adhere.

Chapter 4: The Role of the TPJ in Social Cognition

The temporoparietal junction (TPJ) has consistently been identified as a key brain region involved in social cognition. Several studies suggest that the TPJ controls representations of the self or another individual across a variety of low-level (agency discrimination, visual perspective taking, control of imitation), and high-level (mentalizing, empathy) socio-cognitive processes. Findings from Experiments 1 and 2 suggest that the online control of self-other representations is a common requirement between the inhibition of imitation and visual perspective taking. The experiments described in this chapter aimed to replicate and extend these findings by investigating whether the online control of self - other representations could be modulated using transcranial direct current stimulation (tDCS) of TPJ. In Experiment 3, participants received either excitatory (anodal), inhibitory (cathodal) or sham stimulation of right TPJ before completing the imitation-inhibition, perspective taking and theory of mind tasks. Experiment 4 sought to explore whether TPJ involvement in social cognition is found bilaterally or whether it is limited to the right hemisphere. The results from these experiments are discussed in relation to the TPJ involvement in the online control of self-other representations in social cognition and the efficacy of tDCS as a methodological tool in social neuroscience research.

Experiment 3: Self-Other Representations and the Right TPJ

To date, social cognition studies using fMRI have been the source of the majority of current knowledge concerning the role of TPJ in this domain. Brain stimulation methods such as tDCS are an important addition to fMRI, as they allow cortical excitability to be directly manipulated. In non-social domains, anodal stimulation has proved to be a powerful tool to enhance perceptual (Falcone, Coffman, Clark, & Parasuraman, 2012) and motor (Nitsche et al., 2003b) learning. In contrast, the effects of cathodal stimulation have been found less reliably on cognitive tasks (Jacobson et al., 2012).

Experiment 3 tested the hypothesis that anodal stimulation of TPJ should lead to enhanced socio-cognitive abilities: specifically, by enhancing the ability to control, online, co-activated representations of the self and the other. Participants received either anodal, cathodal or sham stimulation – which produces the same sensation as active stimulation but has no effect on neuronal populations (Nitsche et al., 2008) – of right TPJ for 20 minutes prior to completing the control of imitation and visual perspective taking tasks described in Chapter 2. Additionally, participants also performed a theory of mind task – different from the ones used in Experiments 1 and 2 – in which they were required to make mental and physical judgements either about themselves or a famous person (self-referential task).

All three tasks used in this experiment – including the theory of mind measure (self-referential task) – require representations of the self and the other in three different domains (motor plans, visuospatial perception, mental states). However, although the control of imitation and visual perspective taking require the ability to control online (on a trial-by-trial basis) representations of the self or the other, this requirement is not present in the self-referential task. Prior to presentation of either a mental or a physical judgment in the self-referential task, participants know whether they should judge if the statement describes themselves or another person. An additional distinctive feature of the self-referential task is the inclusion of mental vs. physical judgments. The TPJ has been found to play a crucial role during mental but not physical attributions (e.g., Lombardo, Chakrabarti, Bullmore, & Baron-Cohen, 2011; Saxe & Kanwisher, 2003), therefore a differential effect of stimulation is expected between mental and physical trials. Accordingly, the experimental design employed here allows testing the following predictions: If a difference in performance were only found in the control of imitation and perspective taking tasks but not on the self-referential task – after anodal stimulation – this would suggest that TPJ is causally involved in the online control of self-other representations. Moreover, if TPJ involvement is required for self-other representations in general, it is expected that anodal stimulation – compared to cathodal and sham – will lead to improved performance on the self-referential task for judgments of both 'self' and 'other'. Additionally, if, as suggested by previous research, TPJ selectively differentiates between mental and physical judgements, then it is expected that performance of the anodal group would be better in mental than in physical trials for both self and other. Finally, no differential stimulation effects in either of the tasks would suggest that the TPJ is activated as a consequence of self-other processing (as shown by the fMRI literature) but does not play a causal role in self-other processing itself.

4.1.1 Method

Participants

Forty-nine right-handed adults (24 females, age range 18-45 years, *M* = 26.5, *SD* = 6.7) participated in this study for a small monetary reward. Participants were randomly assigned to the anodal (*N* =17), cathodal (*N* = 17), or control 'sham' (*N* = 15) groups. The groups were matched in terms of age (*F*(2,48) = .35, *p* = .70) and gender ($\chi 2$(2, *N* = 49) = .16, *p* = .92). All participants were healthy volunteers, without any known developmental or neurological disorders and no contra-indications to tDCS. They were all naïve with respect to the experimental hypotheses and remained unaware of what type of stimulation they received until the end of the experiment.

Procedure

Prior to the testing session, all participants were provided with written information about the study and a description of the tDCS procedure. The associated safety/risk warnings were explained and participants were asked to sign an informed consent form. This study received full ethical approval by the local Ethics Committee.

The stimulation was induced using two saline-soaked surface sponge electrodes 35 cm^2 in size and delivered by a battery-driven, constant current stimulator. For the stimulation of the rTPJ, the anodal or cathodal (depending on the group assignment) electrode was placed over CP6 (electroencephalography 10/20 system) (Herwig, Satrapi, & Schönfeldt-Lecuona, 2003). The reference electrode was placed over the vertex, individually measured on each participant. A relatively weak electrical current (1mA) was delivered for 20 minutes. For the sham group, the set-up was identical to the anodal group, but the stimulator was only turned on for 15 seconds; participants felt the initial itching sensation associated with tDCS but received no active current for the rest of the stimulation period. Offline stimulation (i.e. stimulation preceding task performance) was used as previous work suggests that effects are more robust than online stimulation, at least for anodal stimulation (Pirulli et al., 2013).

The control of imitation and perspective-taking tasks used in this experiment have already been described in Chapter 2, the theory of mind task is described below.

The self-referential task was adapted from a previous version used by Lombardo and colleagues, (Lombardo et al., 2010a). Participants were asked to make either mental or physical judgements about themselves or a famous person (Lady Gaga). At the beginning of the task they read a brief bio of Lady Gaga and were told that they would be asked to rate how likely either Lady Gaga (other) or the participant themselves (self) were to have certain opinions, likes, and dislikes. For example, an 'other-mental' judgement would be: *how likely is she to enjoy the adrenaline rush of taking risks?* Whereas, a 'self-physical' judgement could be: *how likely are you to lose and gain weight very quickly?* Prior to each trial, the word 'YOU' or 'LADY GAGA' was presented on the screen for 2 seconds (font size 45pts). Therefore, participants knew before the start of data (RT) collection whether the following opinion judgement would relate to the self or the other. There were 20 items in each trial type (self-mental, self-physical, other-mental, other-physical). Participants made judgements on a scale of 1 – 4 (1= not at all likely, 4= very likely). The self vs. other statements were counterbalanced between groups. To encourage participants to engage with the task and therefore elicit 'other' thoughts in the Lady Gaga condition, they were told that their answers would be compared to the answers given by the artist over a number of interviews and they would receive an 'accuracy score' at the end. This 'score' was randomly generated and presented on the screen at the end of the task. Reaction times for each trial type were recorded.

A surprise memory test was administered immediately after completion of the perspective-taking task, approximately 25 minutes after the self-referential task. Participants were presented with a judgement statement and asked to rate how confident they were that they had seen it before on a scale of 1-6 (1=definitely not seen it, 2=probably not seen it, 3 = possibly not seen it, 4= possibly seen it, 5= probably seen it, 6 = definitely seen it). For items they thought they had seen before (those rated from 4-6) they were further asked to rate how confident they were that the statement was in reference to themselves or to Lady Gaga (1= definitely self, 6= definitely Lady Gaga). Twenty 'old' (previously presented) and twenty 'new' (matched for number of words) statements for each condition were presented.

In order to standardise the memory delay between the self-referential task and the surprise memory test, the tasks were administered to all participants in the following order: control of imitation, self-referential, perspective-taking and memory test for self-referential task. The entire testing session lasted approximately one hour.

4.1.2. Results and Discussion

Control of imitation task

The RT and accuracy data were analysed using ANOVA with Type of Stimulation as the between-subjects factor (anodal vs. cathodal vs. sham) and

Trial Type as the within-subject factor (congruent vs. incongruent). Where sphericity assumptions were not met, Greenhouse-Geisser corrected values are reported. Bonferroni corrections were used for post hoc multiple comparisons.

RT analysis. Figure 4.1 shows the RT data for the Control of imitation task. Prior to the statistical analysis, extreme RT scores identified by the 1.5 x inter-quartile range rule were removed from each participant's dataset. The analysis revealed a significant main effect of Trial Type, $F(1,46) = 46.89$, $p < .001$, $\eta^2_p = .51$; indicating that responses on congruent trials were executed faster than those on incongruent trials – see Figure 4.1A. The main effect of Type of Stimulation was also significant, $F(2,46) = 6.14$, $p = .004$, $\eta^2_p = .21$. Pairwise comparisons showed that this effect was driven by the difference in performance between the anodal and the cathodal stimulation groups ($p = .003$). Crucially, the Type of Stimulation × Trial Type interaction was also significant, $F(2,46) = 4.31$, $p = .019$, $\eta^2_p = .16$. Simple effects analysis showed that in congruent trials, participants who received anodal stimulation responded significantly faster (*M* = 430 ms, *S.E.M.* = 13 ms) than those who received cathodal stimulation (*M* = 484 ms, *S.E.M.* = 13 ms; $p = .004$); however, the anodal vs. sham stimulation contrast was not significant ($p = .21$). During incongruent trials, performance of the anodal stimulation group (*M* = 446 ms, *S.E.M.* = 18 ms) was significantly faster than both the cathodal (*M* = 537 ms, *S.E.M.* = 18 ms; $p = .001$) and the sham (*M* = 506 ms, *S.E.M.* = 19 ms; $p = .026$) conditions. In order to account for the faster performance by the anodal stimulation group in the congruent condition, a one-way ANOVA on the imitation effect (RT incongruent trials – RT congruent trials) was performed. This analysis confirmed that the anodal effect remained significant *F*(2,48)= 4.31, *p* = .019. Pairwise comparisons revealed a difference in performance between the anodal and the cathodal stimulation groups (*p* = .040), while the comparison between anodal and sham approached significance (*p* = .051) – see Figure 4.1B. These results show that anodal stimulation (but not cathodal or sham) of right TPJ results in an increased ability to inhibit the tendency to imitate the stimulus hand on the screen. This finding is consistent with previous studies reporting right TPJ involvement in the control of imitation (Brass et al., 2009; Spengler et al., 2009).

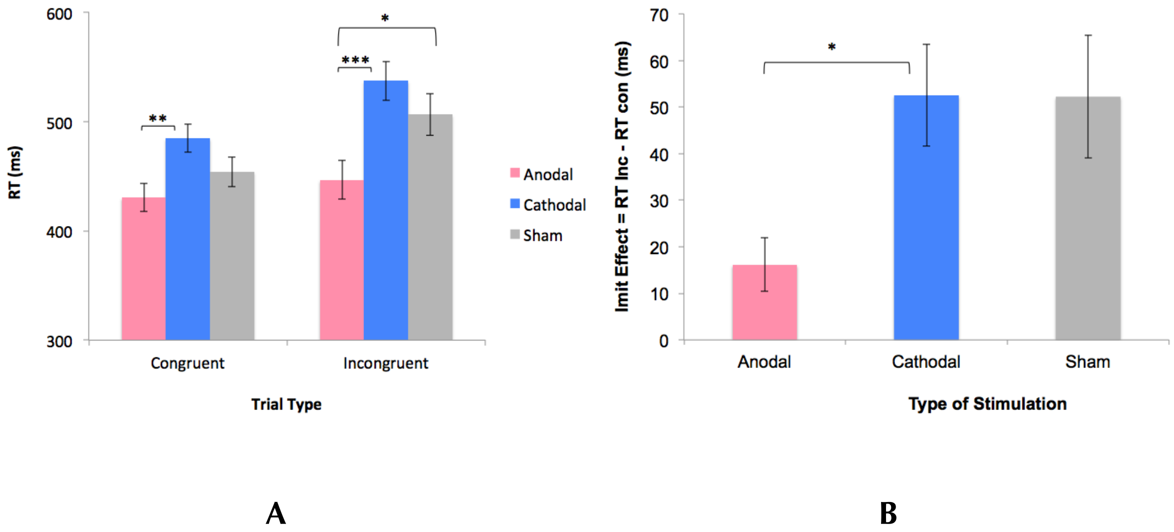

Figure 4.1. *Mean RTs on congruent and incongruent trials (A) and B) imitation effect (RT incongruent trials – RT congruent trials) in the control of imitation task for each stimulation condition. The error bars represent standard error of the mean. *** (p < .001); ** (p < .01); * (p < .05)*

Error analysis. Overall, participants made a small number of errors (*M total*= 6.8, *S.E.M.* = .95). The main effect of Trial Type was significant, $F(1,46) = 19.07$, $p < 0.001$, $\eta^2_p= 0.29$, with participants making more errors in the incongruent ($M = 3.95$, *S.E.M.* = 0.62) than in the congruent ($M = 2.14$, *S.E.M.* = 0.40) trials. The main effect of Type of Stimulation and the Type of Stimulation × Trial type interaction were not significant, ($p =0.84$. and $p =0.49$, respectively*)*, showing that the type of stimulation did not affect accuracy on this task.

Perspective-taking task

The accuracy and RT data were analysed using ANOVA with Type of Stimulation as the between-subject factor and Trial Type (experimental vs. C1 vs. C2) as the within-subjects factor.

Accuracy. Figure 4.2 shows the accuracy data on the experimental trials of the Director task. There was a main effect of Trial Type, $F(1.02,44.96) = 54.52$, $p < .001$, $\eta^2_p = 0.55$. Overall, performance (proportion of correct responses) was worse on experimental trials ($M = .66$, *S.E.M.* = .04) than on control trials: C1 ($M = .96$, *S.E.M.* = .01), C2 ($M = .93$, *S.E.M* = .01), confirming the previously reported difficulty in taking the director's perspective observed using this task. The main effect of Type of Stimulation was also significant $F(2,44) = 4.35$, $p< .02$, $\eta^2_p = .17$. Post-hoc pairwise comparisons showed that performance of the anodal group ($M = .93$, *S.E.M.* = .03) was significantly better than the sham group ($M = .81$, *S.E.M.* = .03, $p = .03$) while the comparison with the cathodal group showed a trend towards significance ($M = .83$, *S.E.M.* = .03,

p = .06). The Type of Stimulation × Trial Type interaction was significant, $F(1.02, 44.96) = 6.37$; $p = 0.003$; $\eta^2_p = .23$. Post-hoc analysis showed that while all stimulation groups performed similarly on control trials (C1: anodal= M = .98, *S.E.M.* = .02, cathodal= M = .96, *S.E.M.* = .02, sham= M = .96, *S.E.M.* = .02; C2: anodal= M = .94, *S.E.M.* = .02, cathodal= M = .92, *S.E.M.* = .02, sham= M = .94, *S.E.M.* = .02), on experimental trials the anodal group (M = .86, *S.E.M.* = .03) performed significantly better than both the cathodal (M = .60, *S.E.M.* = .083, p =.031) and the sham (M = .54, *S.E.M.* = .09, p= .006) groups. Thus, anodal stimulation enhanced performance by making participants better at separating their own perspective from that of the Director's when the two perspectives were in conflict.

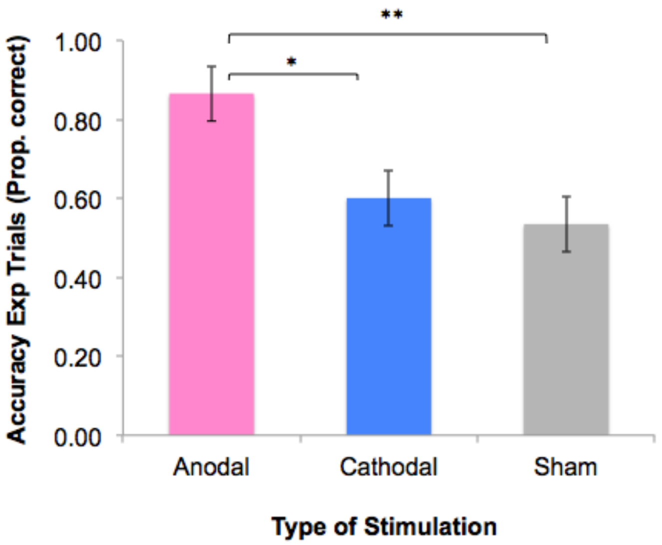

Figure 4.2. *Mean percentage of correct responses on the perspective-taking task task for each stimulation group. The error bars represent standard error of the mean. ** (p <.01); * (p <.05)*

RT. A significant main effect of Trial Type was found, $F(1.75, 77.14) = 80.87$, $p < 0.001$, $\eta^2_p = .65$. Overall, participants responded faster to the C1 ($M = 2.62$s, *S.E.M.* = 48.53) trials than to the experimental ($M = 3.03$s, *S.E.M.* = 74.64, $p < .001$) or the C2 trials ($M = 2.96$s, *S.E.M.* = 65.58, $p < .001$). Neither the main effect of Type of Stimulation nor the Type of Stimulation × Trial Type interaction were significant, (all *p*s > .40).

Self-referential task

In this task, accuracy does not form part of the analysis because of the subjective nature of judgment ratings.

Figure 4.3 shows the RT data for the self-referential task. An ANOVA was performed with Type of Stimulation as a between-subject factor and Target (self vs. other) and Trial Type (mental vs. physical) as the within-subjects factors. There was a main effect of Target, $F(1,46) = 16.33$; $p < 0.001$; $\eta^2_p = .26$. Overall, responses were faster for 'self' ($M = 3.31$ s, *S.E.M.* = .16) than for 'other' trials ($M = 3.56$ s, *S.E.M.* = .17; $p < .001$), replicating previous findings with Western participants on similar versions of this task (Lombardo et al., 2010b; Mitchell, Macrae, & Banaji, 2006). The main effect of Type of Stimulation was also significant $F(2,46) = 6.17$, $p = .004$, $\eta^2_p = .21$). Pairwise comparison showed that the anodal group ($M = 2.72$ s, *S.E.M.* = .28) was faster than the cathodal group ($M = 4.13$ s, *S.E.M.* = .28; $p = .003$) on self- and other-judgments regardless of Trial Type (mental vs. physical). No other main effects or interactions were significant (all *p*s> .24). In order to ensure that the significant main effect of Type of Stimulation did not represent an effect of stimulation on self-other control *between* trials, trials were subdivided into ‘switch’ trials (where a ‘self’ trial is preceded by an ‘other’ trial or vice versa) and ‘no-switch’ trials (where the target of the judgement is the same on trial n and n-1). If there was an effect of stimulation on self-other switching between trials on this task, one would expect this effect to be greater on switch trials than on no-switch trials, resulting in a Type of Stimulation × Trial Type (switch / no-switch) interaction. However, this interaction was not significant (*p* = .33).

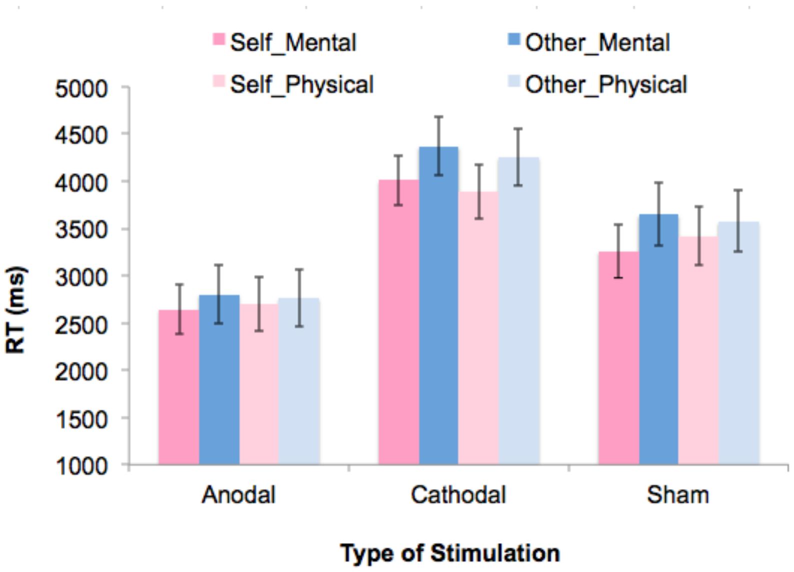

Figure 4.3. *Mean RTs on each trial type of the Self-Referential task for each stimulation group.*

Surprise memory test

The RT and accuracy data were analysed using ANOVAs with Type of Stimulation as a between subject factor and Target (self vs. other) and Trial Type (mental vs. physical) as within subject factors. Accuracy was assessed using Signal Detection Theory (d’ values) (Green & Swets, 1966).

RT. There was a main effect of Target, *F* (1,44) =5.47, $p < 0.024$, η^2_p= .11; overall, responses were faster for self (*M* = 2.5 s, *S.E.M.* = .09 s) than for other trials (*M* = 2.7 s, *S.E.M.* = .11 s). The main effect of Type of Stimulation showed a trend towards significance ($p = .086$). Pairwise comparisons revealed that this trend was driven by overall RT differences between the anodal (*M* = 2.4 s, *S.E.M.* = .1 s) and the cathodal groups (*M* = 2.9 s, *S.E.M.* = .1 s), however, this comparison did not reach significance, $p = .10$. No other main effects or interactions were significant, (all *ps* > .20).

Accuracy. Again, a main effect of Target was found *F* (1,44) =24.19, $p < .001$, η^2_p= .36. Across all groups, participants were better able to remember items that were self-related (*M* = .81, *S.E.M.* = .23) than other-related (*M* = .74, *S.E.M.* = .25), confirming the self-reference effect found in memory research (e.g., Symons & Johnson, 1997). No other main effects or interactions were significant (all *p*s > .42).

In line with the first prediction, the results from Experiment 3 that anodal stimulation enhances performance in both the control of imitation and perspective-taking suggest that within the social cognitive domain, the area of the right TPJ stimulated in this study is recruited in situations where online control of co-activated self and other representations – whether inhibiting 'self' and enhancing 'other' or vice versa –, is crucial for successful social interaction.

In the self-referential task, faster responses of the anodal (compared to the cathodal) group on all trial types suggest that anodal stimulation of right TPJ improved participants' ability to make judgements about both the self and the other. This result therefore provides further support for the commonly reported role of TPJ in representing the self and the other. However, the absence of an interaction between Type of Stimulation × Trial Type in both the self-referential task and the memory test suggests that stimulation of the right TPJ did not have an effect on distinguishing between mental and physical attributions. This contradicts previous findings from fMRI studies that attribute a selective role to the right TPJ for distinguishing between mental and physical judgements (e.g., Lombardo et al., 2011; Saxe & Kanwisher, 2003). However, several fMRI studies have found that processing of trait judgements, for both self and others, are found selectively in the MPFC, (e.g., Mitchell, Banaji, & Macrae, 2005; Spengler et al., 2009, see also Van Overwalle, 2009) for a meta-analytical review).

4.2 Experiment 4 – Self-Other Representations and (bilateral) TPJ

Despite abundant evidence of TPJ involvement in socio-cognitive abilities, the extant literature is far from consistent when it comes to any lateralization of function (See Table 4.1). For example, several neuroimaging studies report bilateral TPJ activation during attribution of mental states such as intentions or beliefs (Gallagher et al., 2000; Jenkins & Mitchell, 2010; Perner, Aichhorn, Kronbichler, Staffen, & Ladurner, 2006; Völlm et al., 2006), while others (and occasionally the same studies) report greater, or exclusive, involvement of right TPJ (false belief: Aichhorn et al., 2009; Perner et al., 2006; Saxe & Kanwisher, 2003; Saxe & Wexler, 2005), moral judgements (Young & Saxe, 2009; Young et al., 2010; Young et al., 2007), experience of agency (David et al., 2006), imitation inhibition (Brass et al., 2005; Spengler et al., 2009), or left TPJ activation (theory of mind (Berthoz, Armony, Blair, & Dolan, 2002a); visual perspective taking (David et al., 2006; Ruby & Decety, 2001; Vogeley et al., 2004; Zacks, Vettel, & Michelon, 2003) – see also meta analysis by (Schurz, Aichhorn, Martin, & Perner, 2013). Furthermore, while some researchers claim a predominant role for right TPJ in social interactions, specifically when understanding other people's minds (e.g., Decety & Lamm, 2007; Saxe 2010), evidence from brain lesion studies show that left TPJ is also necessary (Apperly, Samson, Chiavarino, & Humphreys, 2004; Samson et al., 2004) for mental state attribution. Similarly, neuroimaging evidence from studies of visual perspective-taking tasks report activation of left, but not right, TPJ (Aichhorn et al., 2006; David et al., 2006; Ruby & Decety, 2001; Vogeley et al., 2004).

The results from Experiment 3 are consistent with neuroimaging studies claiming that within the socio-cognitive domain, the right TPJ is involved in self-other representations (e.g., Brass et al., 2009; Decety & Lamm, 2007; Spengler et al., 2009; Van Overwalle 2009). Furthermore, these findings suggest that right TPJ recruitment is necessary for the online control of these representations when they are co-activated on a trial-by-trial basis. Experiment 4 aimed to replicate and extend these findings by investigating whether this TPJ function is lateralized to the right hemisphere or whether it can be found bilaterally. Participants received anodal stimulation of either right TPJ, left TPJ, or the occipital cortex (control site) prior to performing three tasks measuring the three socio-cognitive processes under investigation. Notably, the absence of a stimulation effect in the mental vs. physical judgements of the theory of mind task in Experiment 3 is intriguing because it contrasts with evidence from a substantial number of neuroimaging studies reporting TPJ recruitment during mental state attribution. In this experiment, the self-referential task was replaced by the MASC (described in Chapter 2 – Experiment 2) as an alternative theory of mind measure. The suitability of the MASC was assessed on the basis that it adopts traditional mentalising concepts such as false belief, irony, faux pas and metaphors. Some of these concepts are also present in theory of mind stories, which have been found to activate TPJ. Furthermore, a previous study using this task (Wolf, Dziobek, & Heekeren, 2010) reported left TPJ activation when contrasting scenes requiring mental inferences vs. physical inferences. The findings from this experiment are discussed in relation to the apparent disjointed evidence from neuroimaging studies.

Table 4.1. Example of contrasting evidence of lateralization of TPJ function in socio-cognitive abilities.

	bTPJ	**rTPJ**	**lTPJ**
Visual Perspective Taking (VPT)		- (Santiesteban, Banissy, Catmur, & Bird, 2012) – anodal tDCS of rTPJ enhanced performance in VPT (requiring 3PP) compared to cathodal and sham stimulation	- (Aichhorn et al., 2006) – 3PP vs. 1PP, spatial relation between objects (e.g., in front, behind) vs. comparison of object properties (e.g., small, tall, light). camera vs. comparison of scenes - (David et al., 2006) – Both first (1PP) and third (3PP) person perspective taking (1PP vs. 3PP; 3PP vs. 1PP), inanimate object (camera) perspective vs. comparison of 2 scenes - (Ruby & Decety, 2001) – 1PP vs. 3PP - (Vogeley et al., 2004) – only 1PP - (Zacks et al., 2003) – 1PP
Imitation inhibition	- (Spengler et al., 2010) – TPJ lesion patients (rTPJ *N*= 6, lTPJ *N*= 6, bTPJ *N=1*): correlation between VPT and imit-Inhib	- (Brass et al., 2005) – incongruent vs. congruent trials - (Spengler et al., 2009) – overlapping activation in rTPJ for ToM and imit-Inhib - (Santiesteban et al., 2012) – anodal tDCS of rTPJ reduced automatic imitation compared to cathodal and sham stimulation - (Sowden & Catmur, 2013) – rTMS impaired control of imitation	

Table 4.1. (Cont.)

	bTPJ	rTPJ	lTPJ
Experience of Agency	- (Farrer & Frith, 2002) – action generated by other vs. self	- (David et al., 2006) – passive observation of another's action vs. self-generated action	
Theory of Mind (ToM)			
- Mental state attribution including false beliefs (FB)	- (Gallagher et al., 2000) – ToM vs. non-ToM* stories and cartoons, non-ToM stories and cartoons vs. jumbled sentences or cartoons - (Jenkins & Mitchell, 2010) – Mental inferences of beliefs and preference both ambiguous and unambiguous vs. non-social inference - (Perner et al., 2006) – FB vs. photographs, FB vs. temporal change control (TCC) stories - (Saxe & Kanwisher, 2003) – FB vs. mechanical inference, human action vs. non-human action - (Saxe 2006) – FB vs. Photographs, but more activation in rTPJ than lTPJ during ToM - (Völlm et al., 2006) – mental attribution vs. physical inference cartoons	- (Aichhorn et al., 2009) – FB vs. true beliefs (TB), FB vs. false signs (FS) - (Jenkins & Mitchell, 2010) – Ambiguous vs. unambiguous inferences of belief and preference - (Saxe & Wexler, 2005) – norm-violating mental state of a character from familiar vs. unfamiliar background, normal (congruent) mental state of a character from unfamiliar vs. familiar background - (Perner et al., 2006) – FB vs. photographs, FB vs. FS, FB vs. TCC - (Ruby & Decety, 2004) – other vs. self perspective (both emotional and neutral content)	- (Aichhorn et al., 2009) – FB vs. TB, FB vs. Photographs, FB = FS - (Apperly et al., 2004); (Samson et al., 2004) – patients with damage to lTPJ – impaired in belief reasoning - (Berthoz, Armony, Blair, & Dolan, 2002b) – Stories depicting both intentional and unintentional violation of social norms - (Fletcher et al., 1995) – Comprehension of both mental attribution and physical stories - (Perner et al., 2006) – FB = FS, FS vs. Photographs - (Saxe & Kanwisher, 2003) – Verbal description of theory of mind stories vs. to photographs

Table 4.1. (Cont.)

	bTPJ	rTPJ	lTPJ
- Moral judgments		- (Young et al., 2007) – neutral outcome of moral judgments: negative belief vs. neutral belief - (Young & Saxe, 2009) – Exp 1: moral vs. non-moral facts; negative vs. non-moral, neutral vs. non-moral, neutral =negative outcome. Exp 2: belief: neutral = negative, facts: moral vs. non-moral, outcome: neutral vs. negative - (Young et al., 2010) – TMS of rTPJ lead to judgment of attempted harm (negative belief, neutral outcome) as more permissible than TMS of control site	- (Young et al., 2007) – neutral outcome of moral judgments: negative belief vs. neutral belief, negative outcome: negative vs. neutral - (Young & Saxe, 2009) – Exp 1: no lTPJ activation found. Exp 2: outcome: negative vs. neutral

bilateral (bTPJ), right (rTPJ), left (lTPJ), VPT = Visual Perspective Taking, 1PP = 1st person perspective taking, 3PP = 3rd person perspective taking, FB= false belief, TB = true beliefs, FS = false signs, TMS = transcranial magnetic stimulation, rTMS = repetitive transcranial magnetic stimulation

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* In Gallagher et al 2000, a story was considered ToM if mental states inferences such as false belief or ignorance were required for its interpretation, whereas the non-ToM condition did not require such inferences to understand the meaning

4.2.1 Method

Participants

Forty-five right-handed adults (25 males, age range 18-39 years, *M* = 23.4, *SD* = 4.5) were recruited to take part in this study. They were all university students and as a token for their participation they received a small monetary reward. Upon arrival, participants were randomly assigned to the right TPJ (*N* =15), left TPJ (*N* = 15), or the occipital cortex, Oz (*N* = 15) stimulation condition. The groups were age- (*F*(2,44) = .10, *p* = .91) and gender- (χ^2 (2, *N* = 45) = .72, *p* = .70) matched. All participants were healthy volunteers, without any known developmental or neurological disorders and no contra-indications to tDCS. They were all naïve with respect to the aims of the study and remained unaware of what type of stimulation they received until the end of the experiment.

Procedure

The same protocol described in Experiment 3 was followed for this experiment. All participants received anodal stimulation. For the TPJ stimulation, the anodal electrode was placed over CP6 (right TPJ) or CP5 (left TPJ), according to the EEG 10/20 system. Oz was chosen as the control site as no previous evidence links this occipital area with measures of social cognition. The reference electrode was placed over the vertex, individually measured on each participant. To keep the design consistent with Experiment 3, the stimulation was delivered offline, at 1mA, for 20 minutes.

Following the stimulation, participants completed the three socio-cognitive tasks previously described (the control of imitation, visual perspective taking and theory of mind – MASC) in a randomised order, counterbalanced across participants. The testing session lasted approximately one hour.

4.2.2 Results and Discussion

Control of imitation task

The data from one participant in the Oz group showed extreme scores identified by the 1.5 x IQR rule and were removed from the analysis. The remainder of the RT and accuracy data (rTPJ: *N*=15*;* lTPJ: *N*=15*;* Oz: *N*=14) were analysed using ANOVA with Stimulation Site as the between-subjects factor and Trial Type (congruent vs. incongruent) as the within-subject factor.

RT analysis. Figures 4.4 show the RT data for the control of imitation task. The analysis revealed a significant main effect of Trial Type, $F(1,41) = 97.91$, $p < .001$, $\eta^2_p = .71$; indicating that responses on congruent trials (M = 444 ms; *S.E.*M. = 7.4ms) were executed faster than those on incongruent trials (M = 479 ms; *S.E.*M. = 7.8ms). The main effect of Stimulation Site failed to reach significance, $p = .098$. However, the Stimulation Site × Trial Type interaction was significant, $F(2,41) = 5.68$, $p = .007$, $\eta^2_p = .22$; simple effects analysis showed that RT of incongruent trials were significantly faster after stimulation of both rTPJ and lTPJ compared to Oz (Oz vs. rTPJ, $p = .011$; Oz vs. lTPJ $p = .044$); $F(2,41) = 3.86$, $p = .029$; $\eta^2_p = .16$) – See Figure 4.4A. Furthermore a one-way ANOVA on the size of imitation effect (RT incongruent trials – RT congruent trials) showed a significant effect of Stimulation Site, $F(2,41) = 5.68$, $p = .007$, confirming the improvement in performance by both rTPJ and lTPJ compared to Oz (Oz vs. rTPJ, $p = .044$; Oz vs. lTPJ $p = .008$) – see Figure 4.4B.

Error analysis. The main effect of Trial Type was significant, $F(1,44) = 23.0$, $p < .001$, $\eta^2_p = .36$; with participants making more errors in the incongruent (*M* = 6.7%, *S.E.M.* = .8%) than in the congruent (*M* = 2.3%, *S.E.M.* = .4%) trials. The main effect of Stimulation Site showed a trend towards significance $p=.075$, which was driven by the lTPJ (*M* = 3.4%, *S.E.M.* = .7%) vs Oz contrast (*M* = 5.6%, *S.E.M.* = .7%, $p = .071$). The Stimulation Site × Trial Type interaction was not significant, ($p = .43$), indicating that site of stimulation did not affect accuracy of either congruent or incongruent trials.

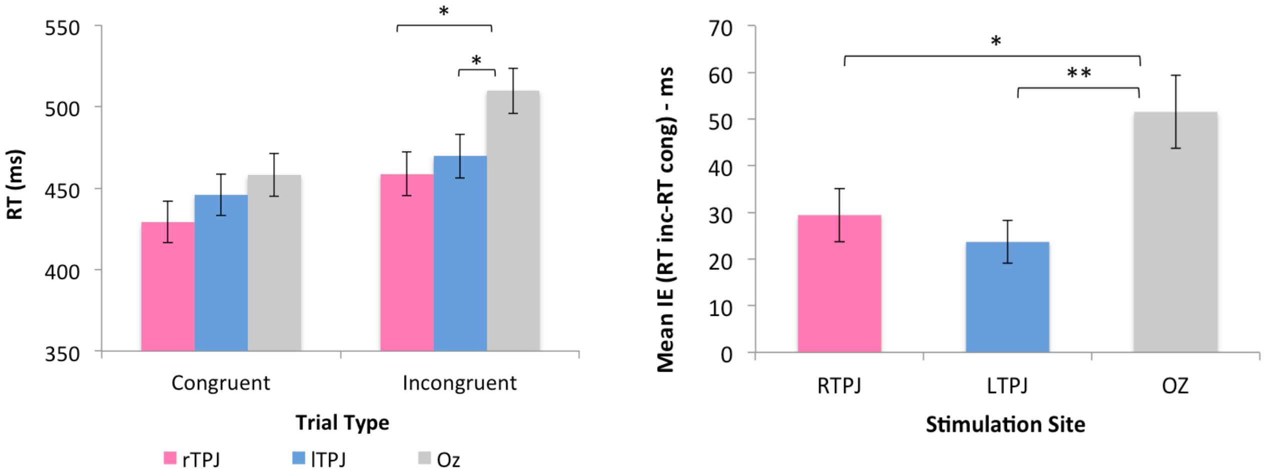

Figure 4.4 *Performance on the control of imitation task. Panel A shows Mean RTs for congruent and incongruent trials while Panel B shows the Mean imitation effect for each Stimulation Site. Error bars represent S.E.M. ** (p <.01); * (p <.05)*

Perspective-taking task

Due to faulty equipment, the data from one participant in the Oz group were not recorded. The remainder of the accuracy and RT data were analysed using ANOVA with Stimulation Site as a between-subject factor and Trial Type (Experimental vs. C1 vs. C2) as the within-subjects factor. Since no differences in accuracy were found between the control trials, the data from C1 and C2 were collapsed for comparison with experimental trials.

Accuracy. Figure 4.5 shows accuracy of experimental trials in the Director task. The analysis revealed a main effect of Trial Type, $F(1,41) = 15.85$, $p < 0.001$, $\eta^2_p = .28$. Overall, performance was better on control trials: (M = 96%, $S.E.M$ = 1%) than on experimental trials (M = 82%, $S.E.M.$ = 3%). The main effect of Stimulation Site was also significant $F(2,41) = 8.12$, $p = .001$, $\eta^2_p = .28$. Post-hoc pairwise comparisons showed that rTPJ stimulation resulted in improved performance compared to Oz stimulation ($p = .001$), while the lTPJ vs. Oz contrast approached significance, ($p = .058$). The Stimulation Site × Trial Type interaction was significant, $F(1,41) = 7.37$; $p = .002$; $\eta^2_p = .26$. Post-hoc analysis showed that while no effects of Stimulation Site were found on control trials ($ps > .05$), on experimental trials, there was an improvement following both rTPJ and lTPJ stimulation which was not seen after Oz stimulation (rTPJ vs. Oz, $p < .001$; lTPJ vs. Oz, $p = .004$); thus, participants were better able to adopt the Director's perspective following stimulation of either right or left TPJ.

RT. A significant main effect of trial type was found, $F(2, 82) = 54.10$, $p < .001$, $\eta^2_p = .57$. Overall, participants responded faster to the C1 (M = 2.4 s, *S.E.M.* = .031 s) trials than to the experimental (*M* = 2.75 s, *S.E.M.* = .055 s, *p* < .001) or the C2 trials (*M* = 2.70 s, *S.E.M.* =.057 s *p* <.001). Neither the main effect of Stimulation Site (*p* =.10) nor the Stimulation Site × Trial Type interaction (*p* = .12) were significant.

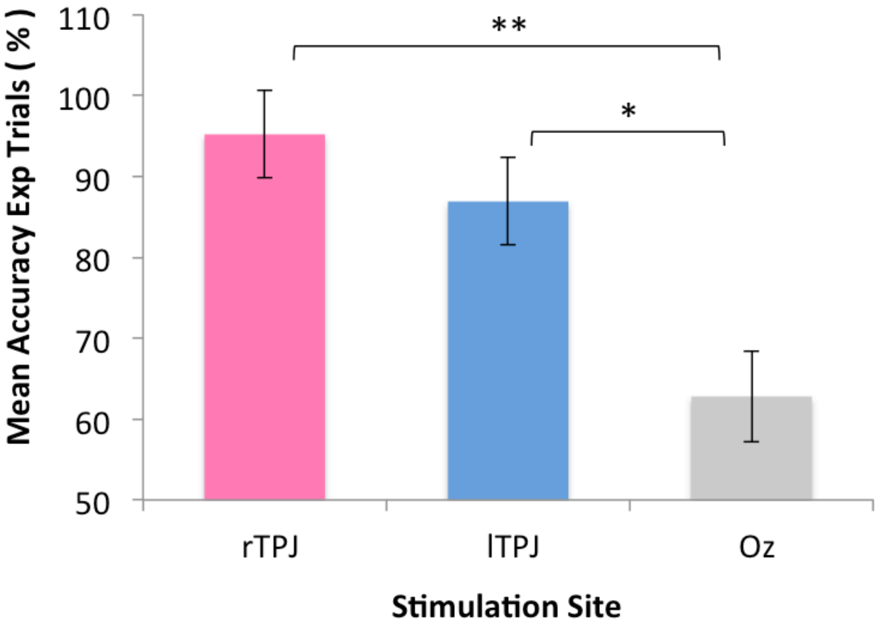

Figure 4.5. *Accuracy performance on the experimental trials of the Director task by each stimulation condition. Error bars represent S.E.M. ** (p<.01); * (p<.05)*

Theory of mind task (MASC)

Two separate analyses were performed on the MASC data. The first analysis included the accuracy rate for theory of mind and control questions and the second sought to investigate if there were group differences in the type of errors participants made. The first analysis revealed that overall, participants' accuracy was higher for control questions (*M* = 89.2%, *S.E.M.* = 1.4%) than for questions requiring mental state attribution (*M* = 78.8%, *S.E.M.* = 1.1%), *F*(1,42)

= 51.69; $p < .001$; $\eta^2_p = .55$. The main effect of Stimulation Site showed a trend towards significance ($p = .10$). Pairwise comparisons revealed this was driven by the overall difference in performance between the Oz group ($M = 87\%$, *S.E.M.* = 1.7%) and the rTPJ group ($M = 82\%$, *S.E.M.* = 1.7%; $p = .12$). The Stimulation Site × Question Type interaction was not significant ($p = .43$).

The analysis of error data revealed a significant main effect of Error Type, $F(2,84) = 25.94$; $p < .001$; $\eta^2 p = .34$; pairwise comparisons showed that overall, participants made fewer errors reflecting a lack of theory of mind ability ($M = 1.69$, *S.E.M.* = .21) than errors reflecting either insufficient theory of mind ($M = 3.38$, *S.E.M.* = .29; $p < .001$) or excessive theory of mind ($M = 4.44$, *S.E.M.* = .36; $p < .001$). No other main effects or interactions were significant (all *p*s > .27). Thus, contrary to findings from fMRI studies of theory of mind suggesting TPJ involvement in the attribution of mental states to others, neither stimulation of rTPJ, nor of lTPJ, resulted in improved performance on this mentalising task.

Is TPJ involvement in self-other representations limited to the right hemisphere?

In the midst of seeming contrasting findings regarding lateralisation of function in the TPJ, this study sought to investigate whether involvement of this brain region in social cognition is limited to the right hemisphere or not. This is the first study attempting to investigate a causal role of bilateral TPJ across different socio-cognitive abilities. The data from Experiment 4 replicated the findings of right TPJ involvement in the control of imitation and visual perspective taking following anodal stimulation in Experiment 3 (Santiesteban et al., 2012a); Hogeveen et al, under review), however, they extend such findings by showing that left TPJ is also recruited during performance of these two socio-cognitive tasks. These results are also consistent with neuropsychological evidence showing that performance in imitation inhibition is correlated with visual perspective taking in patients with lesions to either right, left or bilateral TPJ (Spengler et al., 2010). However, the finding of bilateral TPJ involvement across these tasks is not entirely consistent with the limited evidence available from neuroimaging studies of imitation inhibition and visual perspective taking. For example, as mentioned in the introduction (see also Table 4.1; (Schurz et al., 2013)), fMRI studies of visual perspective taking have generally reported left but not right TPJ activation, whereas imitation inhibition studies have reported activation of right but not left TPJ. Several factors could account for the seemingly contrasting findings between these fMRI studies and the results from Experiment 4, ranging from differences in methodologies employed, experimental design and choice of dependent variables included in the statistical analysis.

The data obtained from fMRI studies is based on changes in the Blood Oxygen Level Dependent (BOLD) signal. Only brain regions showing the strongest BOLD signals and surviving, more often than not, a conservative statistical threshold are reported as showing significant activity during performance of a given task, whereas areas that may be active at a lower threshold are not reported and yet, such activations could represent true effects, resulting in a Type II error. Consistent with this view, Lieberman &

Cunningham, (2009) argue that the extreme focus on avoiding Type I errors (reporting false positives) in fMRI research leads to increasing Type II errors (missing true effects). In the context of the present study, if both right and left TPJ are activated during performance of a specific task, but the activation is stronger in the right and survives the conservative statistical threshold, then activation in the left TPJ might not be considered of interest and therefore is not reported and vice versa. This could explain the reported fMRI findings of both visual perspective taking and imitation inhibition studies. Arguably, weaker activation of one hemisphere over the other would suggest lesser involvement in the specific cognitive process under investigation. However, unless meta-analysis data were available for the smaller/ unreported effects, a conclusion of lesser involvement of the hemisphere showing weaker activation is debatable. At single study level, the sensitivity of random effects analysis (inter-subject variability effects of regional activity) performed within a small number of subjects (as sample size is a constraint in fMRI studies) is low (Thirion et al., 2007; Wei et al., 2004). Therefore, fMRI researchers tend not to report effects that do not meet the statistical criteria. Indeed, Lieberman and Cunningham (2009) argue that if individual studies reported smaller effects (at more lenient thresholds), when included in a meta-analysis, the sum of these effects across studies would emerge as true effects, whereas false positives (Type I errors) will self-erase as they will not be replicated. Yet, since smaller effects are not reported, they can never be considered for future replications.

Thirion et al., (2007) demonstrate this paradox with a sample of 78 participants. They observed that the analysis of 6 different groups of 13 subjects would lead to different reports of activated regions under the same experimental conditions at a standard threshold (*p* < .001 uncorrected for multiple comparisons), whereas including the pooled data from the 78 subjects, would dramatically increase the reliability and sensitivity of the analysis (Thirion et al.,2007) – see Figure 4.6. Considering the small number of fMRI studies for both the control of imitation and visual perspective taking, a combination of future replication of fMRI experiments, including publication of smaller effects, and data from brain stimulation studies such as those presented here, would contribute to the advancement of knowledge about lateralization of TPJ function.

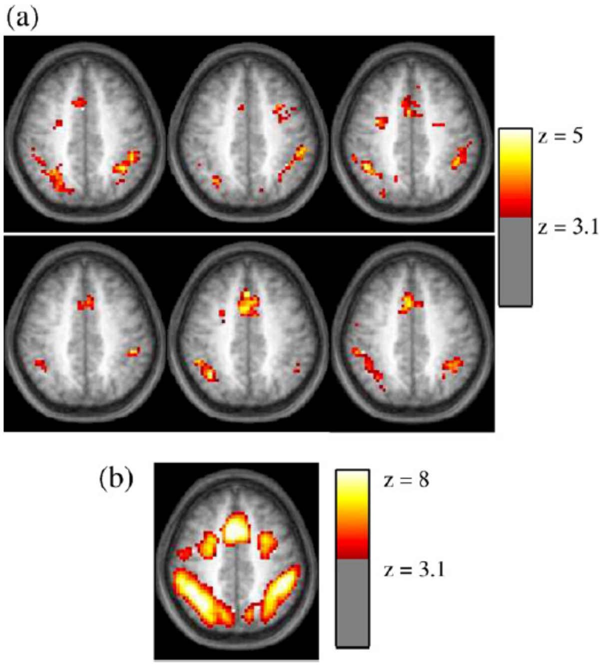

Figure 4.6. *Illustration of activity maps from Thirion et al., (2007). a) Shows different activation patterns in 6 separate groups of 13 subjects each, while b) shows the increased sensitivity and reliability with the combined data from all 78 subjects. Reproduced with permission from Elsevier, © 2007.*

Another potential explanation for the discrepancy between the tDCS findings presented here and previous fMRI studies of visual perspective taking could lie in the choice of contrasts for the statistical analysis. Usually, the key experimental question in fMRI studies of visual perspective taking is to identify brain areas that are more active when participants adopt either a first person perspective (1PP; 1PP vs. 3PP) or a third person perspective (3PP; 3PP vs. 1PP), e.g., David et al., 2006; Vogeley et al., 2004). Therefore, overlapping activity during both 1PP + 3PP would not be reported. It is possible that such overlapping unreported activation lies within right TPJ and only left TPJ activation survives statistical analysis of the contrasts mentioned above. Conversely, the present tDCS data show that stimulating both right and left TPJ results in enhanced control of co-activated representations of self (1PP) and other (3PP). In the context of fMRI, these co-activated representations of self and other would most likely be found in the unreported, overlapping 1PP + 3PP activation.

The TPJ is part of a network of brain regions, also including the medial prefrontal cortex, posterior cingulate cortex, precuneus, superior temporal sulcus, and temporal poles (e.g., Adolphs 2003b, 2009; Frith & Frith, 2003; Mar 2011) that consistently activate when participants perform tasks requiring the attribution of mental states, either to the self or others. In the present study, however, no evidence was found of TPJ involvement, in either hemisphere, during mental state attribution. This finding is consistent with those from Experiment 3 (Santiesteban et al., 2012a) and with the behavioural training-paradigm employed in Experiment 1 (Santiesteban et al., 2012b) and the mirror-touch synaesthesia study (Experiment 2)[1]. In response to a concern about the sensitivity of the theory of mind task used in each of the previous studies, Experiment 4 employed a task, designed to approximate real-life social interactions (MASC, also used in Experiment 2) and which has shown TPJ activation in a previous fMRI study (Wolf et al., 2010). Yet, no differential stimulation effect was found on this task. Unlike the imitation inhibition and visual perspective taking tasks, accurate performance on the theory of mind task (MASC) does not require online control of self-other representations. The MASC requires participants to make mental state attributions to the characters in the film. To understand the plot, participants must separate the facts presented to them (e.g., the character's utterances) from the relevant mental states they attribute to the character (e.g., based on the character's facial expressions). This self vs. other distinction process takes place online. However, when subsequently presented with a question about the character's mental state (i.e. offline), participants can answer correctly by getting into the mindset of the character, without needing to represent simultaneously their own mental states and those of the character in the film. The online processing required in both the perspective-taking and the imitation-inhibition tasks contrasts with the offline measure used in the theory of mind task, and this difference could explain our failure to find a stimulation effect (of right and /or left TPJ) in the MASC.

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[1] The two behaviour examples (Experiments 1 and 2) refer to the lack of differential effects on the theory of mind measure compared to the control of imitation and visual perspective taking tasks.

As mentioned earlier, (Wolf et al., 2010) did find activation of left TPJ. One potential explanation of this discrepancy is that fMRI data are more sensitive than behavioural assessment on this task. However, it is worth noting that although overall performance on the mental inference questions was good across all three groups (right TPJ: *M* = 78%, *S.E.M.* = 6.2%; left TPJ: *M* = 77%, *S.E.M.* = 8.9%; Oz: *M* = 81%, *S.E.M.* = 6.4%), the room for improvement on these scores do not suggest that a ceiling effect prevented an effect of stimulation from being observed. The MASC also has the advantage, compared to other theory of mind measures, of differentiating between the types of errors participants make, ranging from total theory of mind failure to excessive mentalising. Yet, no differences in performance between stimulation groups were found on the error measures either. A second potential explanation for the absence of a stimulation effect on this task could lie in the lack of spatial specificity of tDCS (Faria, Hallett, & Miranda, 2011; Nitsche et al., 2007; Sparing & Mottaghy, 2008), particularly when using large electrodes like the ones used in these experiments, thus preventing the distinction of functional subdivisions in the TPJ. Therefore, it is possible that the areas of the TPJ stimulated in Experiment 4 are distinct from those reported in the study by Wolf and colleagues. However, it could be argued that the large size electrodes used in this study are likely to increase the current spread across a relative large area of the TPJ, making it less likely that the TPJ region activated in the Wolf et al., study was not affected by anodal stimulation. Nevertheless, it will be interesting to examine this potential explanation further, perhaps by employing a paradigm combining both fMRI and tDCS or by using fMRI-guided neuronavigation prior to tDCS, thus ensuring precise positioning of the electrodes in the same region of TPJ. Until such evidence emerges, any interpretations concerning differential regions within TPJ as a potential alternative explanation to our results remain speculative.

4.3 General Discussion

Experiments 3 and 4 describe the first tDCS studies to date investigating the role of TPJ in social cognition. The experimental question they set out to address concerns the involvement of the TPJ in mechanisms of self-other representation within three socio-cognitive domains: the control of imitation, visual perspective taking and theory of mind. Experiment 3 sought to find evidence of a general role of right TPJ in self-other representations across these social abilities, and/or a more selective role in the control of self-other representations when they are co-activated. The findings show that anodal (but not cathodal or sham) stimulation of right TPJ significantly improves performance in the control of imitation and visual perspective taking domains, thereby providing support for the selective role of right TPJ during online control of self-other representations. Interestingly, the observed effects did not differentiate between self vs. other representations. That is, the effects were present regardless of whether such online control required enhancement of 'self' and inhibition of 'other' representations (as required in the control of imitation task) or enhancement of ‘other’ and inhibition of ‘self’ (as required in the visual perspective taking task). However, contrary to previous fMRI studies of theory of mind, the data from Experiment 3 do not suggest a selective role of right TPJ in the attribution of mental states, since no significant differences were found between mental vs. physical judgments in the theory of mind measure. Instead, a significant improvement was observed on RT measures for both self and other judgements following anodal stimulation, a finding that is consistent with the general role of right TPJ in self-other representations. However, because this is the first study investigating the effects of tDCS of TPJ in these socio-cognitive abilities, the present findings would benefit from future replications and perhaps the employment of different measures.

Replication of these findings was one of the aims of Experiment 4, which also investigated whether the effects observed in Experiment 3 were specific to the right hemisphere or whether they could be found bilaterally.

The results from Experiment 4 replicated and extended those of Experiment 3 by showing that anodal stimulation of both right and left TPJ (compared to a control site) led to enhanced performance in the same measures of the control of imitation and visual perspective taking used in Experiment 3. Also in line with the data from Experiment 3, no stimulation effects were found in the theory of mind measure used in Experiment 4. The findings of bilateral TPJ involvement in the control of imitation and visual perspective taking, and the lack of stimulation effect on the theory of mind measure are not consistent with the extant evidence from fMRI studies of these socio-cognitive abilities. However, the limitations of fMRI methodology and choice of contrast included in the statistical analysis could go some way towards explaining these contradictory findings. Taken together, the results from both experiments show the potential contribution of brain stimulation methods to the field of social cognition. Although no currently available methodology for social cognitive neuroscience research is perfect, perhaps future research could benefit from a combination of neuroimaging and brain stimulation methods in an attempt to ease current imperfections.

Chapter 5: The Role of Culture in Self-Other Processes

The experiments described in Chapters 2 and 4 show that self-other representations can be modulated by the specific demands of the social situation and that both behavioural training to control self-other representations and stimulation of the TPJ can enhance this modulation. The experiments described in this Chapter seek to investigate if culture also plays a modulatory role in socio-cognitive processes relying on the control of self-other representations. Specifically, Experiment 5 explores the relationship between migrant's cultural attitudes and imitation, while Experiment 6 seeks to investigate the relationship between self-construal styles and the three socio-cognitive abilities under investigation (the control of imitation, perspective taking and theory of mind).

5.1 Introduction

Migrating to a different country has an impact on various aspects of the self, requiring important redefinitions and reconstruction of both personal and social identities. The redefinition of these identities occurs in the context of, often, conflicting choices between membership in the host culture and attachment to values of the heritage culture (Padilla & Perez, 2003). According to Barry's model of migrant's acculturation (Berry 2005), *integration* is achieved when individuals value both maintenance of the heritage culture and identity but also seek contact with, and take part in, the larger society within the host culture. *Assimilation* refers to a preference for the host culture at the expense of the heritage culture. *Separation* is associated with a preference for the heritage compared to the host culture. Finally, *marginalization* occurs in the presence of little or no interest in either the heritage or the host culture. This bidimensional model of acculturation, comprising attitudes towards both the heritage and host cultures, provides a rich environment in which to study self-other processes. However, to date, there is a lack of empirical research combining this area of social psychology with social cognition. The present study explores the relationship between migrant's cultural attitudes and their imitative behaviour.

5.1.1 The Social Function of Automatic Imitation

The automatic imitation of gestures and behaviour of our interaction partners, also known as mimicry (Chartrand & Bargh, 1999), is considered to have played a fundamental role in evolution, allowing humans to communicate and maintain harmonious relationships with members of their own groups (Lakin et al., 2003). According to Lakin et al. (2003) such an important role in evolution has now evolved to facilitate positive social interactions. Evidence for this claim has been found in studies showing that automatic imitation promotes rapport, affiliation and group harmony. For example, people who engage in imitative behaviour are rated as more likeable by their interaction partners than those who do not imitate (Chartrand & Bargh, 1999). Similarly, when people are imitated they feel closer to their interaction partner and rate the interaction as smoother than when no imitation occurs (Stel & Vonk, 2010). It has also been found that the extent of language mimicry, both during face-to-face and text-based computer-mediated communication, predicts group cohesiveness (Gonzales, Hancock, & Pennebaker, 2010). However, individuals are not always motivated to affiliate and create positive rapport with every person with whom they may interact.

Motivational and situational factors play a role in modulating the extent to which people display imitative behaviour. For example, individuals are more likely to engage in mimicry with in-group members if they share a common goal and cooperation is required, but not when they are competing against each other (LaFrance, 1985). Similarly, in situations where building rapport is perceived as advantageous, individuals with a high degree of self-monitoring, who are motivated and able to control their public appearance (Cheng & Chartrand, 2003), and those who wish to be liked, such as narcissists (Ashton-James & Levordashka, 2013), are more likely to imitate their interaction partner, particularly if their interaction partner is judged to have a superior social status to them (see also Carr et al. (2013). Research also shows that individuals who are particularly motivated to be accepted by their peers, for example, those who are socially excluded from their group, engage in more imitation than those who are included in the group (Lakin & Chartrand, 2005; Lakin, Chartrand, & Arkin, 2008). The primary aim of Experiment 5 is to investigate if automatic imitation can also be modulated by a different motivational / situational factor such as migrants' cultural attitudes towards either the host or the native culture.

5.1.2 Self Construal Styles and Imitative Behaviour

A second line of research from cultural psychology, relevant to self-other processes, relates to how individuals see themselves in relation to others – also known as self-construal styles (SCS). Those with 'independent' self-construals have a sense of the self as autonomous beings, separate from interpersonal context. They tend to value uniqueness, self-promotion and assertiveness. A contrasting view of the self is present in Individuals with 'interdependent' self-construals, who tend to value cooperation and group cohesiveness. They have a sense of self as intertwined with the other, particularly close others, to such extent that meeting another's goals and desires are a requirement to achieving the self's goals and desires (Markus & Kitayama, 1991).

The study of automatic imitation has been extended to the context of cultural differences in SCS. Previous studies have shown that people with an interdependent SCS engage in more imitative behaviour than those with a dependent SCS (van Baaren et al., 2003). The relationship between imitation and SCS seems to be bidirectional. In a set of experiments, (Ashton-James, van Baaren, Chartrand, Decety, & Karremans, 2007) found that being imitated activates an interdependent SCS, and in turn, this effect mediates prosocial behaviour. The role of SCS on imitation is also explored in Experiment 5.

5.2 Experiment 5: Imitation Effects and Acculturation Strategies of Polish Migrants in the UK

This study seeks to extend previous findings of motivational and situational factors modulating automatic imitative behaviour by exploring the effects of acculturation attitudes of Polish migrants in the UK on imitation. This migrant group was chosen because since 2004, when Poland joined the European Union, it has become one of the largest migrant groups in the UK. This is confirmed by the latest UK Census (2011), which revealed that Polish is the second most spoken language in England and third (after Welsh) in the UK. The four acculturation attitudes of the Polish migrants that took part in this study were identified based on their answers to a cultural preference questionnaire. Imitative behaviour towards the native vs. the host culture was measured using an adapted version of the control of imitation task described in Experiment 1 (see Method). This is the first study to explore the relationship between acculturation strategies and automatic imitative behaviour of immigrants towards a member of their native vs. the host culture. Based on the existing evidence from cultural psychology studies of imitation, it is expected that differences in acculturation strategies would modulate automatic imitation. Particularly, the chosen experimental design allows for the following predictions: a) Polish migrants reporting stronger preference for the British culture (assimilation strategy) would imitate a British more than a Polish individual, b) the opposite pattern is expected from those who report higher preference for the Polish culture (separation strategy) – more imitative behaviour towards a Polish individual, c) no differences in the imitation effect towards the British or Polish individuals in the assimilation and marginalization groups.

5.2.1 Method

Participants

The Polish group consisted of 40 healthy adults (26 females) living in the London area, aged between 19 and 54 years (*M* = 31.6, *SD* = 6.0). The length of residence in the UK ranged between 6 months and 32 years (*M* = 7.6 years, *SD* = 6.2)[1]. Based on responses to the cultural attitudes questionnaire (see below), for the second part of the data analysis Polish participants were assigned to one of four acculturation strategies: assimilation (high preference for British over Polish culture, *N* = 9), separation (high preference for Polish over British culture, *N* = 8), integration (high preference for both British and Polish cultures, *N* = 12) and marginalization (low preference for both British and Polish cultures, *N* =11). In the British group there were 20 healthy adults (9 females), aged between 21 and 58 years (*M* = 34.1, *SD* = 10.9). The groups were matched for age ($t(58)= 1.18$, $p = .24$) and gender ($\chi^2 = 2.19$, $p = .14$).

Materials and Procedure

Participants watched a 4-minute video in which two female actors, one British, one Polish living in the UK, introduced themselves and read a brief current affairs article relevant to the UK and Poland respectively (see Figure 5.1A). Participants were encouraged by the actors to pay attention, as they would be required to answer questions about the article's content after the

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[1] Two Polish participants did not disclose the length of residence in the UK, therefore their data were excluded from the correlation analysis.

video. This manipulation was introduced to ensure participants' engagement and identification with either or both cultures. The actors also provided verbal instructions for the control of imitation task. There were two identical videos with only one difference between them, in one video the Polish actor was sitting on the left and the British actor on the right ('Polish left'), and for the second video, the sitting position was reversed ('British left'). Half of the participants watched the 'Polish left' video while the other half watched the 'British left' video. Then participants were required to perform the imitation-inhibition task.

Control of imitation task: This was a modified version of the procedure used in Experiments 1-4. The main modification was made to the onscreen stimulus, which now showed the lower arm and hand of either the British or Polish actor previously seen on the video. Although, they could not see the actors' faces, participants were able to identify the hand by the colour of the jumper's sleeve, red for the Polish actor and blue for the British actor (as worn in the video, see Figure 5.1A). The remainder of the procedure was kept the same as described in Experiment 1. Participants were instructed to respond with an index or middle finger lifting action to a number cue that appeared between the fingers of the stimulus hand. If the number cue was 1, they had to lift their index finger, if it was 2, then they had to lift their middle finger. Simultaneously to the appearance of the number cue, there was a lifting movement of the index or middle finger of the stimulus hand. The relationship between the observed movement and the movement required by the number defined two trial types. On congruent trials, the required finger movement was the same as the observed movement (Figure 5.1B); whereas on incongruent trials, the required finger movement was different from the observed movement (Figure 5.1C). Thus, on incongruent trials participants were required to inhibit an imitative response and perform the pre-instructed movement. There were thirty trials in each of the four combinations of observed and executed finger movements (congruent British, congruent Polish, incongruent British, incongruent Polish), presented in a random order in two blocks of 60 trials each. The Polish and British hands were presented on the same side of the screen as the actors were sitting in the video, for participants who watched the 'British left' video, the British hand appeared on the left side of the screen and the Polish hand on the right. This order was reversed for those who watched the 'Polish left' video. The duration of the task was approximately 8 minutes.

Following completion of this task, Polish participants were asked to complete a questionnaire asking for information such as their age and length of stay in the UK and a Cultural Attitudes questionnaire. The latter consisted of 28 items designed to produce a preference score for British and Polish cultures, with half of the items relating to each culture. Among the items included were preference for food, TV programs, films, support for sports team, newspapers, web pages, politics, friends, spouse, child naming, language, and intention to remain in the UK or return to Poland. The British and Polish preference questions were mixed and the order of presentation was counterbalanced across participants (the Cronbach's α coefficient of internal consistency for the British and Polish preference items were .65 and .67 respectively). Based on the answers to this questionnaire, each participant received a score for British and Polish preference. Using a median split, a value was obtained for high and low preference in each culture, which allowed the assignment of participants to each of the 4 cultural attitudes group mentioned above.

Additionally, thirty-four participants (British *N*=10*,* Polish *N* = 24*)* had been recruited as part of a pilot study for a different project and were also asked to complete the Self-Construal Scale[1] (Singelis 1994). This is a frequently used measure of self-construal in cross-cultural studies. The administered version contained a total of 30 items (Hardin, Leong, & Bhagwat, 2004), 15 items each for independent and interdependent SCS. An independent SCS item in this scale could be “I enjoy being unique and different from others in many respects”, whereas an interdependent SCS item would be “It is important for me to maintain harmony within my group”. Each item is rated on a likert scale ranging from 1 (Strongly disagree) to 7 (Strongly agree). Reliability of this scale in the current sample was between moderate and acceptable, Cronbach’s α independent = .59, interdependent = .75.

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[1] To avoid confusion, throughout the text the name of the measure Self-Construal Scale is spelled throughout, while the term self-construal styles, referring to independent vs. interdependent, is used in its acronym form: SCS.

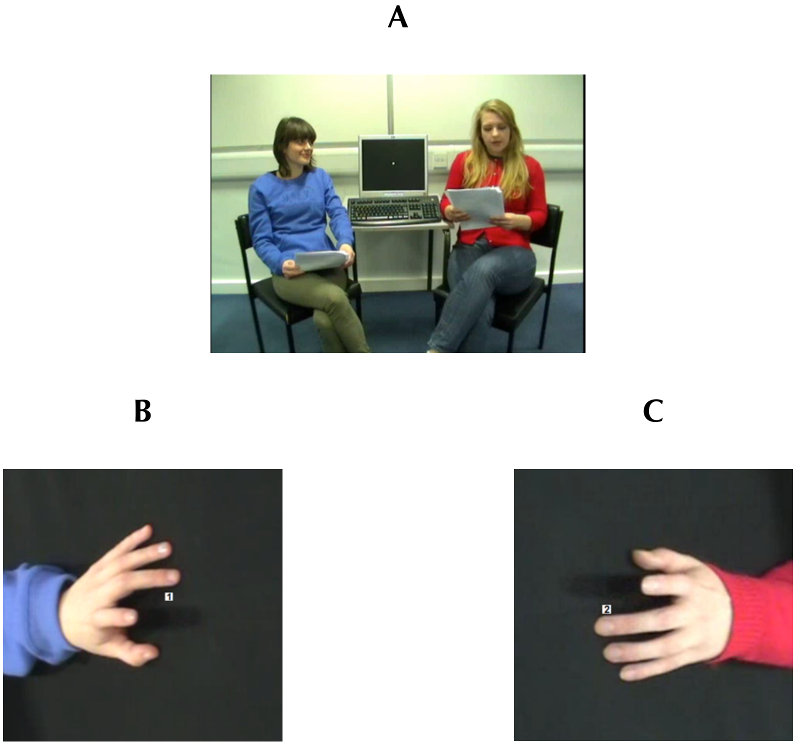

Figure 5.1. *Examples of the stimuli presented. Panel A shows a frame from the video that participants watched prior to performing the imitation-inhibition task. The British actor is wearing a blue sweater while the Polish actor is wearing a red sweater. Half of the participants were presented with the British actor sitting on the left (BL), while the other half were presented with the Polish actor sitting on the left (PL). Panel B shows an example of a congruent trial performed by the British actor and Panel C shows an example of an incongruent trial performed by the Polish actor from the imitation-inhibition task for participants who watched the BL video.*

5.2.2 Results and Discussion

Prior to the statistical analysis, extreme RT scores identified by the 1.5 x inter-quartile range rule (IQR, (Tukey 1977a)) were removed from each participant's dataset. The RT analysis excluded incorrect responses (6% of the data). RT and accuracy data were analysed with a 2 x 2 x 2 ANOVA, Congruency (congruent vs. incongruent) and Hand Identity (British vs. Polish) were the within-subject factors and Group (British vs. Polish) the between-subject factors. Where sphericity assumptions were not met, Greenhouse-Geisser corrected values are reported. Bonferroni corrections were used for post hoc multiple comparisons. No effect of side of presentation was found, all *ps* >.11.

RT Analysis. A main effect of Congruency was found, *F*(1,58) = 22.97; $p < .001$, $\eta^2_p = .28$. Overall, responses were faster for congruent trials (*M* = 529 ms, *SEM.* = 7.42) than for incongruent trials (*M* = 544 ms, *SEM.* = 8.04). The main effect of Hand Identity was also significant, *F*(1,58) = 6.03; $p = .017$, $\eta^2_p = .09$. Responses were faster when the stimulus hand was believed to be that of the British actor (*M* = 532 ms, *SEM.* = 7.73) than the Polish actor (*M* = 540 ms, *SEM.* = 7.76). However, the main effect of Group was not significant ($F < 1$, *p* = ns), in fact, Mean RTs were identical for both Groups (British [*M* = 536 ms, *SEM.* = 12.37], Polish [*M* = 536 ms, *SEM.* = 8.75]). The Congruency × Hand Identity interaction was significant, *F*(1,58) = 5.54; $p = .022$, $\eta^2_p = .09$. Simple effects analysis revealed a larger imitation effect (RT incongruent – RT congruent trials) for the hand of the British actor (*M* = 13 ms, *SEM.* = 3.69) compared to the hand of the Polish actor (*M* = 2.2 ms, *SEM.* = 4.29); *F*(1,58) = 13.42; $p = .001$, $\eta^2_p = .19$). The 3-way interaction of Congruency × Hand Identity × Group was also significant, *F*(1,58) = 5.40; $p = .024$, $\eta^2_p = .19$. Simple effects analysis showed that this interaction was driven by the British group showing a significantly greater automatic imitation effect (RT Incongruent – RT congruent) when the stimulus hand was British (*M* = 24.19 ms, *SEM.* = 6. 65) but not when it was Polish (*M* = 1.71 ms, *SEM* = 6.21), *F(*1,58) = 8.21; *p* =

.006, $\eta^2_p = .12$), whereas the same contrast in the Polish group was not significant (British hand: *M* = 17.06, *SEM* = 4.71, Polish hand: *M* = 16.92, *SEM* = 4.39; *p* = .98) – *See Figure 5.2*. This result indicates that while association of the stimulus hand with the British actor facilitates an in-group imitation bias for the British participants, the equivalent association failed to elicit the in-group bias in their Polish counterparts.

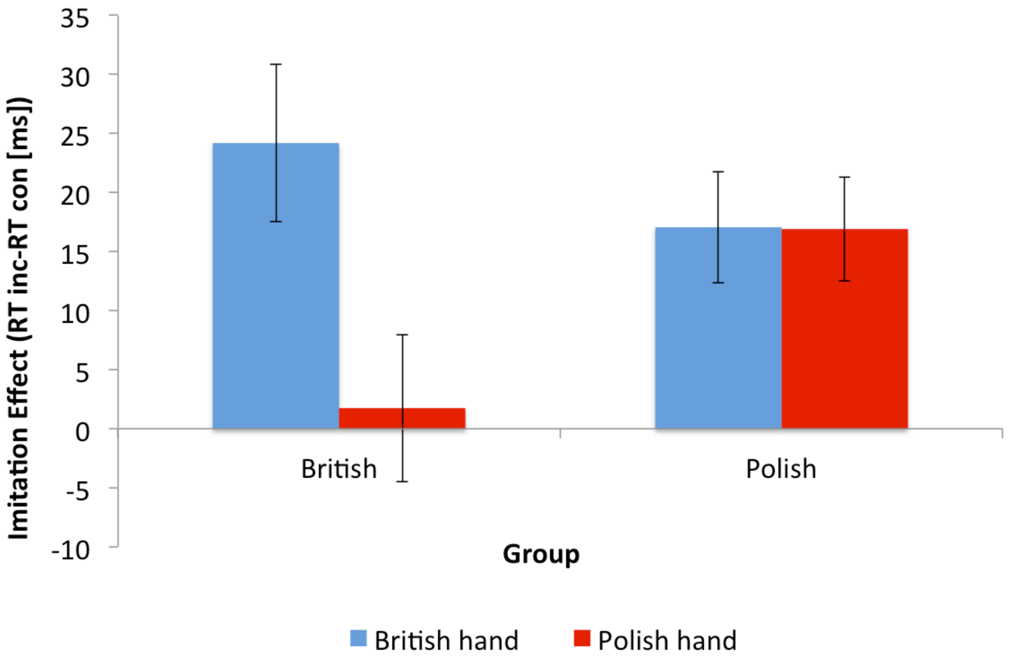

Figure 5.2 *Group × Hand Identity interaction. The blue line represents the imitation effect (RT incongruent – RT congruent trials) for the British hand and the red line represents the imitation effect for the Polish hand. Error bars represent SEM.*

Error Analysis. Equivalent analyses of the error data showed that the main effect of Congruency failed to reach significance (*p* = .07), with a trend towards more errors on incongruent (*M* = .06%, *SEM.* = .012) than on congruent (*M* = .04%, *SEM.* = .009) trials. No other main effects or interactions were significant (all *p*s > .47), confirming the absence of speed-accuracy trade-offs.

Cultural Attitudes. To aid further exploration of the lack of in-group imitation bias in the Polish group, an additional analysis was performed on the imitation effect (RT incongruent – RT congruent trials) for both the British and the Polish hand with a 2 × 4 ANOVA with Imitation Effect (British hand vs. Polish hand) as the within-subjects factor and Acculturation Strategy (assimilation, separation, integration, marginalization) as the between-subjects factor for both RT and accuracy.

The main effect of imitation failed to reach significance, $p = .99$. Although the main effect of Acculturation Strategy was significant, $F(3,36)= 3.15$, $p = .037$, $\eta^2_p = .21$, post hoc pairwise comparisons revealed that the only contrast approaching significance ($p = .08$) was the integration ($M = 33.4$ ms, *SEM.* = 6.42) vs. the assimilation ($M = 7.9$ ms, *SEM.* = 7.41) strategies. Notably, the Imitation Effect × Acculturation Strategy interaction was also significant, $F(3,36) = 4.63$, $p = .008$, $\eta^2_p = .28$. This interaction is illustrated in Figure 5.3. Simple effects analysis confirmed that while the assimilation group showed a significantly reduced imitation effect when the stimulus hand was that of the Polish actor ($M = -7.8$ ms, *SEM.* = 8.91) compared to the hand of the British actor ($M = 23.5$ ms, *SEM.* = 9.65); $F(1,36) = 7.78$; $p = .008$, $\eta^2_p = .18$), the inverse was true for the separation group (British actor's hand: [$M = -3.2$ ms, *SEM.* = 10.23], Polish actor's hand: [$M = 23.5$ ms, *SEM.* = 9.45]; $F(1,36) = 5.06$; $p = .031$, $\eta^2_p = .12$). The same contrasts for the integration and marginalization groups failed to reach significance, both *ps*>. 05. Simple effects analysis also revealed more variability in the data when the stimulus hand was Polish than when it was British. Accordingly, the following contrasts reached significance in the Polish hand condition: assimilation vs. separation (*p* = .021), assimilation vs. integration (*p* = < .001) and integration vs. marginalization, *(p* = .015); whereas in the British hand condition the only contrast that reached significance was separation vs. integration, (p = .02) with a trend towards significance in the assimilation vs. separation (*p* =.066). Crucially, as illustrated in Figure 5.3, all groups show a pattern of imitation towards the British or Polish hand that fits in with the styles of cultural adaptation of the quadripolar model described by Berry et al. (1989) and Hutnik (1991).

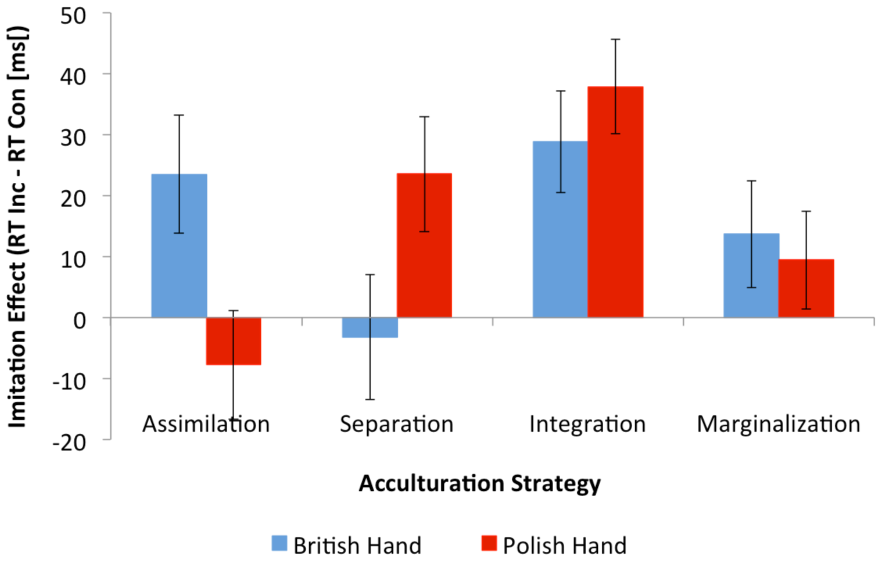

Figure 5.3. *Imitation effects for the British and Polish hand in each of the Acculturation Strategy groups. Light bars indicate the imitation effect for the British hand and dark bars indicate the imitation effect for the Polish hand. Error bars represent S.E.M.*

Self-Construal Scale. A 2 × 2 ANOVA was conducted with SCS (independent vs. interdependent scores) as the within-subjects factor and Group (British vs. Polish) as the between-subjects factor. The analysis revealed a significant main effect of SCS, $F(1,34) = 13.52$, $p = .001$, $\eta^2_p = .29$. Overall, scores for the independent scale ($M = 5.06$, $SEM = .10$) were higher than for the interdependent scale ($M = 4.45$, $SEM = .13$). Neither the main effect of Group ($p = .15$) nor the Group × SCS interaction ($p = .29$) were significant.

Correlations. Since the Polish data did not meet the normality assumption, a Spearman's Rho was used for correlation analyses. The first of these analyses revealed that the interdependence scores were positively related to preference scores for Polish culture, $r_s = .48$, $p = .018$, and negatively correlated to the length of time spent in the UK, $r_s = -.50$, $p = .014$. Moreover, after controlling for the imitation effect when the stimulus was the hand of the Polish actor, a partial correlation analysis confirmed that the size of the imitation effect when the stimulus was the hand of the British actor was related to preference scores for British culture, $r(37) = .327$, $p = .042$; and similarly, when controlling for the imitation effect when the stimulus hand was that of the British actor, the size of the imitation effect when participants viewed the hand of the Polish actor was related to the preference scores for Polish culture, $r(37) = .508$, $p = .001$. Finally, no significant correlations were found between SCS scores and imitation effects (all $ps > .25$). Therefore, these data provide no evidence of a relationship between SCS and automatic imitation.

The first finding of interest from these data is that while the British participants show an in-group imitation bias towards the hand of the British actor, the equivalent in-group bias is not present in the Polish group. The fact that there were twice as many Polish as British participants in this sample, rules out the lack of statistical power as a plausible explanation for the absence of an in-group bias in the Polish group. Furthermore, this finding replicates those of Mondillon, Niedenthal, Gil, & Droit-Volet (2007) in which they report that French Caucasians imitate the facial expressions of another French Caucasian more than those of a Chinese person; however, Chinese participants living in France imitated the facial expressions of the Chinese person just as much as the French Caucasian's. Mondillon and colleagues interpret the lack of in-group bias in the Chinese participants in terms of their motivations to understand the emotional expressions of the host culture. The experimental design of this study allows expansion of Mondillon et al's findings, as the present results indicate that differences in acculturation strategies are the most likely explanation for the absence of an in-group imitation bias in the Polish participants.

Consistent with the predictions, Polish migrants adopting the assimilation strategy show a larger imitation effect towards the British compared to the Polish actor; conversely, those with a separation strategy imitate the Polish more than the British actor. Also as predicted, no in-group imitation bias was found in either the integration or marginalization strategy groups. As far as we are aware, this is the first study to investigate and demonstrate that acculturation strategies can modulate automatic imitation of immigrants towards an individual from either the native or the host culture. Although the data do not allow to tease apart the precise cognitive mechanisms responsible for such modulation, these findings are not entirely surprising if one takes into account the increasing research evidence, some of which is discussed in the introduction, showing that motivational and situational factors can determine the extent to which we imitate other people's actions. When migrating to a different culture, individuals can choose how to adapt to their new environment. Some will be motivated to learn and absorb the customs and practices of the host culture and in order to do so, they will seek and maintain contact with members of the new community in which they choose to settle. Migrants with this assimilation strategy would be motivated to affiliate and integrate with members of the host culture. For example, the assimilative Polish immigrant in the UK would perceive a British rather than a Polish individual as a member of the in-group, or rather the group with which he/she prefers to affiliate. Conversely, those who adopt a separation strategy would favour the Polish culture they left behind and instead would prefer to affiliate with fellow Polish immigrants in the UK. In both cases, automatic imitation could foster positive relationships, functioning as the 'social glue' (Lakin et al., 2003) to provide a harmonious environment within the preferred group of affiliation. This assumption is compatible with the present results showing that preference scores for British culture are correlated with the extent to which participants automatically imitate the hand believed to be British rather than Polish, and that preference for Polish culture is related to imitation of the Polish actor's hand. As for the integration and marginalization strategies, as described by Berry et al., (1989) and Hutnik (1991), individuals with these acculturation attitudes are capable of either integrating and assimilating with both the native and host cultures (integration) or show little or no prominent interest for either (marginalization). Interestingly, these data also fit in with these models of acculturation - no evidence of a difference in automatic imitation of the British or Polish hands was found in these groups, and the magnitude of the imitation effect – as seen in Figure 5.3 – resembles the description of these acculturation strategies in that integrators showed a high level of automatic imitation of both hands while those with a marginalized view showed little imitation of either hand.

In sum, these findings show that the acculturation strategies that Polish migrants adopt when living in the UK modulate the extent to which they allow self-other representations to overlap or to separate. In the context of imitation, such control of self-other representations is determined by the migrants' motivational attitudes towards the host or the heritage culture, which are reflected on their automatic imitative behaviour towards members of the host vs. the heritage culture. Nevertheless, causation cannot be derived from correlations and further research will be needed to unravel the precise cognitive processes underlying the relationship between acculturation strategies and automatic imitation.

A secondary finding of interest is the set of results from the SCS. Although Polish culture is usually considered more interdependent (Cialdini, Wosinska, Barrett, Butner, & Gornik-Durose, 1999), (Reykowski 1998) than Western cultures such as the UK, in the present sample no evidence of differences between independent and interdependent scores was found between the two cultural groups. However, this finding is consistent with research suggesting that economically motivated or voluntary migrants tend to have a more independent self-construal orientation (Kitayama, Ishii, Imada, Takemura, & Ramaswamy, 2006), (Chen, Wagner, Kelley, Powers, & Heatherton, 2013). Therefore, it is plausible that this sample of Polish migrants a) already possessed a more independent SCS, which led them to voluntarily migrate in the first place, or b) their mindsets became more independent as a consequence of migrating to a more independent culture. Although the former explanation is highly plausible, evidence for the latter was found in the present study. A negative correlation was found between interdependent scores and length of time spent in the UK, suggesting that the longer Polish migrants remain in the UK, the more independent their mindset becomes. Also of interest was the positive correlation found between interdependent scores and Polish preference scores, suggesting perhaps that the Polish participants associate their native culture with a more interdependent view of the self.

Finally, no evidence was found to suggest that interdependent self-construal style is associated with increased mimicry (van Baaren et al., 2003), (Ashton-James et al., 2007). This could be due to: a) overall, these participants favoured an independent vs. an interdependent self-construal style, therefore, it is plausible that the data lacked statistical power to show such relationship, or b) the acculturation strategies that individuals choose to adopt when migrating to a new culture could play a stronger modulatory role in imitation than self-construal styles. Future cross-cultural research into the factors that modulate automatic imitation could provide answers to these hypothetical explanations.

5.3 Experiment 6: Culture and Social Cognition

In addition to its relationship with automatic imitative behaviour, the effects of independent vs. interdependent SCS have also been studied in the context of visual perspective taking. Wu & Keysar, (2007) used a real life version of the Director task, described in Experiment 1, with American and Chinese participants. They found that Americans, a culture that favours the independent SCS, were significantly worse in adopting the Director's perspective compared to the Chinese, a culture that favours the interdependent SCS. The poor performance of the American participants compared to their Chinese counterparts was evident in accuracy, RT and eye-tracking measures during experimental trials. Wu and Keysar interpreted these results in relation to the differences in SCS between the two cultures. They argue that for interdependent cultures, the self is defined in relation to others, therefore focusing attention on other's actions, knowledge and needs is more important to them than it is for individuals with an independent view of the self (Wu & Keysar, 2007).

In recent years, a new interdisciplinary approach combining theories from cultural psychology and neuroscience research has given rise to cultural neuroscience. This emerging field of research aims to explore the relationship between culture, cognitive processes and the brain (Kitayama & Park, 2010). In one, frequently cited, Cultural Neuroscience study, Zhu et al. (2007) used a self-referential task in which Chinese and Western (North Americans and Europeans) participants had to judge the appropriateness of trait attributes to describe themselves, their mother or a culture-relevant famous person. They found medial prefrontal cortex (MPFC) activation for self-judgements (contrast self vs. other) in all participants. However, while Chinese participants also showed increased activation in the MPFC when making mother-judgements (contrast mother vs. other), Western participants did not show the same pattern of activation, instead, the same contrast showed increased activation in the anterior cingulate cortex (ACC) in this cultural group. Furthermore, the self vs. mother contrast showed no difference in activation of MPFC in Chinese but it did in the Americans. The authors interpreted these findings in relation to differences in SCS between the two cultures and argued that different processing styles of information related to the self and close others observed by social psychologists are also found at neural level. Therefore, the interpersonal connectedness emphasised by the Chinese culture results in an overlap of neural representations of the self and a close other such as mother, whereas the emphasis on independent SCS in Western cultures leads to measurable neural differences in the representation of the self and others – including close others such as mother – (Zhu et al., 2007).

Noticeably, the majority of cultural psychology and cultural neuroscience studies relating to SCS have predominantly focused on comparisons between Americans (with a small number of studies including European participants) and East Asians (Chinese, Japanese, South Koreans). Therefore, it is not known if these findings replicate in other cultures that might or might not show such remarkable differences in processing styles concerning self and others. For example, do all Western cultures emphasise independent

SCS? Or are there other cultures, besides East Asians, that show such markedly different SCS when compared to Western cultures? Are SCS limited to the independent vs. interdependent dichotomy? Do these differences, if they exist, lead to measurable differences in performance of social cognition abilities requiring self-other representations?

Experiment 6 compared performance of individuals from two seemingly different cultures, UK and Cuba, on the three measures of social cognition employed in Experiments 1-4: the control of imitation, visual perspective taking and theory of mind tests. The self-referential paradigm from Experiment 3 was employed as the theory of mind test. This paradigm was adapted for this experiment so that in addition to *self* and *other* mental and physical judgements, it also included *mother* judgements. The independent and interdependent SCS were measured with the Singelis (1994)'s self-report scale.

Cuba has been a communist country for over 50 years. Communism encourages collectivist/ interdependent thinking. Reliance on others and interpersonal relations are a necessity for everyday life and for success. The Communist system deters individual thinking and behaviour that deviates from the communist ideas, deep rooted in the communities. Such constraints in individual thinking are seen in the education system, the work place and the political system, which does not legally allow or recognise any other political affiliations than the communist party. All this contrasts with the way of life in the UK, a society that emphasises personal achievement, independent thinking, creativity, competitiveness, all of which epitomises an independent SCS.

Therefore, it is expected that the SCS scores of Cuban and British participants would reveal these cultural differences, so that Cuban participants would affiliate to the interdependent SCS while British participants would favour the independent SCS. If this pattern of results is found, the findings from the control of imitation and visual perspective taking are expected to replicate those from previous cross-cultural studies, (e.g., van Baaren et al., 2003; Wu & Keysar, 2007). Specifically, it is expected that Cuban participants, if indeed they are more interdependent than the British, would a) show a higher tendency to imitate, resulting in a larger imitation effect in the control of imitation task and b) be better able to adopt the Director's perspective in the visual perspective-taking task, than the British participants. In terms of the self-referential task, the prediction (based on Zhu et al., 2007) is that self vs. other judgements would be different in both groups, but that self vs. mother judgements would not differ (in terms of RTs) in the Cuban group, but that they would differ in the British sample. Since the Zhu & Han study did not include mental vs. physical judgements in their design, no predictions are made in relation to these trial types.

5.3.1 Method

Participants

Fifty-five adults (29 M, 26 F) from both Cuban and British cultures participated in this study (Cuba: *N* = 27, UK: *N* = 28), age ranged between19-45 years, (*M*= 26.5, *SD* = 6.7). There were no age, *F*(1,54) = .69, *p* = .41, or gender, χ^2(1, *N* = 55)=.17, *p* = .79 differences between the groups.

Materials and Procedure

The Cuban sample was tested in Cuba (in the city of Santiago de Cuba) and only included Cuban nationals. To the best of our knowledge, no previous studies have been published concerning SCS in Cuba, but according to (Markus & Kitayama, 1991), Latin American cultures are considered to favour the interdependent SCS. Recruitment of the UK participants, who were tested in London, ensured that only British Caucasians, without a mixed-culture background, were invited to take part in the experiment, thus ensuring the absence of influence from interdependent cultures within the participants' household in the UK sample.

All participants performed three tasks: the control of imitation, visual perspective taking and the self-referential task (described in Chapter 2). The visual perspective taking task was modified by replacing the picture of the British Director and his recorded voice with a Cuban Director (see Figure 5.4) who instructed participants (in Spanish) to move objects from the shelves array. This manipulation aimed to encourage participants to identify with the director as a member of their own cultural group. The self-referential task, described in Experiment 2, was also modified, so this time participants were required to make mental and physical judgements of themselves, their mother and a culture-relevant famous person (UK: Lady Gaga, Cuba: Israel Rojas, lead singer of a popular Cuban band). RTs for each type of judgements were the dependent variable of this task. The order of the tasks was counterbalanced between participants

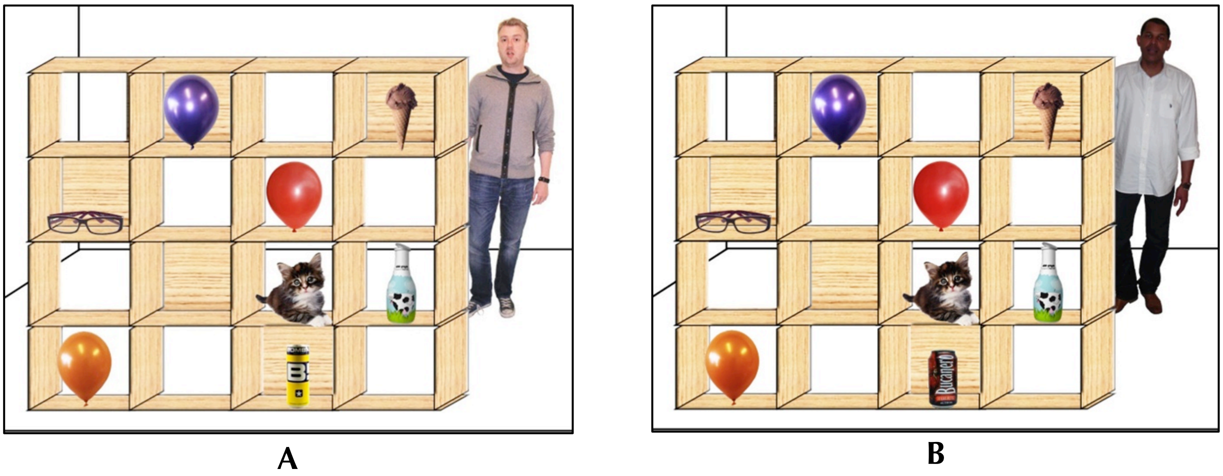

Figure 5.4. *Example of the stimuli presented in the visual perspective-taking task to each cultural group (UK – panel A; Cuba – panel B). The images show an example of experimental trials for which the corresponding (auditory) instruction would be to 'move the top balloon left'.*

5.3.2 Results and Discussion

Self-Construal Scale

Table 5.1 below shows the scores of the self-construal scale. The reliability analysis of this scale indicates poor internal consistency of both types of SCS (Cronbach's α independent= .45, interdependent= .51).

An ANOVA was conducted with SCS (independent vs. interdependent) and Group as the within-subject and between-subject factors respectively. This analysis revealed no significant main effects or interactions, all *ps* > .29.

Table 5.1. Mean (S.E.M.) for the independent and interdependent scores of the Self-Construal Scale for each Cultural Group.

	Independent	**Interdependent**
Cuba (*N* = 27)	4.75 (*0.11*)	4.61 *(0.10)*
UK (*N* = 28)	4.66 *(0.10)*	4.58 (*0.10)*

Control of imitation task

As described in previous analysis, extreme within-subjects RT scores in the control of imitation task were removed from the analysis. The RT and accuracy data were analysed using ANOVA with Cultural Group as the between-subjects factor (Cuba vs. UK) and Trial Type as the within-subject factor (congruent vs. incongruent).

RT analysis. Figure 5.5A shows the RT data for the Control of imitation task. There was a main effect of Trial Type, $F(1,53) = 103.18$, $p < 0.001$, $\eta^2_p = .66$; as expected, responses on congruent trials were executed faster than those on incongruent trials. The main effect of Group was also significant, $F(1,53) = 4.08$, $p = .048$, $\eta^2_p = .07$. Pairwise comparisons showed that Cubans were slower overall than the British participants. However, the Group × Trial Type interaction was not significant ($F < 1$, $p = .70$); Paired Samples T-test showed that the imitation effect (RT incongruent trials – RT congruent trials) was significant within each Group (Cuba: $t(26) = 7.44$, $p < .001$, $d = .96$; UK: $t(27) = 6.93$, $p < .001$, $d = .40$). As the lack of a significant interaction shows, the size of the imitation effect between the two Groups did not differ, (Cuba: $M = 55.34$, *S.E.M.* = 7.43; UK: $M = 51.30$, *S.E.M.* = 7.40$p = .70$).

Error analysis. A similar pattern was observed in the error analysis (see Figure 5.5B). Overall, participants made a small number of errors (*M total*= 7.4, *S.E.M.* = .70). The main effect of Trial Type was significant, $F(1,53) = 35.45$, $p < 0.001$, $\eta^2_p = 0.40$; with participants making more errors in the incongruent ($M = 5.30$, *S.E.M.* = 0.50) than in the congruent ($M = 2.10$, *S.E.M.* = 0.30) trials.

The main effect of Group and the Group × Trial type interaction were not significant, (*ps* >.65), showing that the Groups did not differ on accuracy in this task.

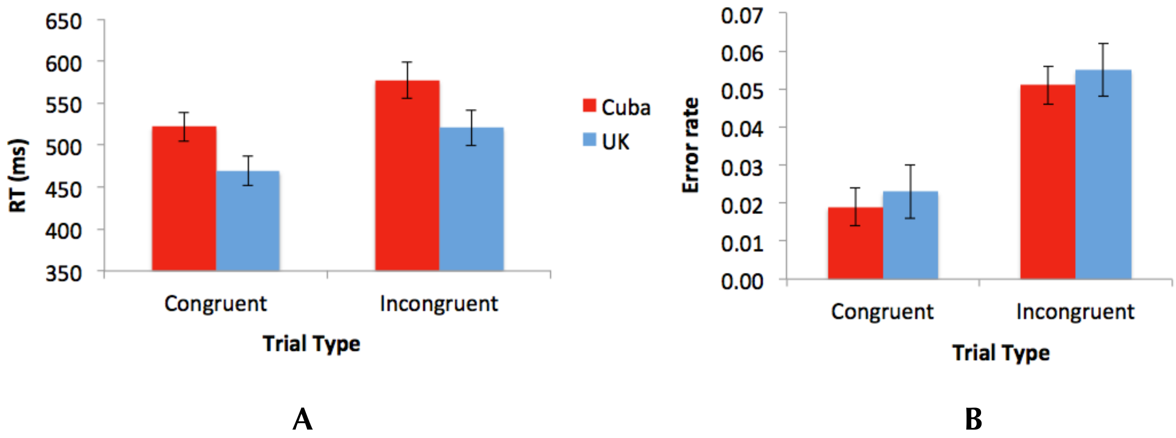

Figure 5.5. *Mean RT (A) and error rate (B) for the control of imitation task. Error bars represent S.E.M.*

Perspective-taking task

The accuracy and RT data were analysed using ANOVA with Cultural Group as a between-subject factor and Trial Type (experimental vs. C1 vs. C2) as the within-subjects factor.

RT. A significant main effect of Trial Type was found, $F(2,104) = 179.20$, $p < 0.001$, $\eta^2_p = .78$. Overall, participants responded faster to the C1 (M = 2.80s, *S.E.M.* = 66.36) trials than to the experimental (M = 3.30s, *S.E.M.* = 82.66, $p < .001$) or the C2 trials (M = 3.28s, *S.E.M.* = 85.93, $p < .001$). The main effect of Group was also significant, $F(1,52) = 7.48$, $p = .009$, $\eta^2_p = .78$. Overall, Cuban participants were slower at responding (M = 3.34 s, *S.E.M.* = 1.10 s) than the British participants (M = 2.92 s, *S.E.M.* = 1.06 s). Slower RTs were also observed in the control of imitation task; taken together, this could indicate a lack of practice of the Cuban participants at performing psychology experiments compared to the British participants, who were drawn from a psychology testing database and are therefore more adept at completing speeded tasks. The Group × Trial Type interaction was not significant, (F <1, p = .59).

Accuracy. Since no differences were found in performance of the control trials, the C1 and C2 trials were collapsed; therefore, the analysis included 2 Trial Types (experimental and control). There was a main effect of Trial Type, $F(1,52) = 14.46$, $p < 0.001$, $\eta^2_p = .22$. Overall, performance (proportion of correct responses) was lower on experimental trials[1] (M = .83, *S.E.M.* = .04) than on control trials: (M = 0.97, *S.E.M.* = .005). Neither the main effect of Group, nor the Group × Trial Type interaction were significant, (*ps* >.57). Taken together, these results indicate that participants from both Cultural Groups show comparable ability at separating their own perspective from that of the Director's when the perspectives were in conflict.

Self-referential task

An ANOVA was performed with Cultural Group as a between-subject factor and Target (self vs. mother vs. other) and Trial Type (mental vs. physical) as the within-subjects factors. A preliminary analysis confirmed the longer RTs

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[1] Notably, both groups scored higher than most neurotypical adults tested with this task in all the other experiments reported in this thesis (except in the conditions of training and anodal tDCS). No obvious explanation can account for this discrepancy. It is possible that because the Cuban sample are less adept at experimental testing, they were more motivated and therefore paid more attention to the instructions. The British sample, were carefully screened during recruitment so that only British Caucasians with no influence of another culture in their household were recruited. The reasons for this screening were carefully explained to the participants prior to testing. It is also possible that they became motivated to perform well on this task. However, these motives are purely speculative.

for the Cuban Group found in the previous tasks. Therefore, Mean Total RT was included in the analysis as a covariate (thereby accounting for the variance on overall RTs). The main effect of Target was significant, $F(2,102) = 3.61$; $p < .03$; $\eta^2_p = .07$. Overall, responses were faster for *mother* ($M = 3.28$ s, *S.E.M.* = .03 s) than for *self* ($M = 3.97$ s, *S.E.M.* = .03 s; $p < .001$) or for *other* trials ($M = 4.00$ s, *S.E.M.* = .03 s; $p < .001$). The main effect of Trial Type was not significant, ($p = .66$). The Target × Trial Type interaction was significant, $F(1,52) = 8.05$; $p = .006$; $\eta^2_p = .13$. Simple effects analysis revealed that while mental responses ($M = 3.86$ s, *S.E.M.* = .04 s) were faster than physical responses ($M = 4.07$ s, *S.E.M.* = .05 s; $p = .001$) for *self*-judgements, the opposite pattern was true for both *mother* (physical: $M = 3.21$ s, *S.E.M.* = .03 s; mental: $M = 3.36$ s, *S.E.M.* = .04s, $p = .002$) and for *other* judgements (physical: $M = 3.82$ s, *S.E.M.* = .04 s; mental: $M = 4.17$ s, *S.E.M.* = .04s, $p < .001$), where responding was faster for physical than for mental judgements. Neither the main effect of Group, nor the 2-way interactions involving Group were significant, (all *ps* >.09). The 3-way, Group × Target × Trial Type, interaction approached significance ($p = .063$), and was therefore further explored. Simple effects analysis showed that while the contrast self-mental vs. other-mental in the Cuban Group was not significant ($p = .19$), the same contrast was significant in the UK Group ($p < .001$), where responses to self-mental ($M = 2.90$ s, *S.E.M.* = .20) were significantly faster than other-mental judgements ($M = 3.40$ s, *S.E.M.* = .21). In the physical trials, the contrast self-physical vs. other-physical was significant in the Cuban Group ($p = .017$) and showed a trend towards significance in the UK Group ($p = .072$). Although, this pattern of dissociation between mental and physical judgements for self and other between the Cultural Groups lends itself to further interpretation, doing so in the absence of a significant 3-way interaction would be highly speculative. It is possible that the 3-way interaction failed to reach significance due to lack of statistical power and therefore, these data would require replication with larger sample sizes before meaningful interpretations can be made.

This study compared performance of Cuban and British adults in a range of social cognition tests. The experimental design was conceived on the assumption that the two cultural groups would show differences in SCS, which in turn would predict the replication of previous findings in imitation (van Baaren et al., 2003), visual perspective taking (Wu & Keysar, 2007) and self-referential judgements (Zhu et al., 2007)[1]. However, no differences between the groups were found on any of the measures, including the Self-Construal Scale.

As mentioned in the introduction, previous cross-cultural studies of independent vs. interdependent SCS have almost exclusively focused on differences between the East (Chinese, Japanese, Koreans) and West (Americans), with a few including both Western Europeans and Americans as representative of Western cultures. One exception is a study by (Kitayama, Park, Sevincer, Karasawa, & Uskul, 2009), in which they include three groups of participants, Americans, Japanese and Western Europeans (British and Germans). Kitayama and colleagues used a battery of implicit measures to assess SCS. For example, in a visual perception task, they measured wether

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[1] Although the Zhu and Han study was a neuroimaging study, their behavioural data also show cross-cultural differences in the predicted direction of the SCS model.

participants attended to the stimuli in an analytic or holistic manner. Previous studies (e.g., Nisbett & Masuda, 2003; Nisbett & Miyamoto, 2005) have found that while individuals with interdependent SCS tend to process visual information in a holistic manner, by focusing on the relationship between the objects and the context in which it is placed, those with independent SCS show a more analytic processing style, by focusing attention on a salient object independent of its contextual setting. In their study, Kitayama et al (2009) found that overall, although British and Germans show a more independent SCS than Japanese, they are less so than Americans, thus indicating the presence of systematic cross-cultural variations of SCS among cultures that affiliate to the independent SCS.

In the context of the present study, the finding that British participants are neither more independent than interdependent in a within-group comparison, or more independent than the Cuban participants in a between-group comparison, and vice versa for the Cuban sample, would suggest that neither of these cultural groups are representative of the extreme dichotomy commonly associated with SCS.

However, another – and perhaps more important – factor could explain the pattern of results in this experiment. The poor internal consistency found in the Singelis (1994) self-construal scale, seriously challenge its suitability as a reliable SCS measure. Although, probably the most popular self-construal scale in cross-cultural psychology (Cross, Hardin, & Gercek-Swing, 2011), it has been the subject of criticism by several researchers, who question the validity of this scale, (e.g., Cross et al., 2011; Levine et al., 2003). Interestingly, Kitayama et al., (2009) also used the Singelis (1994) scale as an explicit measure of SCS, in addition to their battery of implicit measures. They describe the obtained pattern of results with the SCS measure as anomalous, since their British sample showed the lowest independent scores (compared to Americans, Germans and Japanese); while the Americans showed the highest interdependent scores from all groups. Based on the unacceptable level of reliability of this scale in the present experiments, no further conclusions can be drawn regarding the SCS of either the British or Cuban participants in this study.

Another potential limitation of this study, as discussed above in relation to the results from the self-referential task, is the relatively small sample size for cross-cultural comparisons using behavioural measures. In the cultural psychology literature is not unusual to find studies with hundreds of participants. However, in the study by van Baaren et al., (2003) the sample size in Experiment 3, which investigated automatic imitation of Japanese and American participants, was smaller (15 Japanese and 16 Americans) than the number of participants in the current sample. Similarly, Wu & Keysar, (2007) tested 20 Chinese and 20 Americans using the Director task, and in the Zhu et al., (2007) study – which used the self-referential task – there were 13 Chinese and 13 Westerns. The fact that these studies found significant cross-cultural differences in these three socio-cognitive domains[1] with smaller number of

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[1] It is worth pointing out that the actual tasks and dependent variables (DVs) used in the three studies(van Baaren et al., 2003; Wu & Keysar, 2007; Zhu et al., 2007) were not exactly the ones used in the current experiment. For example, (van Baaren et al., 2003) measured automatic imitation (mimicry) in the context of real-life interactions – with a confederate. Similarly, (Wu & Keysar, 2007) used a real life version of the Director task and their DVs included eye-tracking measures. Finally, in their behavioural assessment, (Zhu et al., 2007) looked at number of items remembered for either self, mother or other in a memory task related to the self-referential task.

participants, while the current study failed to find them, suggests that sample size might not explain the absence of cross-cultural differences observed here. Clearly, further replication of these data with larger sample sizes would be required to provide more conclusive evidence. In the meantime, the argument that socio-cognitive abilities do not differ between Cuban and British cultures is one worthwhile considering.

However, taking into account the results from Experiments 1-4, which employed the same measures as this experiment, it is unlikely that differences in DVs from the 3 cross-cultural studies can explain the absence of significant cross-cultural effects in the current study.

5.4 General Discussion

The experiments described in this Chapter were deigned to explore the role of culture in processes of social cognition that rely on the control of self-other representations such as imitation (Experiment 5 and 6), visual perspective taking and theory of mind (Experiment 6). In Experiment 5 it was found that acculturation strategies of Polish migrants in the UK modulate imitative behaviour when they observe either a Polish or a British actor perform an action. For example, those with an assimilation strategy would favour the host over the native culture, thereby showing increased imitation when observing the actions of a British actor than when observing the same actions performed by a Polish actor. The opposite pattern was found for migrants who adopt a separation strategy. Participants in this group showed less imitation-inhibition when they observed the actions of a Polish actor than those of a British actor. Consistent with these effects, Polish migrants who adopt either integration or marginalization strategies show no differences in imitation effects towards either the Polish or British actors. However, the size of the imitation effects of these groups fits in with the adopted strategies, so that the integration group – who assimilates the two cultures – shows large imitation effects for both the Polish and British actors, whereas the marginalization group – who does not feel strong connections to either culture – show small imitation effects for both the Polish and British actors.

The findings contribute to the increasingly expanding research on imitation by providing the first empirical evidence that acculturation strategies are another situational/ motivational factor that affects automatic imitative behaviour. However, it is worth noting that the sample size of each acculturation strategy is small and while the observed effect sizes are not small, these findings would benefit from future replication with larger samples.

The results from the self-construal scale in Experiment 5 showed no evidence of a relationship with imitation. As mentioned earlier, several potential explanations could account for this findings, ranging from lack of statistical power to detect effects, or the lack of variability on the two measures (independent vs. interdependent) due to the fact that the Polish migrants show a more independent than interdependent SCS. The suitability of this scale as an appropriate measure of SCS (as discussed in Experiment 6) should also be considered as a potential explanation.

Experiment 6 aimed to investigate if the way individuals see themselves in relation to others impacts performance in social cognition tasks requiring representations of the self and another individual. Borrowing concepts from cultural psychology, this experiment aimed to find, first, differences in self-construal styles between two seemingly different cultures such as Cuba and the UK and, second, if such differences would lead to differential performance in the three social cognition tasks from previous experiments. However, the results do not provide support for either of the above assumptions. Null results are difficult to interpret as many different factors endogenous and / or exogenous to the experimental design could account for them. Therefore, future studies addressing the issues mentioned in the discussion of this experiment would be required before solid conclusions could be drawn.

Chapter 6: Discussion

This chapter summarises the findings from the experiments reported in this thesis. The three themes concerning each of the empirical chapters will be individually addressed. The first section relates to the findings from Chapter 2, which investigated the effect of training self-other representations on socio-cognitive abilities and the presence of atypical self-other representations in mirror-touch synaesthesia. The second section addresses the role of the TPJ, a brain region commonly associated with self-other processing, in social cognition (Chapter 4). Finally, the third section of this chapter relates to the influence of culture on socio-cognitive abilities that rely on the control of self-other representations (Chapter 5). Within each of the sections, the main empirical findings will be summarised (subsection 1), the strengths and limitations of the studies will be discussed (subsection 2) and outstanding questions and future directions will be highlighted (subsection 3).

6.1 Self-Other Representations: From Imitation to Theory of Mind

6.1.1 TRAINING SOCIAL COGNITION

Experiment 1 aimed to test two contrasting theories relating to self-other representations in social cognition. The MNS theory, posits that imitation, and its neural substrate the MNS, is at the core of higher-order socio-cognitive processes such as mental state attributions (e.g., Gallese & Goldman, 1998; Oberman, Pineda, & Ramachandran, 2007; Rizzolatti & Craighero, 2004). A recent alternative account, the self-other control theory (Brass et al., 2009), suggests that the control of shared representations (pertaining to self and others) underlie common processes in the control of imitation and mental state attributions. In Experiment 1, a training paradigm allowed to test both theories. Three groups of participants received different types of training: imitation, imitation-inhibition, or general inhibitory control training prior to completing three social cognition tasks: control of imitation, visual perspective taking and theory of mind.

6.1.1.1 Summary and Interpretation of Main Findings

The results showed that the group receiving imitation-inhibition training was better able to adopt the visual perspective of another person (whose viewpoint differed from that of the participants) than both the imitation and inhibitory control groups. However, there was no effect of training on the theory of mind task. Therefore, although no evidence was found in support of the MNS theory – there was no effect of imitation training on visual perspective taking or theory of mind –, the improved performance of the imitation-inhibition training group on the visual perspective taking task provides some support for the self-other control theory, advanced by (Brass et al., 2009). Both, imitation-inhibition and visual perspective taking abilities require the online control of co-activated self-other representations. Notably, the requirement of online control differs in both abilities. Successful performance in the control of imitation depends on enhancing representations of the self (by focusing on the intended action) and inhibiting representations of the other (by ignoring the observed action of another agent); whereas the visual perspective taking paradigm requires inhibiting self representations (by ignoring the objects you can see) and enhancing representations of the other (by only choosing the objects the director can see). The results of Experiment 1 suggest that regardless of the direction in which self-other control is needed, there appears to be a link between imitation-inhibition and visual perspective taking.

6.1.1.2 Strengths and Limitations

This is the first empirical study to test the relationship between imitation, perspective taking and theory of mind. The increased ability to adopt the perspective of others observed after imitation–inhibition training (but not after imitation or inhibitory control training) provides support for a novel theory of social cognition suggesting that the same self-other distinction process underlies imitation inhibition and perspective taking. In addition to their implications regarding the interrelatedness of socio-cognitive processes, these findings provide positive evidence for the efficacy of socio-cognitive 'brain training'. There is very little evidence that the beneficial effects of standard brain-training programmes extend beyond the particular tasks in which participants are trained (Owen et al., 2010; c.f. Klingberg, 2010). Experiment 1 shows that training in one socio-cognitive task (the control of imitation), has a transferable effect on a very different socio-cognitive task (perspective taking). Noticeably, imitation–inhibition training had a positive effect, not only on manual responding in the perspective-taking task, but also on participants' eye-movements. After imitation–inhibition training, participants looked less at the self-referenced object than those who received imitation or inhibitory control training. This suggests that the training had a deep effect – influencing, not only final choice behaviour, but also the way in which attentional resources were allocated when differing perspectives were to be resolved.

A potential limitation of this study concerns the choice of theory of mind measure. Accuracy scores in the Strange Stories task were very high. It is possible that a baseline ceiling effect would have prevented a differential effect of training being seen on this task, and that therefore the task was not sufficiently sensitive to detect improved theory of mind performance in the imitation–inhibition group. Further investigation with alternative theory of mind tasks is therefore necessary to determine the selectivity of the effect of imitation–inhibition training on theory of mind performance.

6.1.1.3 Outstanding Questions and Future Directions

The findings from Experiment 1 could be extended in several directions. For example, future research could test the impact of imitation and counter-imitation training on other socio-cognitive abilities relying on self-other processes such as empathy. They could also explore whether the same effects can be found with different processes thought to utilise theory of mind, such as understanding of false beliefs and irony, deception, or moral judgements. These findings could contribute towards a deeper understanding of the construct known as theory of mind, which currently is used as an umbrella term for a range of socio-cognitive processes ranging from visual perspective taking to action understanding, attribution of mental states, and false belief understanding. Future research could derive an empirically based, finer-grained taxonomy of theory of mind, improving our understanding of this essential social skill.

Another direction for future research could explore the replicability of the current findings in clinical populations. The ability to control self-other representations is impaired in individuals with autism (Spengler et al., 2010;

Williams & Happé, 2010; Williams 2008) and schizophrenia (Bailey & Henry, 2010; Liepelt et al., 2012), with resultant impairments of social interaction. These impairments deprive affected individuals of social support and reduce opportunities for employment, exacerbating the effects of their primary illness. The current results raise the possibility that carefully designed training interventions could be used to enhance the control of self-other representations in these clinical populations.

Finally, future studies could investigate whether the mechanisms underlying self-other processes are intrinsic to the social domain or whether they represent domain-general processes subserving a social function when required by task demands. The design of Experiment 1 included a non-social control condition in which a group of participants received general inhibitory control training. Performance on the visual perspective-taking task was poorer in the control group than in the imitation-inhibition training group. This finding indicates that although general inhibitory control is required in the perspective-taking task (Apperly et al., 2010), this alone is not sufficient for accurate performance on the task. Results therefore provide evidence that common (social) domain-specific processes are shared between imitation-inhibition and visual perspective taking. It should be noted however, that recent theoretical (Heyes, in press) and empirical work (Santiesteban, Catmur, Coughlan Hopkins, Bird, & Heyes, 2013); Santiesteban, Shah, White, Bird, Heyes, under review) have started to question the domain specificity assumption in visual perspective taking tasks, and propose that domain general processing such as attentional orienting could explain some of the effects often attributed to third-person perspective taking. For example, a commonly used measure of visual perspective taking is the 'dot' task[1] (McCleery, Surtees, Graham, Richards, & Apperly, 2011; Qureshi, Apperly, & Samson, 2010; Samson, Apperly, Braithwaite, Andrews, & Bodley Scott, 2010), in which participants are presented with a picture of a room with dots on the walls. A human-like figure (avatar) stands in the middle of the room. The dots could be placed on the wall in front of the avatar, on the wall behind the avatar, neither or both. Participants are required to make judgements about the number of dots they can see or the number of dots the avatar can see. Sometimes the number of dots that participants can see is the same as the number of dots the avatar can see (consistent trials), but sometimes the number of dots is different for the participant and the avatar (inconsistent trials).

A robust finding from studies using this task is that when making self-inconsistent judgements, participants' responses are slower than when making self-consistent judgements. This self-consistency effect has been interpreted as evidence of implicit theory of mind since the mere presence of the avatar figure (representing another human being) slows participants' responses during self-inconsistent trials, suggesting that participants cannot help but adopt the avatar's perspective, even when not required to do so (Samson et al., 2010). However, (Santiesteban et al., 2013) found that the self-consistency effect is also present when the avatar is replaced by a non-social stimulus like an arrow. The arrow in this study shared the same directional, but not the agentive, features of the

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[1] None of the studies cited above refer to this task as the 'dot' task. This term is used by Heyes, (in press) and by Santiesteban et al., (2013).

avatar. The self-consistency effect in the arrow condition is present when participants have not had prior experience with the avatar condition, ruling out potential transfer effects from the avatar to the arrow, and also when they are only required to make self-judgements, ruling out other-to-self transfer effects. Therefore, these findings challenge the implicit theory of mind interpretation in the dots task and suggest that domain general processes such as attentional orienting could explain the self-consistency effect.

A separate study (Santiesteban et al, under review) tested the domain-specificity of the Director task described in Chapter 2 and used in Experiments 1-4 and 6. Following an earlier study reporting that individuals with autism do not show impaired performance on the Director's task (Begeer, Malle, Nieuwland, & Keysar, 2010), this study showed that the same pattern of results is obtained, in typically developing adults and in adults with autism, when the director figure is replaced by an inanimate object, in this case a camera. In light of these recent data, a prominent question for future research concerns the generalizability of the findings from Experiment 1 outside of the social domain. To what extent is the online control of self-other representations limited to social cognition? Are mechanisms of self-other processing relying on domain general attentional processes? Specifically, could the observed improved performance in the Director task after imitation-inhibition training also be obtained with the camera condition?

6.1.2 WHEN SELF-OTHER REPRESENTATIONS GO AWRY: THE CASE OF MIRROR-TOUCH SYNAESTHESIA

Experiment 2 tested the socio-cognitive abilities of individuals with mirror-touch synaesthesia, a condition that has been related to atypical self-other representations – (Banissy & Ward, 2013; Banissy et al., 2009). This experiment aimed to expand on the findings from Experiment 1 by using the same measures of the control of imitation and visual perspective taking but with a different theory of mind task. The performance of the mirror-touch synaesthetes was compared to a non-synaesthetic control group.

6.1.2.1 Summary and Interpretation of Main Findings

The mirror-touch synaesthesia group performed significantly worse in the control of imitation task compared to the control group. This was evident not only with RT but also with accuracy measures, suggesting that the synaesthetes found it harder to separate their own intended actions from those performed by another agent. This finding provides further evidence in support of the atypical self-other representations account of mirror-touch synaesthesia. Performance of the synaesthetes on the visual perspective-taking task was comparable to that of the non-synaesthete control group, as no effects of groups were found on this task. The fact that mirror-touch synaesthetes perform similarly to controls on perspective taking could indicate that the control of self-other representations is impaired in this type of synaesthesia, only in situations when representations of the ‘other’ should be inhibited (as in imitation-inhibition) but not when they should be enhanced (as in perspective taking). However, since overall performance on both groups was not very high, no firm conclusions can be made about the perspective taking abilities of mirror-touch synaesthetes until future evidence emerge corroborating or contradicting this view. Finally, no differences were found between the groups in the theory of mind measure, performance was very high for both synaesthetes and controls. Thus, suggesting that the ability to attribute mental states to others is not impaired in individuals with mirror-touch synaesthesia.

6.1.2.2 Strengths and Limitations

This is the first study investigating the extent of impairment of a range of socio-cognitive abilities in mirror-touch synaesthesia. The contributions of these findings are twofold. First, they facilitate further understanding and characterisation of this rare condition by providing an insight into which social cognition abilities appear to be impaired and which remain intact. Second, they contribute to a better understanding of the ways in which the control of self-other representations typically functions and of the interrelatedness of these different socio-cognitive skills.

In terms of limitations, the relatively small sample size and the choice of task could have precluded a differential effect been seen on the perspective taking measure. Therefore, further replications, using different measures would improve the understanding of the visual perspective taking abilities in mirror-touch synaesthesia.

6.1.2.3 Outstanding Questions and Future Directions

Research in mirror-touch synaesthesia is a relatively new field. Therefore, a myriad of research avenues remain to be explored. Future research could expand upon the present findings by testing other socio-cognitive abilities. For example, it has been found that mirror-touch synaesthesia is related to empathy (Banissy & Ward, 2007). Banissy & Ward used a self-report measure of empathy: the emotional reactivity subscale from the Empathy Quotient (EQ, (Baron-Cohen, Richler, Bisarya, Gurunathan, & Wheelwright, 2003)). Future work employing an empirical (instead of self-report) measure of empathy could provide further evidence of this finding.

Furthermore, based on the results from Experiments 3-4 and recent reports of atypical grey matter volume in the right TPJ in mirror-touch synaesthetes (Holle, Banissy, & Ward, 2013), it will be interesting to assess whether tDCS of TPJ results in enhanced performance on the control of imitation and perspective taking abilities of individuals with this condition.

6.2 The Role of TPJ in Social Cognition

6.2.1 Summary and Interpretation of Main Findings

Experiments 3 and 4 (Chapter 4) aimed to investigate the role of the TPJ in social cognition, in particular, its involvement in the control of self-other representations required for imitation-inhibition, visual perspective taking and theory of mind. Two different tDCS protocols were employed. In Experiment 3, three groups of participants received anodal, cathodal or sham stimulation of right TPJ. The results revealed that anodal stimulation (compared to cathodal and sham) significantly improved performance on the control of imitation and visual perspective taking task, whereas no differential effect of stimulation was found on the theory of mind measure.

Experiment 4 aimed to replicate and extend these findings under a different tDCS procedure. This time only anodal stimulation was delivered to right TPJ, left TPJ or the occipital cortex (Oz) to three groups of participants, prior to performing the control of imitation and perspective taking tests from Experiment 3 and a different theory of mind. The choice of left TPJ was motivated by the contrasting evidence regarding lateralization of function of this brain region in social cognitive processes.

The results were consistent with Experiment 3 as performance improvements were observed following anodal stimulation of right TPJ on the control of imitation and perspective-taking task; however, such improvements were also seen on participants who received left TPJ stimulation (but not on those in the Oz condition). These data therefore provide evidence of bilateral TPJ involvement in these two socio-cognitive abilities. Also compatible with Experiment 3, no effect of stimulation was found during performance of the (different) theory of mind task.

6.2.2 Strengths and Limitations

Experiments 3 and 4 are the first tDCS studies to provide evidence of causal TPJ involvement in social cognition. An important strength of these studies lies on the selected method for assessing the role of this brain region in socio-cognitive abilities. For example, contrary to fMRI studies reporting selective right TPJ involvement in the control of imitation (Brass et al., 2005; Spengler et al., 2009), Experiment 4 shows that this involvement is found bilaterally. Similarly, the findings from the visual perspective taking measure also reveals bilateral TPJ recruitment, challenging previous reports of selective left TPJ involvement during perspective taking (e.g., Schurz et al., 2013). Therefore, the results from these experiments highlight the potential of tDCS as a powerful methodological tool, which can provide evidence to complement and extend current knowledge from existing neuroimaging methods.

A potential explanation for the failure to find a stimulation effect on the theory of mind measures could be the lack of spatial specificity of tDCS (Faria et al., 2011; Nitsche et al., 2007; Sparing & Mottaghy, 2008). It is possible that the region of the TPJ where activation is found during theory of mind tasks in fMRI studies, differs from the area of TPJ stimulated in these tDCS experiments. To address this problem, future theory of mind research involving tDCS of TPJ could employ fMRI-guided neuronavigation (Moos, Vossel, Weidner, Sparing, & Fink, 2012; Weiss et al., 2013) to ensure precise positioning of the electrodes in the same region of TPJ.

An alternative interpretation of the results from Experiment 4, and therefore a potential limitation of the experimental design, concerns the likelihood of tDCS effects spreading across hemispheres. if true, hemispheric transmission would challenge the interpretation of bilateral TPJ involvement in the control of imitation and perspective taking. Evidence of interhemispheric tDCS effects from studies stimulating the motor cortex are somewhat mixed. For example, (Lang et al., 2005) found increased regional cerebral blood flow (rCBF) in contralateral M1 following both cathodal and anodal tDCS. They suggest that such contralateral cortical effects may represent a lasting reduction in left-to-right transcallosal inhibition between the two cortices (Lang et al., 2005); similar effects have been found in TMS studies, (e.g., Schambra, Sawaki, & Cohen, 2003). However, the contralateral cortical effects do not necessarily lead to measurable behavioural effects. For example, Lang, Nitsche, Paulus, Rothwell, & Lemon, (2004) delivered tDCS to the left M1 and measured motor evoked potentials (MEPs) from both right and left hands. They found no contralateral effect, as there was no change in MEPs evoked from the right hand after anodal or cathodal tDCS. Yet other studies suggest that the contralateral behavioural effects following tDCS of M1 are dependent on the dominance of the stimulated hemisphere. Vines, Nair, & Schlaug, (2008) found that stimulating the dominant (left M1) hemisphere had an effect on both contralateral and ipsilateral hands (anodal: right hand > left hand; cathodal: left hand > right hand); whereas when stimulating the non-dominant (right M1) hemisphere, anodal stimulation had an effect on the contralateral hand but no effect was seen with either type of stimulation on the ipsilateral hand. Similar findings have been reported earlier with TMS (Netz, Ziemann, & Hömberg, 1995), suggesting that hemispheric dominance plays an important role in the complex relationship between interhemispheric inhibition of the motor cortices. However, given the regional restrictions of the tDCS effects even within the motor cortex (.e.g., Nitsche et al., 2007) and taking into account the electrode positioning used in this experiments, it is unlikely that the observed bilateral effects are due to current spread. One could still argue that there might be connectional effects between the homologous TPJ sites, however, given that interhemispheric connections between the stimulated TPJ areas are inhibitory (Koch et al., 2011) these effects should be antagonistically directed (Michael Nitsche, march 2014, via personal communication). Furthermore, two recent rTMS studies (Heinisch, Dinse, Tegenthoff, Juckel, & Brüne, 2011; Uddin, Iacoboni, Lange, & Keenan, 2007) stimulated both right and left TPJ and found selective rTPJ involvement in self (vs. other) face recognition tasks, while no effect was seen on the lTPJ. The findings from these studies do not support the alternative hypotheses that current spread or connectional effects caused the bilateral effects observed in Experiment 4.

6.2.3 Outstanding Questions and Future Directions

Similarly to the training paradigm, the effects of tDCS could be studied in clinical populations known to show impairment in the control of self-other representations such as autism and schizophrenia. In the non-social domain, recent studies looking at the therapeutic effects of tDCS in neuropsychiatric conditions show encouraging results in the treatment of depression (Kalu, Sexton, Loo, & Ebmeier, 2012; Nitsche et al., 2009). The effect of tDCS on impaired cognitive function (visuospatial attention) has been recently explored in patients with schizophrenia (Ribolsi et al., 2013), and there is currently one study listed on ClinicalTrials.gov that will investigate the effect of tDCS on language and memory impairment in autism. Although cognitive neuroscience research is beginning to tap into the potential therapeutic effects of tDCS in the cognitive domain, to date, no research has explored the potential benefits of tDCS in social cognition. Therefore, carefully designed protocols could explore the potential effects of tDCS as a tool to enhance self-other representations in autistic and schizophrenic patients.

Along with the TPJ, neuroimaging studies have consistently reported activation of the medial prefrontal cortex (MPFC) during social cognition tasks requiring mental representations of the self and other agents (e.g., Denny, Kober, Wager, & Ochsner, 2012; Gilbert et al., 2006; Mitchell et al., 2006; Van Overwalle 2011). A recent meta-analysis (Van Overwalle 2009) advocates dissociable roles for these two regions, so that the TPJ is recruited for temporal goals and intentionality inferences at a perceptual level whereas the MPFC serves as a *"module that integrates social information across time and allows reflection and representation of traits and norms, and presumably also of intentionality, at a more abstract cognitive level"* (Van Overwalle 2009, pp. 829). Such presumed dissociation between the TPJ and MPFC presents an interesting line for future research using either tDCS[1] protocols or a combination of tDCS and fMRI.

The findings from Experiments 3 and 4 could also be extended to address the on-going debate concerning the role of TPJ in social cognition and attentional re-orienting (Corbetta et al., 2008; Mitchell 2008; Saxe 2010). For example, HD-tDCS (using smaller size electrodes) to maximise focality of stimulation or a combined tDCS-fMRI design could be employed to further investigate causal TPJ involvement in the social vs. non-social domains.

6.3 The Role of Culture in Self-Other Processes

6.3.1 Summary and Interpretation of Main Findings

Experiments 5 and 6 (Chapter 5) were designed to investigate the role of culture in socio-cognitive processes that rely on the control of self-other representations. Experiment 5 explored whether the acculturation attitudes (Berry et al., 1989) of Polish migrants in the UK modulates their automatic imitative behaviour towards a member of their heritage culture vs. a member of the host culture. Based on participants' answers to a cultural preference questionnaire, the four acculturation attitudes were identified in Polish migrants:

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[1] The extant tDCS literature suggests that stimulating a subcortical region such as MPFC could pose a few challenges. For example, it has been estimated that approximately 45% of the total current applied to the scalp passes through the cranial cavity, therefore the peak current density is found on the cortices directly under the electrode (Lang et al., 2005a; Rush & Driscoll, 1968). Although Lang et al. (2005) reported widespread rCBF changes in remote brain areas following anodal tDCS, it should be taken into account that the current density reaching deeper structures would be reduced compared to the areas directly under the electrode. Furthermore, although a small number of studies have reportedly delivered tDCS of MPFC, the exact positioning of the electrodes is not consistent in these studies. For example, Antal et al. (2013) positioned the stimulating electrode between F2 and Fpz (10-20 EEG system); whereas Bellaïche, Asthana, Ehlis, Polak, & Herrmann, (2013) placed it horizontally over Fpz.

integration, assimilation, separation and marginalization. The behavioural measure of automatic imitation was adapted from the control of imitation task (Brass et al., 2000). The results showed that, as predicted by the acculturation model, Polish migrants adopting the assimilation strategy showed more imitative behaviour towards the British than towards the Polish actor, whereas the opposite pattern was found in those with a separation strategy, who imitated more the Polish than the British actor. Although no differences in the magnitude of imitation effects for either the Polish or the British actor were found in the integration and marginalization groups, their pattern of imitative behaviour matched the prediction from the acculturation model. Thereby, those adopting the integration strategy showed larger imitation effects towards both the British and Polish actors, whereas the marginalized migrants displayed small imitative behaviour towards both nationalities.

Experiment 6 compared performance of two cultures (Cuban vs. British) in a range of social cognition tests. It was expected that these two cultures would show different self-construal styles (SCS) as assessed by the Self-Construal Scale (Singelis 1994), whereby Cubans would show preference for the interdependent SCS and British would prefer the independent SCS. Based on this initial assumption, the data from this experiment were expected to replicate previous findings of cross-cultural differences in automatic imitation (van Baaren et al., 2003), visual perspective taking (Wu & Keysar, 2007) and self-referential judgements (Zhu et al., 2007). Nevertheless, contrary to expectations, no differences were found in any of these measures, including the Self-Construal Scale.

6.3.2 Strengths and Limitations

The findings from Experiment 5 bring together two separate areas of research in the fields of cultural and cognitive psychology by providing the first empirical evidence in support of a modulatory role of acculturation strategies on automatic imitation. Additionally, this study also shows that under the appropriate experimental manipulations, as suggested by Heyes (2011), automatic imitation tasks normally used in a laboratory setting can be successfully employed to investigate mimicry in a social context.

The data from Experiment 5, however, are unable to disentangle the specific cognitive mechanisms mediating the relationship between acculturation strategies and automatic imitative behaviour. Future work in this area could include variables to investigate, for example, the allocation of attentional resources to each stimuli type, or the priming effects from the videos presented prior to the testing session (e.g., whether the same results would be found in the absence of the familiarisation phase – including actors and news from the heritage and the host culture). Another limitation of this study is the small sample size in each of the acculturation strategies. A larger sample would add more statistical power and allow for more reliable statistical analysis to be performed, which in turn would make the evidence presented here more robust. Furthermore, self-report measures could be combined with empirically based paradigms to obtain objective and more reliable measures of cultural attitudes. For example by using RT and or physiological measures (e.g., GSR – galvanic skin response) while migrants are exposed to images / videos representing the heritage and the host culture.

Experiment 6 aimed to expand previous cross-cultural studies, which have mostly focused on North American and East Asian cultures, by contrasting socio-cognitive abilities from two cultures that have not been compared before, Cuba and the UK. Although the experimental design employed tried and tested paradigms in the three measures of social cognition, no cultural effects were found on any of the measures. A considerable weakness of this experiment is the poor internal consistency of the Self-Construal Scale found with this sample.

6.3.3 Outstanding Questions and Future Directions

The modulatory role of acculturation strategies on socio-cognitive abilities provides an interesting avenue for future research. The findings from Experiment 5 could be extended to other social cognition domains such as perspective taking, empathy and pro-social behaviour. For example, would those with an assimilation strategy find it easier to adopt the perspective of/ empathise with/ be more generous or altruistic towards others from a host vs. heritage culture and would the opposite be true for those who adopt a separation strategy? Similarly, what are the benefits of adopting an integration strategy? Does it result in more flexible socio-cognitive processing of self and others, thereby, allowing them to equally adopt the perspective of/ empathise with/ be altruistic towards others regardless of their cultural background (i.e. heritage vs. host)? It would also be of interest to investigate whether the adoption of a certain acculturation strategy remains stable over time or changes as a function of factors such as the amount of time spent living in the host culture, or the extent of contact with members of the host culture. For example, is there a linear progression between the different strategies - so that those who adopt a separation or marginalization strategy at first become more assimilative and ultimately become integrated? If so, does the imitative behaviour towards a member of the heritage vs. host culture change as migrants adopt different strategies?

In spite of the null results from Experiment 6, its aims are worthwhile pursuing. Future research should endeavour to widen the focus of cross-cultural studies beyond the established North American vs. East Asian boundaries by adopting a more inclusive attitude towards other cultures. However, should no significant effects be found between those cultures, researchers are faced with the challenge that null findings are difficult - and at times, impossible – to interpret.

6.4 Conclusions

The set of studies presented in this thesis provide an insight into self-other processes in social cognition. Previous research has studied these processes as a single class of representation (e.g., mental states, motor plans, emotional states) 'bound' to the socio-cognitive ability under investigation (theory of mind, imitation, empathy). Experiments 1-4 and 6 explored whether shared underlying mechanisms of self-other representations can be found in three different social domains, the control of imitation, visual perspective taking and theory of mind; and Experiment 5 investigated whether different acculturation strategies of migrants to a new culture modulate self-other representations in the control of imitation.

The results from Experiments 1-4 reveal a relationship between the control of imitation and visual perspective taking. Furthermore, these data suggest that the underlying mechanism of this relationship may relate to the online control of co-activated self-other representations, which at the neural level is supported by the TPJ (Experiments 3-4), an area of the brain that has been consistently identified as part of a wider network of regions playing an essential role in social cognition. Although much work still needs to be done to determine the specific role of each component of this network, the findings from these experiments make some contribution towards achieving that goal. Based on these findings, a number of interesting areas for future research have been identified, some of which include the potential for carefully designed behavioural training and brain stimulation protocols to be used in clinical populations known to show impairment of self-other representations such as individuals with autism and schizophrenia.

Future research could also address the failure to find a relationship between theory of mind and the control of imitation or between theory of mind and visual perspective taking. Performance on all of the theory of mind tasks was very high, therefore this null result could be due to the lack of performance variability when using these tasks with neurotypical adults. Although all the three tasks employed in these experiments have been successfully used in clinical settings and neuroimaging research, it is possible that neurotypical adults are so competent at the attribution of mental states to others that capturing performance variability at the behavioural level poses a considerable challenge. A combination of brain stimulation and neuroimaging methods could be used in the future to address this challenge.

Finally, the results from Experiment 5 revealed that in the context of imitation, the control of self-other representations within a migrant population could be modulated by the adopted acculturation strategy. If the preferred strategy is to assimilate the host culture, then there is an imitation bias towards a member of the host culture, whereas the imitation bias in a separation strategy is towards a member of the heritage culture. These findings have implications in the field of social cognition research, specifically within the imitation literature, by revealing that yet another factor can modulate self-other representations, with resulting impact on the quality of social interactions.

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