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Automatic Imitation: Antecedents and Individual Differences

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SOBA Laboratory
Social Brain in Action

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SUMMARY

Automatic imitation is a nonverbal behaviour that is central to social cognition and influences social connectedness. Despite a recent interest in examining the factors that influence imitation behaviour, there is still much that is unknown. The following studies employ a range of methods to investigate how features of oneself and of an interaction partner impact on imitation behaviour. In the first empirical chapter (Chapter 2), a series of behavioural experiments elucidate the influence of facial signals from an interaction partner on subsequent imitation behaviour. Chapters 3 and 4 employ large sample behavioural approaches to investigate the relationship between automatic imitation and individual differences in one's own stable personality characteristics. In Chapter 4 this approach is combined with a functional magnetic resonance imaging (fMRI) study. This chapter examines an unpredicted individual difference result from Chapter 3, and the brain regions involved in supporting this difference in the control of automatic imitation compared to a non-social inhibitory control task. As a whole, the results from this thesis suggest that imitation is sensitive to facial cues from an interaction partner that signal information pertinent to a current social interaction, rather than cues about the interaction partner's long-term behaviour. Additionally, imitation is relatively resistant to individual differences in one's own stable personality characteristics. This thesis has implications for social cognitive neuroscience research more broadly and advocates the use of large sample behavioural studies in combination with fMRI studies in order to increase reproducibility in the field and confidence in neuroimaging findings.

TABLE OF CONTENTS

LIST OF FIGURES AND TABLES

Chapter 1. General Introduction

Chapter 2. Facial features that signal transient emotional states, but not enduring personality traits, modulate automatic imitation of hand actions

Chapter 3. Investigating the Relationship Between Stable Personality Characteristics and Automatic Imitation

Chapter 4. Sex differences in the inhibition of automatic imitation

Appendices

CHAPTER 1

GENERAL INTRODUCTION

A friend once told me that a quick upward nod of the head indicates acknowledgement of a friend or an accomplishment, whereas a slow downward nod of the head indicates respect. I do not know the strength of empirical evidence behind this claim, however, I have since read that over 60 different types of 'nod' can be distinguished (Poggi et al., 2011). Given that such a simple movement of only one body part can lead to so many different interpretations it is a wonder that humans navigate their social environment so proficiently, with only the odd faux pas. Indeed, there is a wealth of empirical evidence that supports the idea that we are experts at understanding the intricacies of nonverbal behaviours and social interactions more generally. Humans are adept at navigating their social environment despite social interactions being incredibly complex, relatively hard to predict, and responsive to one's own behaviour (Adolphs, 2001). It is thought that living in complex social groups has required unmatched levels of cognitive processing and this has driven our intellectual and neurological development (Adolphs, 2001; Emery, 2005). The growing field of social cognitive neuroscience provides great insight into social processes by integrating social and cognitive neuroscience domains (Ochsner & Lieberman, 2001). Using this approach I will investigate the social process of imitation using cognitive and neuroscience approaches.

Imitation of individuals with whom we interact is one of many important social processes and is a behaviour that is considered central to social cognition (Heyes, 2009). Imitation behaviour is considered an important tool for learning and a key behaviour for non-verbal communication (Brass & Heyes, 2005; Hamilton, 2014; Heyes, 2011). Although investigation of imitation spans many domains, including developmental psychology, social psychology, biological evolution, and the nascent field of social cognitive neuroscience (Heyes, 2009), much of this research has focused on the role of imitation in learning (Hamilton, 2014). Recently, however, there has been a call for a shift in focus toward investigating the influence of imitation in nonverbal communication, in order to more fully understand the central role of imitation behaviour in social interaction (Hamilton, 2014). Research is moving in this direction, however, there are many open questions that will aid understanding and characterisation of this behaviour. For instance, there is still much to learn about the factors in our social environment that impact on imitation behaviour, as well as how our own characteristics relate to our imitation behaviour. Finally it remains to be seen how these factors modulate the neural systems supporting imitation.

In this thesis I will provide evidence that adds to understanding of these influences and relationships with imitation behaviour. As such, throughout the rest of this chapter I will provide a background by outlining current understanding of imitation in relation to these topics. Section 1.1. will be a general introduction to imitation, comprising causes, consequences, and methods of measurement. Section 1.2. will describe neural systems supporting automatic imitation behaviour, and what we know about modulation of these systems. Section 1.3. will outline what we currently know about antecedents to, and individual differences related to, automatic imitation behaviour. Finally, in Section 1.4. I will present the structure of the thesis and the aim of each chapter.

1.1. Imitation background

1.1.1. What is imitation and specifically what is automatic imitation?

Imitation refers to the act of copying the behaviours of another individual, and as such is a fundamentally social phenomenon; without another person present, imitation cannot occur. Furthermore, it is a ubiquitous behaviour; we imitate facial expressions, emotions, speech patterns and characteristics, postures, gestures, and mannerisms of the people we interact with (Chartrand & van Baaren, 2009). This behaviour serves two broad roles: skill acquisition and social development (Brass & Heyes, 2005; Heyes, 2011). Anecdotally, skill acquisition, or the learning of a novel behaviour, seems easier when we copy another person compared to receiving verbal or written instruction, for example, when learning to dance, play piano, or ride a bike. Imitation also enables social development, at a personal and cultural level (Heyes, 2009, 2011). For example, when we are in a new situation, it is likely that we pick up on the behaviour of those around us and adjust our own behaviour accordingly. In the case of learning a novel behaviour, imitation is likely to be a conscious process, whereas the case of imitation in social situations is more likely to be unintentional and automatic, occurring without either interaction partner's awareness (R. Cook et al., 2012a; Chartrand & Lakin, 2013; Chartrand & van Baaren, 2009; Heyes, 2011; van Baaren et al., 2009). Given the ubiquity and functional roles of imitation behaviour, it is accordingly considered a process central to social cognition (Heyes, 2009). The focus of my PhD is the second form of imitation, the nonconscious, automatic behaviour. The rest of this section will outline the importance of automatic imitation behaviour in the social environment by discussing the causes and consequences of automatic imitation, and outline the different methods by which automatic imitation is measured.

1.1.2. The importance of automatic imitation: Causes and consequences

Automatic imitation occurs without awareness of the observed behaviour or the intention to copy it and yet appears to have important social consequences (Stel & Vonk, 2010; van Baaren et al., 2009). Nonconscious, automatic imitation has positive effects on the dyad, the currently interacting individuals, by facilitating smooth interactions, and by increasing liking and affiliation between social partners (Chartrand & Bargh, 1999; Chartrand & Lakin, 2003). Automatic imitation also has positive effects on the individual by promoting subsequent pro-social behaviour (Chartrand & Lakin, 2003; van Baaren et al., 2009). In terms of social success, it seems that the more you imitate those around you, the better. Indeed, evidence suggests that automatic imitation is a pervasive, rapid behaviour that is difficult to inhibit, even in contexts where inhibition of automatic imitation is beneficial to the individual. For example, in a game of "rock, paper, scissors", where imitation reduces payoffs by leading to more draws and fewer wins, participants were still more likely to imitate the gesture of the other player (R. Cook et al, 2012a).

However, this behaviour is not impervious to external influences. In fact, there are a number of factors that cause modulation of automatic imitation. Research has shown that context, characteristics of the interaction partner, and one's own characteristics cause imitation to a greater or lesser degree. There is a bidirectional relationship between automatic imitation and liking or rapport between individuals (Stel & Vonk, 2010). Greater imitation leads to greater rapport, but a pre-exiting rapport also leads to increased imitation (Chartrand & van Baaren, 2009; Stel & Vonk, 2010). Thus imitation can also be used as a nonconscious regulator of social interactions; increasing imitation will increase affiliation and social closeness, whereas decreasing imitation can be used to disaffiliate and decrease social closeness when an individual does not intend to affiliate with their interaction partner (Chartrand & Lakin, 2003; Chartrand & van Baaren, 2009; van Baaren et al., 2009).

1.1.3. Measurement of automatic imitation

Two main approaches have been taken in order to measure automatic imitation. In both approaches participants are involved in a primary task and automatic imitation is incidental to this primary task, thus occurring without intention or awareness on behalf of the participant.

Taking the first approach, Chartrand and Bargh (1999) characterised automatic imitation during naturalistic social interactions as the chameleon effect, as individuals take on the characteristics and mannerisms of those around them much like a chameleon takes on the colour of its environment. In this way it has been suggested that the nonconscious imitation of the behaviour of one's interaction partner allows us to "blend in" or "merge" with our social environment (Chartrand & Lakin, 2003; Rauchbauer et al., 2015). Following this approach, a participant and a confederate perform the primary task together, such as describing photographs. Whilst the primary task is completed, the confederate displays a specific behaviour and the number of instances of copying by the participant is covertly recorded. Automatic imitation, often known as mimicry in this literature, has been documented for a variety of behaviours, including foot shaking and facial expressions (Chartrand & Bargh, 1999; Stel & Vonk, 2010). This measure provides a high level of ecological validity, but lower experimental control of factors that impact on automatic imitation.

The second approach provides higher experimental control and a very precise temporal measure of automatic imitation, and any moderating influences, by utilising a computer-based reaction-time (RT) paradigm (Brass et al., 2000; Stürmer et al., 2000).

During this approach, the primary task requires participants to make a movement, for example lifting a finger in response to a visual cue. Incidental to this task they will simultaneously observe another person's finger movement. The observed finger movement is either congruent with their own (i.e., lifting the same finger), or incongruent with their own (i.e., lifting a different finger). When observed movements are congruent with the visually cued movement facilitation occurs, observed as speeding of RTs. Whereas observed movements that are incongruent with the visually cued movement produces interference, observed as a RT cost. This difference in RT is considered an index of automatic imitation (Heyes, 2011) as it reflects the tendency to automatically imitate an observed action despite the action being incidental to, and in the case of an incongruent trial detrimental to, task performance. This measure of imitation partially indexes spatial compatibility (Catmur & Heyes, 2011) and shares some task demands with more general cognitive control tasks requiring the inhibition of task irrelevant responses, for example the Flanker task (Erikson & Erikson, 1974) or cueing tasks (Bayliss et al., 2005). However, this task provides additional social conflict in the form of automatic representation of an observed action that must be inhibited in order to perform the task, and thus provides a robust laboratory based measure of automatic imitation behaviour (Catmur & Heyes, 2011; Heyes, 2011; Heyes et al., 2005).

These two approaches to measuring automatic imitation consist of differences that are important to consider when interpreting the mechanisms underlying the observed behaviour (Hogeveen et al., 2014). In the first measure increasing imitation behaviour is advantageous to performance in terms of building affiliative bonds with an interaction partner (Chartrand & Bargh, 1999; Chartrand & Lakin, 2003). Additionally, imitation behaviour occurs asynchronously, with a typical temporal delay of a few seconds from observation of the interaction partner's action (Bailenson & Yee, 2005). In contrast, better performance in the computer-based RT measure of automatic imitation requires decreasing imitation behaviour, temporally simultaneous to observing the interaction partners action (Brass et al., 2000; Stürmer et al., 2000). As such, the RT measure of imitation requires separation of self-generated and other-generated action representations in trials where participants simultaneously observe an action that is incongruent with their own task-required motor response (Brass et al., 2000; Brass et al., 2009). Therefore interpretation of behaviour measured by the RT measure involves greater consideration of the control of social interactions in terms of inhibition of automatic imitation; a consideration that has received increased attention recently and will be discussed in more detail later in this chapter (Cook & Bird, 2012; J. Cook et al., 2012; Hogeveen et al., 2014; Southgate & Hamilton, 2008; Wang & Hamilton, 2012;).

1.1.4. Summary of imitation background

Automatic imitation is a pervasive behavioural phenomenon that is central to social cognition and occurs across face processing, emotion, language, and motor domains. This behaviour occurs nonconsciously and automatically, is subject to moderating influences and has a significant impact on social interactions for the dyad and the individual. Additionally, automatic imitation can be measured as an incidental behaviour during naturalistic social interactions or during a laboratory-based paradigm that measures the inhibition of automatic imitation. Throughout my PhD I use the RT measure of automatic imitation due to the greater level of experimental control afforded by this method, and the ability of this paradigm to lend itself well to use in functional magnetic resonance imaging (fMRI) studies in order to examine the neural systems underpinning the inhibition of automatic imitation behaviour.

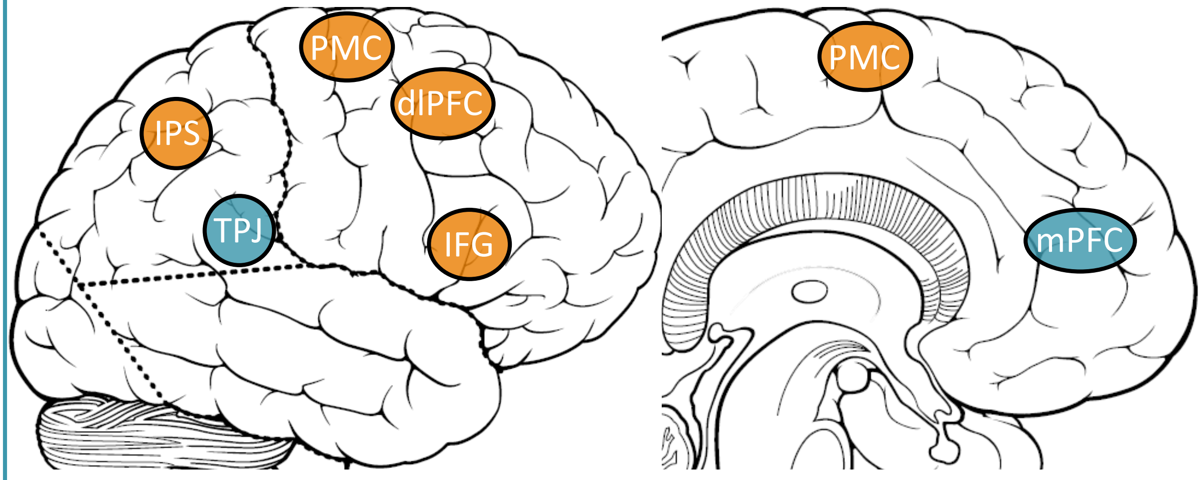
The following sections will first outline the neural systems involved in the inhibition of automatic imitation and what we currently know regarding modulation of these neural systems (section 1.2.), and then the behavioural modulation of inhibition of automatic imitation by antecedents and individual differences (section 1.3.).

1.2. Neural systems and automatic imitation

Investigation of the neural systems that are recruited during the inhibition of automatic imitation will shed light on the mechanisms by which regulation of automatic imitation behaviour occurs. A recent debate regards the extent to which social processes rely on domain general and domain specific neural architecture (Adolphs, 2001; Barrett & Satpute, 2013; Kanwisher, 2010). Those regions that show specialised responses for social processes have also been shown to be responsive in non-social tasks (Baetens et al., 2014; Spunt & Adolphs, 2015) and general processing areas have been shown to interact with those areas specialised for social processing (Baldauf & Desimone, 2014;

Quadflieg et al., 2011; Zaki et al., 2010). As such, modulation of automatic imitation based on antecedents or individual differences could occur via neural systems engaged during general inhibitory control or those specifically recruited during the regulation of automatic imitation (see Figure 1.1.).

Figure 1.1. – Neural regions involved in inhibitory control



Lateral view **Medial view**

Figure 1.1. Inhibitory control regions that are (🔵) specific to the inhibition of automatic imitation, comprising medial prefrontal cortex (mPFC) and temporo-parietal junction (TPJ), and those that are (🟠) involved across multiple inhibitory control tasks, comprising dorsolateral frontal regions (dorsolateral prefrontal cortex (dlPFC); premotor cortex (PMC); inferior frontal gyrus (IFG)), medial frontal cortex (PMC), and parietal cortex (inferior parietal sulcus (IPS))

1.2.1. Neural systems engaged in general inhibitory control

Neural systems underpinning general, non-social inhibitory control have been identified (see Figure 1.1., orange clusters). Non-social tasks requiring response inhibition, such as go/no-go, flanker, and stimulus response compatibility tasks consistently engage parietal, and dorsolateral and medial frontal cortices (Bunge et al., 2002; Hazeltine et al., 2007; Nee et al., 2007; Wager et al., 2005). The functional roles of these areas have been dissociated suggesting that parietal areas are involved in maintaining a representation of possible responses during a task. Dorsolateral and medial frontal areas, including premotor cortex, have been shown to be involved in selecting among competing response alternatives during a task, which involves inhibition of the incorrect response or responses (Bunge et al., 2002; Hazeltine et al., 2007; Nee et al., 2007; Wager et al., 2005).

1.2.2. Neural systems engaged in inhibition of automatic imitation

Imitation is a crucial component of social functioning and as such it has been suggested that evolution might have favoured specialised mechanisms in order to facilitate this behaviour (Chartrand & van Baaren, 2009). Indeed, inhibition during social contexts has been shown to rely on neural substrates partly distinct from those involved in inhibition during non-social contexts (see Figure 1.1.). Two key brain regions, medial prefrontal cortex (mPFC) and right temporo-parietal junction (rTPJ), have been consistently implicated in the inhibition of automatic imitation using a triangulation of methods across fMRI (see Figure 1.1., blue clusters; Brass et al., 2001, 2005, 2009; Klapper et al., 2014), brain stimulation (Santiesteban et al., 2012b; Sowden & Catmur, 2015), and patient studies (Brass et al., 2003; Spengler et al., 2010).

A seminal fMRI paper showed regions in mPFC and rTPJ were recruited during the inhibition of automatic imitation (Brass et al., 2001). Support for the role of frontal cortex in inhibiting imitation behaviour specifically came from a study that showed that patients with frontal lesions showed a deficit in inhibiting imitative responses compared to both a posterior lesion group and a healthy control group, whilst both lesion groups showed a deficit compared to healthy controls on a non-social inhibitory control task (Brass et al., 2003). This dissociation between inhibition of imitation and inhibition in a non-social task was further supported by an fMRI study showing activation in mPFC and rTPJ for inhibition of imitation but not during inhibition in a non-social task (Brass et al., 2005). Finally, dampening of activity in rTPJ by way of repetitive transcranial magnetic stimulation (TMS) impairs imitation inhibition but not spatial compatibility (Sowden & Catmur, 2015). Together these studies identify those regions engaged in the inhibition of automatic imitation and suggest that these regions are specialised for the inhibition of imitation rather than general inhibitory control.

However, the functional roles of mPFC and rTPJ during this task have been dissociated (Brass et al., 2009) and are shown to share neural recruitment with other social processes (Santiesteban et al., 2012b; Spengler et al., 2009, 2010). This suggests that inhibition of imitation might not rely on a special purpose mechanisms dedicated specifically to the control of imitation behaviour but maybe those specialised for the control of social processing more generally (Brass & Heyes, 2005). The first study to show a functional dissociation of the roles of mPFC and rTPJ manipulated the timing of the hand action to occur simultaneous to, or delayed from, the presentation of the participant's cue (Brass et al., 2009). This provided evidence that the role of rTPJ is to provide a self/other distinction of the agent responsible for the action whereas the role of mPFC is to enforce one's own action in the face of conflict provided by viewing a simultaneous incongruent action. This fractionation of roles for mPFC and TPJ is supported by evidence that these regions show overlapping activation with other social processes (Spengler et al., 2009). Both regions show overlap of activation between inhibition of imitation and a Theory of Mind (ToM) task, requiring understanding and attribution of mental states to other people. However, activation produced by inhibition of imitation overlapped in rTPJ with an agency task where participants judged whether or not they caused an event to occur. Conversely, activation resulting from inhibition of automatic imitation overlapped in mPFC with a self-referential task.

These findings of shared neural circuitry between imitation and other social-cognitive tasks, as well as a dissociation of roles for mPFC and TPJ are supported by complementary findings in patients with deficits in the inhibition of imitation. Deficits in inhibition of imitation correlated with deficits in mental state attribution in patients with frontal lesions but correlated with deficits in visual and cognitive perspective taking in patients with temporo-parietal lesions (Spengler et al., 2010). Additionally, training in imitation-inhibition improves performance on a visual perspective-taking component of ToM (Santiesteban et al., 2012a), and excitatory stimulation of rTPJ by way of anodal transcranial direct current stimulation (tDCS) causes increased performance on imitation and perspective taking tasks (Santiesteban et al., 2012b).

Taken together, these studies identify neural systems involved in the inhibition of automatic imitation. These regions demonstrate dissociation from non-social inhibitory control, as well as specific roles during the inhibition of imitation that demonstrate some overlap of activation with other social processes. Additional research has begun to investigate whether the response of neural systems recruited during inhibition of imitation is rigid or whether it is flexible and sensitive to modulation by additional factors, such as priming or features of the putative interaction partner.

1.2.3. Modulation of the neural system during inhibition of automatic imitation

Additional evidence that mPFC and TPJ maintain different roles during the inhibition of imitation come from studies that have investigated the sensitivity of the neural system responsible for inhibition of imitation to modulation by other factors.

Evidence that rTPJ is recruited in order to distinguish self- from other- initiated actions comes from the investigation of the neural processes occurring during the modulation of automatic imitation. For example, Klapper et al. (2014) showed that rTPJ is engaged to a greater extent when participants believe that the putative interaction partner is human and when this agent also appears to be human, compared to when only one, or neither of these animacy cues are present. Also, Rauchbauer et al. (2015) showed that rTPJ is recruited to a greater extent when participants simultaneously observe a putative interaction partner looking happy, thus giving a socially salient affiliative signal, compared to when they look angry. The authors suggest that when observing a strong affiliative cue the self/other distinction is harder to achieve, thus rTPJ is activated to a greater extent in order to maintain the distinction between self- and other- generated actions and avoid boundless imitation of an affiliative interaction partner (Rauchbauer et al., 2015).

Additionally, mPFC has been shown to be sensitive to social cues during automatic imitation. An anterior portion of mPFC (amPFC) shows greater activity when imitation must be inhibited if participants are primed with first person prosocial, or third person antisocial sentences (Wang & Hamilton, 2014a). Activity in amPFC during priming was positively correlated with the prime modulated amount of interference participants experienced behaviourally during imitation control. The authors suggest that the priming activates a prosocial self-schema held in amPFC, which results in greater processing demands in order to inhibit automatic imitation. Additionally, activity in mPFC, along with superior temporal sulcus (STS) and inferior frontal gyrus (IFG), is greater as a result of direct eye gaze during imitative responses, but also greater as a result of averted eye gaze when imitative responses must be inhibited

(Wang et al., 2011b). Functional connectivity analyses suggested that mPFC provides a top-down influence on STS and IFG during imitation control (Wang et al., 2011b). Therefore, mPFC appears to provide either an enhancement or an inhibition of imitation in response to the social context.

Rauchbauer and colleagues (2015) also showed that activity was greater in regions including left inferior parietal lobule (IPL) and ventral premotor cortex (vPMC) when the putative interaction partner was an ethnic outgroup compared to an ingroup member. The authors suggest recruitment of these regions is indicative of an increased focus on the hand stimuli during the task, in order to increase imitation and appease a potentially threatening outgroup member. This provides additional evidence that neural system activity during the control of automatic imitation appears flexible depending on the social context.

Taken together, these studies suggest that neural systems subserving the inhibition of automatic imitation are not rigid, but are in fact flexible and demonstrate sensitivity to social context (Klapper et al., 2014; Rauchbauer et al., 2015; Wang et al., 2011b; Wang & Hamilton, 2014a). These data also show that in some contexts, additional regions are recruited (Rauchbauer et al., 2015; Wang et al., 2011b) and suggest that mPFC and rTPJ interact with other neural circuits during inhibition of imitation (Wang et al., 2011b). This supports the idea that a distributed neural network is functionally connected during the inhibition of automatic imitation (Cross & Iacoboni, 2013). Thus, rTPJ and mPFC may be specialised for inhibiting the urge to imitate but they do not act alone; they also exchange signals with a broader brain network.

1.2.4. Individual differences in the neural system during inhibition of imitation

As it stands, the majority of investigation into neural system differences during the control of automatic imitation has focused on external or transient cues (Klapper et al., 2014; Rauchbauer et al., 2015; Wang et al., 2011b; Wang & Hamilton, 2014a). Some behavioural research has suggested that individual differences in stable characteristics impact on automatic imitation (Ainley et al., 2014; Chartrand & Bargh, 1999; Hogeveen & Obhi, 2013; Obhi et al., 2013; Santiesteban et al., 2015), but similar work on a neural level of description is largely absent. As such the relationship between within-individual differences in stable characteristics and the functioning of this neural system is unknown.

It is suggested that imitation may be a crucial mechanism underlying the understanding of other people's thoughts and feelings, and thus forms a basis for empathy (Carr et al., 2003; Iacoboni, 1999; Leslie et al., 2004). However, these studies (Carr et al., 2003; Leslie et al., 2004) have focused on the role of facial expression imitation leading to empathy, and have not investigated differences in neural system engagement during inhibition of automatic imitation behaviour as a function of individual differences in empathy. Consequently, it is currently unknown whether individual differences in empathic traits, and indeed in other stable personality characteristics are related to differences in functioning of the neural system that controls automatic imitation.

1.2.5 Summary of neural systems and automatic imitation

In conclusion, inhibitory control of automatic imitation recruits neural regions distributed throughout the brain (Brass & Heyes, 2005; Cross & Iacoboni, 2013; Rauchbauer et al., 2015; Wang et al., 2011b), that show dissociation of function (Brass et al., 2009; Santiesteban et al., 2012a; Spengler et al., 2009, 2010) and interaction across regions (Cross & Iacoboni, 2013; Wang et al., 2011b). Furthermore, the activity within and across these regions is dissociable from non-social tasks (Brass et al., 2003, 2005; Sowden & Catmur, 2015) and shows some overlap with other social processes (Santiesteban et al., 2012a, 2012; Spengler et al., 2009, 2010). Finally, these neural systems are sensitive to modulation by social context (Klapper et al., 2014; Rauchbauer et al., 2015; Wang et al., 2011b; Wang & Hamilton, 2014a) and potentially by individual differences in stable characteristics, although this is as yet unknown.

Given that social factors provide input to and modulate the neural circuits subserving the inhibition of imitation, and it is presumed that the neural system regulates outputs in terms behavioural measures of imitation (Heyes, 2011). As such, behavioural measures of automatic imitation would also be expected to be flexible and sensitive to social factors.

1.3. Antecedents to automatic imitation

Despite the ubiquitous and automatic nature of imitation behaviour recent studies have begun to reveal that the propensity to imitate is not fixed or constant, but is in fact sensitive to antecedents such as the context in which the interaction occurs, including features of the environment and of the individuals involved in the interaction (Chartrand & Lakin, 2003; Table 1.1.). These antecedents provide modulation of imitation in terms of a relative increase or decrease in imitation behaviour based on these factors. Given the social consequences of imitation (Chartrand & Lakin, 2003), characterising the influence of these factors on automatic imitation is key to understanding imitation and its role in social interactions. This section will outline the evidence that is building to suggest that automatic imitation, focusing on the RT measure of automatic imitation (Brass et al., 2000), is not impervious to modulation, but in fact varies across social context, and depends upon the characteristics of both interaction partners. The final subsection will identify gaps in knowledge that will be addressed in later chapters.

Table 1.1. – Summary of studies that have investigated the modulation of automatic imitation

Broad category	Specific category	Effect on automatic imitation	References
A) Experience	**Counter-mirror training**	Counter-mirror training decreases automatic imitation as measured by reaction time and motor evoked potentials	Catmur et al., 2007; Heyes et al., 2005
	Physical context	Decrease in automatic imitation from counter-mirror training is specific to the context in which the training occurred	R. Cook et al., 2012b
	Situational demands	Task instructions to counter imitate decreases automatic imitation	Bardi et al., 2015
B) Prosocial state	**Sentence priming**	Automatic imitation is greater following prosocial compared to antisocial priming	Cook & Bird, 2011, 2012; Leighton et al., 2010; Wang & Hamilton, 2013; Wang & Hamilton, 2014a
	Administration of oxytocin	Oxytocin administration increases imitation compared to a placebo	De Coster et al., 2014
C) Interaction partner's facial features	**Eye gaze**	Direct compared to averted gaze increases automatic imitation	Wang et al., 2011a; Wang & Hamilton, 2014b
	Emotional expression	No clear effect of negative facial expressions compared to neutral, and greater imitation when viewing happy compared to angry expressions	Crescentini et al., 2011; Grecucci et al., 2013; Rauchbauer et al., 2015*
D) Individual differences	**Narcissism**	Individuals with higher narcissism showed lower automatic imitation	Hogeveen & Obhi, 2013; Obhi et al., 2013
	Interoceptive awareness	Greater automatic imitation in individuals with higher interoceptive awareness	Ainley et al., 2014
	Mirror-touch synaesthesia	Increased automatic imitation in individuals with mirror-touch synaesthesia	Santiesteban et al., 2015

Table 1.1. A summary of studies that show modulation of automatic imitation as measured by the imitation-inhibition task (Brass et al., 2000). This table is not an exhaustive summary of all studies that have investigated modulation of automatic imitation, but includes those I believe to be representative and most relevant to my PhD. *Rauchbauer et al. (2015) also showed that the group membership of the interaction partner modulated automatic imitation.

1.3.1. Experience and social state

Evidence suggests that automatic imitation is a flexible behaviour that is sensitive to experience, situational demands, and physical context (see Table 1.1., section A; Bardi et al., 2015; Catmur et al., 2007; R. Cook et al., 2012b; Heyes et al., 2005). When participants are trained to produce counter-imitative responses, for example making a little finger movement when they see an index finger movement and making an index finger movement when they see a little finger movement, the tendency to produce imitation behaviour is decreased (Catmur et al., 2007; Heyes et al., 2005). This decrease in automatic imitation is specific to the physical environment in which participants received the counter-imitation training (R. Cook et al., 2012b), and can even occur if participants are simply instructed to produce counter-imitative responses (Bardi et al., 2015). In addition, prosocial states have been related to increased automatic imitation (see Table 1.1., section B; Cook & Bird, 2011, 2012; De Coster et al., 2014; Leighton et al., 2010; Wang & Hamilton, 2013; Wang & Hamilton, 2014a). Induction of a prosocial state, via a scrambled sentence completion task (Cook & Bird, 2011, 2012; Leighton et al., 2010; Wang & Hamilton, 2013; Wang & Hamilton, 2014a) or via oxytocin administration (De Coster et al., 2014) increased automatic imitation behaviour compared to priming of an antisocial state or administration of a placebo.

1.3.2. Interaction partner's facial features

Furthermore, transient facial features of the interaction partner have been shown to impact on automatic imitation, specifically eye gaze and emotional facial expression (see Table 1.1., section C). Direct compared to averted eye gaze from the interaction partner has been shown to increase the tendency to imitate by facilitating imitative responses (Wang et al., 2011a; Wang & Hamilton, 2014b). Following up on a study showing that affective priming by negative images increased imitation compared to positive or neutral images (Grecucci et al., 2011), two studies failed to show a reliable impact on automatic imitation of negative compared to neutral facial expressions (Crescentini et al., 2011; Grecucci et al., 2013). A more recent study showed that positive facial expressions increased automatic imitation compared to angry facial expressions (Rauchbauer et al., 2015). Although no studies have directly compared positive, negative, and neutral facial expression, taken together, these studies suggest that imitation is comparable whilst viewing neutral and negative facial expressions, and enhanced when viewing positive facial expressions.

1.3.3. Individual differences

As well as sensitivity to contextual cues, priming of a prosocial state, and facial features of the interaction partner, a few studies have investigated how stable personality characteristics may predispose an individual to imitate to a greater or lesser extent (see Table 1.1., section D). Two studies have linked automatic imitation to individual differences in narcissism (Hogeveen & Obhi, 2013; Obhi et al., 2013). This personality trait, which is characterised by self-interest and lack of empathy, was related to a decreased sensitivity to another's actions and lower automatic imitation behaviour (Hogeveen & Obhi, 2013; Obhi et al., 2013). Conversely, individuals who experience greater sensitivity to the actions of others, those who are higher in empathy or with mirror-touch synaesthesia show increased automatic imitation (Chartrand & Bargh, 1999[1]; Santiesteban et al., 2015). Additionally, Ainley et al. (2014) showed that individuals with higher interoceptive awareness, which is how aware an individual is of their internal body signals, show greater automatic imitation. Ainley and colleagues suggest that those individuals with high interoceptive awareness generate a stronger interoceptive representation upon observing another persons action thus leading them to imitate more. Taken together, these studies suggest that individuals with a stronger other-focus, or stronger internal representations of observed actions, automatically imitate others to a greater extent than individuals with a stronger other-focus, or weaker internal representations of observed actions.

Furthermore, atypical intentional imitation has been observed in both individuals with autism spectrum disorders (ASD; Williams et al., 2004) and those with schizophrenia (Park et al., 2008). However, some research has suggested that automatic imitation is intact in individuals with ASD (Bird et al., 2007; Cook & Bird, 2012; Press et al., 2010). As such, the relationships between automatic imitation and ASD and schizophrenia are less than clear (Hamilton, 2013; Southgate & Hamilton, 2008).

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[1] Chartrand and Bargh (1999) measured automatic imitation using a naturalistic paradigm involving interaction with a confederate.

1.3.4. Summary of antecedents to automatic imitation

Overall these studies show that the mechanisms involved in the inhibition of automatic imitation are flexible, and sensitive to a variety of environmental, contextual, and social cues that are informative to social interactions, as well as individual differences in some stable personality characteristics. However, the full extent of this sensitivity is not entirely understood. This section will identify areas where further research would help to characterise the sensitivity of automatic imitation to facial signals from others, and the relationship to one's own stable personality traits.

Faces are an extremely salient social cue and as such the cognitive and neural systems underpinning perception of social signals from faces have been the focus of extensive study (Haxby et al., 2000; Kanwisher, 2010; Said et al., 2011). It is well established that imitation is at play during the detection and recognition of facial expressions in order to understand the interaction partner's emotional state (Goldman & Sripada, 2005; Moody et al., 2007; Niedenthal et al., 2011; Oberman et al., 2007; Rychlowska et al., 2014; Sato et al., 2013). However, this imitation is of the facial expression itself. Only recently has investigation begun into the consequences of recognising facial signals for the control of nonverbal social interactions, specifically the influence of recognising an expression on subsequent imitation behaviour (Crescentini et al., 2011; Grecucci et al., 2013; Rauchbauer et al., 2015). Additionally, as it stands no single study has investigated the influence of positive, negative, and neutral facial expressions. This would provide further insight into the mechanisms by which facial expressions impact on imitation behaviour.

Moreover, although some evidence suggests that facial expression cues from faces, those that give insight into how someone might behave in the current interaction, modulate automatic imitation we do not know whether mechanisms controlling automatic imitation are sensitive to facial cues that signal stable personality characteristics, those that might give insight into how someone is likely to behave in social interactions generally. Individuals who are more extraverted or agreeable exhibit more prosocial behaviour (Ashton et al., 1998; Barrio et al., 2004; LePine & van Dyne, 2001) and may be a good choice of interaction partner to build affiliative bonds through imitation. Additionally, these traits can be accurately perceived when viewing only static images of emotionally neutral faces (Kramer & Ward, 2010; Penton-Voak et al., 2006). However, it is currently unknown whether facial signals of an interaction partner's stable personality characteristics modulate the extent to which one automatically imitates their actions.

In terms of automatic imitation and individual differences in one's own stable personality characteristics relationships have been identified with interoceptive awareness, empathy, narcissism, and mirror-touch synaesthesia (Ainley et al., 2014; Chartrand & Bargh, 1999; Hogeveen & Obhi, 2013; Obhi et al., 2013; Santiesteban et al., 2015). These studies have typically recruited relatively small samples (interoceptive awareness sample: n=43; empathy sample: n=50; narcissism samples: n=18, n=24; mirror-touch synaesthesia sample: n=29). Although recent studies have begun to control for confounding variables (Ainley et al., 2014; Santiesteban et al., 2015) not all have controlled for variables that may vary with these traits (e.g., sex or age of participant) or with automatic imitation as a result of the measure used (e.g., mean RT). Given that larger samples represent the population more accurately (Maxwell et al., 2008) and recent failures to replicate landmark findings in psychology (Pashler et al., 2012; Shanks et al., 2013), further investigation with a large sample whilst controlling extraneous variables is necessary (Cumming, 2014).

Investigation of additional variables would provide a broader understanding of how individual differences in stable characteristics relate to automatic imitation behaviour. It is currently unknown whether stable personality traits of extraversion and agreeableness are related to automatic imitation, despite having been associated with prosocial behaviour more generally (Ashton et al., 1998; Barrio et al., 2004; LePine & van Dyne, 2001). In addition, the relationship between automatic imitation and ASD and schizophrenia is unclear (Southgate & Hamilton, 2008; Hamilton, 2013). It has been suggested that autistic-like and schizotypal traits lie on a continuum from subclinical to clinical populations (Nelson et al., 2013). Therefore investigation of the relationship between automatic imitation and fluctuations of autistic-like and schizotypal traits within the healthy population will shed light on the cognitive mechanisms involved and aid characterisation of imitation abilities in these clinical populations.

1.4. Overview of the thesis

The chapters comprising this thesis explore those factors that shape our automatic imitation behaviour. Chapter 2 will investigate how social signals from others, specifically facial signals, impact on automatic imitation across a series of behavioural experiments. Chapters 3 and 4 will investigate how our own stable characteristics predict our imitation behaviour in large sample behavioural studies (both chapters), and neurally using fMRI (Chapter 4).

Chapter 2 investigates the impact of facial signals on automatic imitation of an interaction partner across four behavioural experiments. In this Chapter we pair faces that signal high, low, and neutral stable trait agreeableness, and happy, angry, and neutral transient emotional expression with the automatic imitation task. This allows us to examine the influence of facial expressions relative to a neutral face, and is the first study to investigate the influence of trait representative faces on subsequent automatic imitation behaviour.

Chapter 3 investigates the relationship between automatic imitation and individual differences in stable personality and subclinical traits in a large behavioural study (n=230). This is the first study to use multiple regression analyses in a large sample whilst interrogating the relationship between individual differences in automatic imitation and allows us to examine the variance in imitation behaviour explained by each of these stable characteristics, whilst controlling for potentially confounding variables such as mean RT or participant sex.

Chapter 4 comprises a large sample behavioural experiment (n=165) and an fMRI experiment (n=28) in order to follow up on an unpredicted individual difference from Chapter 3.

CHAPTER 2

Facial features that signal transient emotional states, but not enduring personality traits, modulate automatic imitation of hand actions

Across four behavioural experiments this chapter examines the impact on automatic imitation of facial signals from an interaction partner. In this Chapter we pair faces that vary on two dimensions in order to characterise the sensitivity of automatic imitation to facial signals. Faces vary by cue type (stable personality features, and transient emotional expression) and by valence (positive, negative, and neutral). This allows us to examine the influence of positive and negative facial expressions relative to a neutral face, and is the first study to investigate the influence of trait representative faces on subsequent automatic imitation behaviour

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2. FACIAL SIGNALS AS ANTECEDENTS TO AUTOMATIC IMITATION

Abstract

Imitation and facial signals are fundamental social cues, but little is known regarding the relationship between these behaviours. It is clear that *during* expression detection, we imitate observed expressions by engaging similar facial muscles. It is proposed that a cognitive system, which matches observed and performed actions, controls imitation and contributes to emotion understanding. However, the *consequences* of detecting facial signals on subsequent imitation behaviour are unclear. The current study investigated the hypothesis that facial cue valence would modulate imitation of hand actions. To test this hypothesis, we paired different types of facial cue with an automatic imitation task. The first two experiments demonstrated that invariant facial cues, which signal trait-levels of agreeableness, had no impact on imitation. Despite readily identifying trait-based facial signals, levels of agreeableness did not differentially modulate automatic imitation. Experiments three and four demonstrated that the impact of happy expressions on imitation was dissociable from angry and emotionally neutral expressions. Therefore, we show that imitation systems are more sensitive to prosocial facial signals that indicate "in the moment" states than enduring trait characteristics. These findings demonstrate that particular facial signals are an antecedent to multiple forms of imitation, not just facial imitation. Further, we add to growing evidence that the control of imitation is not limited to a system that matches observed and performed actions. Instead, social interactions depend on interplay between cognitive systems that extract facial signals and those that regulate imitation.

Keywords: imitation ; automatic ; face signals ; social cognition.

Introduction

Imitation and facial signals are key social cues that help guide behaviour. Imitation between interaction partners increases affiliation and rapport (Chartrand & van Baaren, 2009; van Baaren et al., 2009), whilst information from faces can convey what someone thinks, feels and desires (Haxby et al., 2000; Blakemore et al., 2004). Recent research has started to identify social antecedents to imitation, including a desire to affiliate and pre-existing rapport (Chartrand & Lakin, 2013; Heyes, 2011). However, less research has shown how facial signals regulate imitative behaviour during social interactions. The aim of the current study is to elucidate the impact of recognising facial signals on nonverbal social interactions.

Faces signal a vast array of social information, which can be used to infer intentions and predict behaviour (Haxby et al., 2000; Blakemore et al., 2004). Changeable aspects of faces, such as frowning and smiling expressions, convey emotional states, such as anger and happiness (Tottenham et al., 2009). By contrast, invariant facial features, such as jaw shape or skin tone, are perceived as signalling stable personality features. For example, invariant facial features have been found to indicate trait levels of trustworthiness and dominance (Todorov et al., 2008; Todorov et al., 2015), as well as extraversion and agreeableness (Kramer & Ward, 2010; Penton-Voak et al., 2006). As such, faces signal information about a person's current state as well as enduring trait characteristics, both of which influence the regulation of social interactions (Frith, 2009).

The cognitive and neurobiological mechanisms that underpin perception and detection of facial signals have been studied extensively (Haxby et al., 2000; Kanwisher, 2010; Said et al., 2011). With respect to expression perception, motor theories suggest that expressions are represented, at least partly, within motor structures of the observer's brain. It is claimed that motor system engagement reflects a process of simulating or automatically imitating observed expressions, which contributes to understanding another's emotional state (Goldman & Sripada, 2005; Moody et al., 2007; Niedenthal et al., 2011; Oberman et al., 2007; Rychlowska et al., 2014; Sato et al., 2013). As such, prior research has aimed to understand how imitative mechanisms operate *during* the detection and recognition of facial signals. In contrast, the current study investigates how imitative mechanisms operate *following* the recognition of facial signals. In other words, the current research investigates the *consequences* of recognising facial signals for the control of nonverbal social interactions.

To date, only four studies have investigated how detection and recognition of facial signals impacts subsequent imitative behaviour (Crescentini et al., 2011; Grecucci et al., 2013; Rauchbauer et al., 2015; Wang et al., 2011a). These studies used a lab-based reaction time measure of imitation, which involves making a finger movement, whilst simultaneously observing the finger movement of another person (Brass et al., 2000). Interference to reaction time occurs when participants observe a finger movement that is incongruent with their intended movement. It is suggested that interference, in part, represents the cost of inhibiting an imitative response (Brass & Heyes, 2005; Heyes, 2011). One study showed that eye contact facilitates imitation (Wang et al., 2011a). A further study showed that happy expressions increased the tendency to imitate compared to angry expressions (Rauchbauer et al., 2015). By contrast, two other studies failed to show that negative facial expressions had a reliable impact on imitation compared to neutral expressions (Crescentini et al., 2011; Grecucci et al., 2013). As such, except for eye contact (Wang et al., 2011a) and happy expressions (Rauchbauer et al., 2015), the consequences of recognising facials signals for imitation remain largely unknown.

In sum, although many studies have investigated the role of imitation during the detection and recognition of facial expressions (Niedenthal et al., 2011), there is little known about the consequences of recognising facial signals for the regulation of imitation during subsequent social interactions. Indeed, no study to date has investigated the consequence of perceiving both positive and negative facial expressions compared to emotionally neutral faces on subsequent imitation. Furthermore, although faces signal stable trait information that could indicate whether to approach or avoid someone (Kramer & Ward, 2010; Penton-Voak et al., 2006; Todorov et al., 2008), it remains unknown how such signals influence imitation.

The aim of the current study is to investigate the consequence of recognising facial signals for automatic imitation during subsequent social interactions. Across a series of experiments, faces that emit enduring trait or transient state signals are presented prior to completing an automatic imitation task (Brass et al., 2000). Two hypotheses can be distinguished. The prosocial sensitivity hypothesis predicts that automatic imitation will be specifically sensitive to pro-social signals. Previous research has shown that prosocial signals lead to affiliative tendencies and such tendencies are associated with an increase in imitative behaviour (Chartrand & Lakin, 2013; Heyes, 2011; van Baaren et al., 2009). By contrast, the general social sensitivity hypothesis predicts that automatic imitation will be sensitive to a wider class of social signal, which extend beyond prosocial signals. In other words, as long as they are instructive for guiding social interactions, both prosocial and antisocial signals should provide inputs to automatic imitation.

Experiments 1 and 2 investigate how trait information from faces influences automatic imitation, whereas Experiments 3 and 4 investigate how facial expressions impact automatic imitation. By doing so, the current study can reveal similarities and differences between the way imitative mechanisms operate following the detection of stable and transient information from faces.

Experiment 1

Method

Participants

Thirty-one students (24 female, 7 male; M_{age} = 20.1 years, SD = 3.36) from Bangor University participated for course credit. All participants had normal or corrected-to-normal vision and reported being right handed. The Edinburgh Handedness Inventory showed that two were ambidextrous. However, they were retained in the sample, as they were predominantly right-hand users. Throughout all experiments, participants were removed from analyses if mean accuracy or mean RT for congruent or incongruent trials was greater than three standard deviations (>3SD) from the group mean. In Experiment 1, no participants were removed. All participants gave written, informed consent and were fully debriefed. The Research Ethics and Governance Committee of the School of Psychology at Bangor University granted ethical approval.

Task and stimuli

Figure 2.1. – Stimuli, task, and trial structure for the automatic imitation task

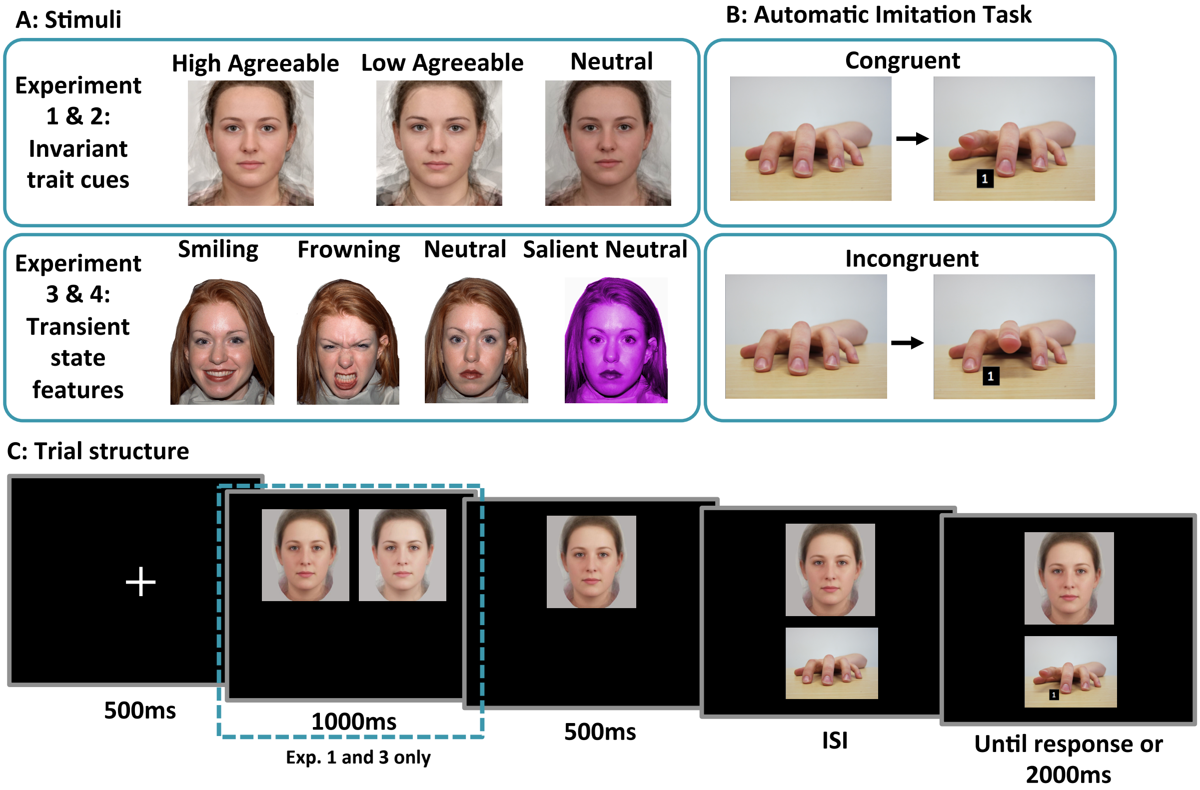

Figure 2.1. **(A)** Stimuli. In Experiments 1 & 2, the hypothesis that invariant trait cues would influence automatic imitation was tested. In Experiment 1, high and low agreeable composites, as well as neutral composites were presented. In Experiment 2, to focus on the distinction between high and low agreeableness, neutral faces were not presented. In Experiments 3 & 4, the hypothesis that transient state cues would influence automatic imitation was tested. In Experiment 3, smiling, frowning and neutral individuals were presented. In Experiment 4, an additional condition was added, which was salient but emotionally neutral. **(B)** Automatic imitation task. Congruent trials involved responding to a number cue, whilst simultaneously observing a matching action. Incongruent trials involved responding to a number cue, whilst simultaneously observing a non-matching action. A number one cued participants to lift their index finger, and a number two cued participants to lift their middle finger. **(C)** Trial structure. In Experiments 1 & 3, faces were first paired together, before a single face remained onscreen. Initially pairing faces together in this manner enabled the distinction between facial signals to be highlighted. In Experiments 2 and 4, faces were presented singularly on each trial to avoid possible contamination between different facial signals. ISI = interstimulus interval.

Face evaluation tasks: Over several years of data collection at Bangor University, participants have been photographed whilst holding an emotionally neutral expression before completing self-report measures of various personality and subclinical traits (Jones et al., 2012; Kramer & Ward, 2010; Scott et al., 2013). We used these existing datasets to generate average images of individuals that are indicative of high levels of agreeableness and low levels of agreeableness. Composite face images were made that represent high and low agreeableness by using a software package that enables multiple individual faces to be combined into one average face (JPyschomorph; Tiddeman et al., 2001). Face images from 15 individuals who reported the highest levels of agreeableness were morphed into one average high agreeable composite. The same morphing procedure was also performed on the 15 individuals who reported the lowest levels of agreeableness. Previous reports demonstrate a correct consensus for these composites across a range of inventory questions for trait agreeableness (Kramer & Ward, 2010).

Composite face images were created from one of three different datasets. Pair one was taken from Kramer and Ward (2010), pair two was taken from the faces photographed for Jones et al. (2012) and pair three was from the faces photographed for Scott et al. (2013). This resulted in three pairs of high-low agreeable composite images with each pair including one high and one low agreeable face. To produce neutral images, a high agreeable composite and a low agreeable composite image were averaged together. Four neutral images were created and paired together into two neutral pairs. In total, therefore, ten individual composite images of faces were used: three were high agreeable, three were low agreeable and 4 were neutral in terms of agreeableness features (Figure 2.1.A.).

Participants completed two face evaluation tasks to examine whether they could accurately judge agreeableness from these faces. The first face evaluation task was a 20-trial two-alternative forced choice (2AFC) task. Participants' viewed five face pairs, three of which comprised a high and a low agreeable face and two pairs comprised neutral faces. On each trial, participants were presented with a face pair and the task was to choose which face best represented one of the four agreeableness-relevant statements from the mini International Personality Item Pool (mini-IPIP; Donnellan, Oswald, Baird, & Lucas, 2006). At the beginning of the 2AFC section, participants saw a fixation cross for 1500ms, followed by presentation of a pair of faces with a question underneath. The face pair and question remained on screen until the participants responded. Therefore, responses were not speeded, however, participants were encouraged to respond with their initial reaction, or 'gut instinct', to the stimuli. Participants were asked to indicate which of the faces best matched the statement underneath by pressing the 'n' key for the left face and the 'm' key for the right face.

On each trial, the high and the low agreeable face was presented next to each other on the screen with the high agreeable face randomly on the left or the right of the pair. It was expected that for pairs comprising a high and a low agreeable face, participants would accurately discriminate them at a level significantly greater than chance (Kramer & Ward, 2010; Penton-Voak et al., 2006; Todorov et al., 2008; Todorov et al., 2015). For the neutral face pairs, which were not trait-diagnostic, performance should be at chance level.

The second face evaluation task was a 40-trial ratings task where participants rated all ten faces on the four agreeableness-relevant statements from the mini-IPIP in a random order. In this task, each face was presented with a statement underneath. The statement remained on screen until participants had given a response. Participants' task was to rate, based on 'gut instinct', how well they agreed that the face matched the statement using the number keys 1-9, where 1 was strongly disagree and 9 was strongly agree.

Automatic imitation task: The automatic imitation task was based on the paradigm developed by Brass, Bekkering, Wohlschläger and Prinz (2000). Stimuli were a female left hand in a neutral position, resting on a flat surface and four target images of the same hand lifting its index or middle finger whilst a target number '1' or '2' appeared between the index and middle fingers of the hand. A number '1' cued the participant to lift their index finger and a number '2' cued the participant to lift their middle finger (Figure 2.1.B.). Thus there were four target trial types, two of which were congruent and two of which were incongruent. During congruent trials, the observed hand action was the same as the participants cued action (observed index finger lift and '1', or observed middle finger lift and '2') whereas during incongruent trials, the observed hand action and the participants cued action were not the same (observed index finger lift and ‘2’, or observed middle finger lift and ‘1’).

Each automatic imitation trial adhered to the following structure (summarised in Figure 2.1.C.). Participants were presented with a fixation cross for 500ms and then a face pair was presented side-by-side for 1000ms. This presentation of a face pair emphasised the differences between the two faces which was intended to give rise to a stronger trait representation than if the faces were only presented singularly. Next, one of the two faces would disappear and a single face, one of the two shown previously in the face pair, would be shown for 500ms in the centre of the screen. A neutral hand would appear underneath the face for a variable duration (500ms, 700ms, or 1000ms) before the imperative stimulus was presented. The imperative stimulus displayed a finger in a raised position with a number cue between the index and middle finger. The imperative stimulus remained onscreen until participants made their response, but for no longer than 2000ms. Thus, trial duration varied but was never longer than 5000ms.

Prior to the start of the task, participants were instructed to hold down the ‘n’ key with the index finger of their right hand and the ‘m’ key with their middle finger. On each trial, upon presentation of a number cue, participants’ instructions were to lift their index finger if it was a ‘1’ and their middle finger if it was a ‘2’ as quickly and as accurately as possible. Reaction time (RT) and accuracy rates were recorded. RTs were measured from the presentation of the number cue until participants lifted one of their fingers. Accuracy rates were recorded as the percentage of total trials in which participants made correct responses.

Catch trials were included at the end of 10% of trials. On catch trials, there was an additional 500ms fixation at the end of the trial followed by the presentation of a single face with the text “Same or different?” underneath. For half of the catch trials, the face was the same as the one that preceded it. This face remained on screen until the participant responded, but for no longer than 10,000ms. If participants thought the face was the same as the one they had just seen, they lifted their index finger from the ‘n’ key and if they thought it was different, they lifted their middle finger from the ‘m’ key. Accurate performance on catch trials required participants to attend to the face stimuli.

Design and procedure

The automatic imitation task employed a mixed 2 x 3 factorial design, with factors of congruency (congruent, incongruent) and face type (high agreeable, low agreeable, neutral). There were 16 repetitions of each face, resulting in 96 trait representative and 64 trait neutral trials. Of the trait representative trials, half were high and half were low agreeable. For all conditions, congruent and incongruent trials were evenly distributed. For half of the congruent and incongruent trials the face had been presented on the left in the pair previously in the trial. Automatic imitation trials were pseudorandomised such that no face pair was shown consecutively and no target hand image was shown more than three times in succession.

Participants completed an 8-trial practice of the automatic imitation task, before completing three tasks. Before the imitation task proper, participants completed the face ratings task and a 20-trial 2AFC task. Participants completed four 40-trial blocks of the automatic imitation task. Blocks of the automatic imitation task alternated with another three blocks of the 2AFC task. The function of alternating between the tasks was to highlight to participants the trait diagnostic value of the faces throughout the experiment. After the last automatic imitation block, participants completed a final 2AFC and a second face ratings task.

Data analysis

Face evaluation: The percentage of correct responses from the trials where participants viewed pairs of high and low agreeable faces was calculated. This was compared, using a one-sample t-test, to the percentage that participants would be expected to get if they were performing at chance (i.e., at 50% as it was a 2AFC task). For pairs of neutral faces, the percentage of trials that participants chose one face from each neutral pair consistently as the high agreeable face was calculated. The percentage for trait representative trials and trait neutral trials was compared using a one-sample t-test to chance (i.e., 50%).

For the rating task, the mean score was calculated for the extent to which participants agreed that each face type (high, low and neutral) looked agreeable on the scale from 1 to 9. A 2 (rating task: first completion, second completion) x 3 (face type: high, low and neutral) ANOVA was used to assess differences in scores for each of the face types and whether ratings differ between the first and second completion of the ratings task.

Automatic imitation: Prior to analysis, trials were removed if participants gave an incorrect response, lifted their finger from the ‘n’ or the ‘m’ key during the ISI, or took longer than 2000ms to respond. For each participant, accuracy was calculated as the percentage of correct responses that participants made. To investigate the hypothesis that trait representative (high and low agreeable) face signals would influence task performance compared to trait neutral face signals, we calculated mean RT for congruent and incongruent trials separately. Analyses can be conducted by way of differences on congruency effect (incongruent RT minus congruent RT) between face conditions, or as an interaction between congruency and face conditions. In the following experiments we will analyse RT data and analyses of interest will therefore be the interaction between congruency and face condition.

A 3 (face type: low, high, neutral) x 2 (congruency: congruent, incongruent) ANOVA was computed on RT data. A main effect of face type would show whether low, high, or neutral agreeable faces (collapsed across congruency) influence RT generally. A main effect of congruency (collapsed across face type) should show that RT on congruent trials is faster than on incongruent trials (Brass et al., 2000). The primary test of our hypothesis lies in the face type by congruency interaction. An interaction between face type and congruency would show that the influence of the faces on congruency differs between low, high, or neutral agreeable faces. If we found an interaction between face type and congruency we followed up with separate ANOVAs on congruent and incongruent trials to investigate which condition, or whether both, drive the observed interaction. If either of these separate ANOVAs were significant they were followed up with paired samples t-tests to investigate which of the faces drive the differences in the ANOVA. Finding that both the low and high agreeable faces influence differences on RT compared to the neutral agreeable face would support the general social signal hypothesis. To support the prosocial hypothesis, we would expect to see the high agreeable face influence differences on RT differently to low agreeable and neutral faces.

Firstly, this analysis was carried out for all participants. Then, the same analysis was performed on a subset of participants who showed high accuracy in the 2AFC face evaluation task. This analysis would assess whether trait detection accuracy influences imitation.

Results

Face evaluation

Results from the face discrimination task (Figure 2.2.A.) showed that participants were significantly more accurate than chance (64.46% correct; SD: 21.46; t(30)=3.75, p=.001, Cohen's d_z=0.67) when discriminating high and low agreeable pairs. When discriminating neutral pairs, participants chose the neutral faces at a rate no different than chance (49.44% correct; SD: 4.90; t(30)=-0.64, p=.526).

For the ratings task, a 2 (rating task: first completion, second completion) x 3 (face type: high, low and neutral) ANOVA showed that there was a main effect of face type (F(2,60)=6.47, p=.003, η_p^2=.177), no main effect of block (F(1,30)=1.22, p=.277), and no interaction between ratings of each face type and block (F(2,60)=0.60, p=.550). As there was no interaction, data was collapsed across the two ratings blocks and the differences between ratings of each face type were analysed with a one-way ANOVA. As expected based on the previous ANOVA, the one-way ANOVA collapsed across the two ratings blocks shows a difference in ratings between the face types (F(2,60)=6.47, p=.003, η_p^2=.177). Follow up paired-sample t-tests show that low agreeable composites were rated significantly less agreeable (M: 5.15; SD: 0.89) than the high agreeable composites (M: 5.69; SD: 0.77; t(30)=-2.52, p=.017, Cohen's d_z=1.01) and the neutral composites (M: 5.65; SD: 0.63; t(30)=-4.20, p<.001, Cohen's d_z=0.51). There was no difference in ratings of agreeableness between the neutral and the high agreeable composites (t(30)=-0.27, p=.790).

Figure 2.2. – Experiment 1 face evaluation and imitation task results

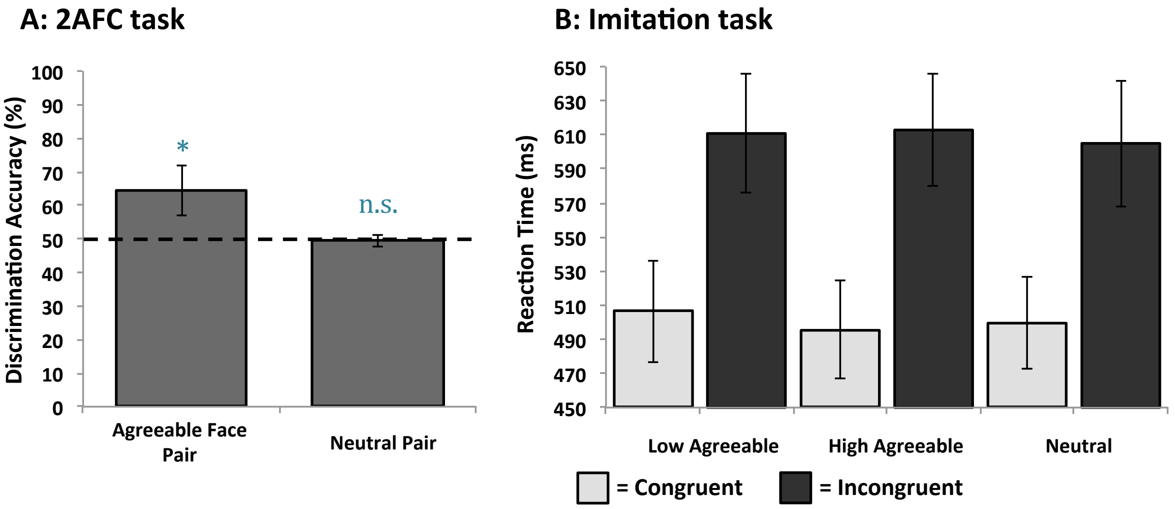

Figure 2.2. Results for Experiment 1. In a 2 alternative-forced-choice (2AFC) task, discrimination performance was greater than chance (dashed line) for high and low agreeable face pairs, but not for neutral face pairs **(A)**. For the imitation task reaction time (RT) for congruent and incongruent trials are compared following facial cues to low, high, and neutral agreeable faces **(B)**. As shown by the trial structure in Figure 2.1.C, faces were presented in pairs at the beginning of each trial in Experiment 1 to highlight the trait-representative features of the faces. However, facial cues to an individual's stable personality traits do not provide an antecedent to automatic imitation. Error bars represent 95% confidence intervals. n.s. = not significant. * = <.05

Automatic imitation

Prior to analysis, trials were removed if participants gave an incorrect response (5%), lifted their finger from the 'n' or the 'm' key during the ISI (0.06%), or took longer than 2000ms to respond (0.18%). Accuracy on catch trials was 61.89% (SD: 11.34) and significantly greater than chance (t(30)=5.84, p<.001, Cohen's d_z=1.05). Paired-samples t-tests showed that participants were significantly faster (t(30)=-13.99, p<.001, Cohen's d_z=2.51) and more accurate (t(30)=8.83, p<.001, Cohen's d_z=1.59) on congruent than incongruent trials.

Illustrated in Figure 2.2.B., a 3 x 2 ANOVA showed no main effect of face type (F(2,60)=0.66, p=.518), a main effect of congruency (F(1,30)=197.21, p<.001, η_p^2=.868), and no interaction between face type and congruency (F(2,60)=1.10, p=.340). All mean RTs and standard deviations are presented in Appendix 1. Next, the same analysis was performed only including participants who were correct on the 2AFC task at 80% or higher (N=9; no participants reached 100% accuracy), but results were the same with no main effect of face type (F(2,16)=2.36, p=.127), a main effect of congruency (F(1,8)=110.78, p<.001, η_p^2=.933) and no interaction between face type and congruency (F(2,16)=1.02, p=.383).

Discussion

In Experiment 1 we tested whether invariant features of faces that signal high or low agreeableness influence automatic imitation in comparison to a trait neutral face. Despite clear recognition of facial features that are indicative of high and low agreeableness, imitation performance was no different compared to the presentation of trait neutral faces. Thus, these data suggest imitative tendencies are indifferent to invariant facial cues to agreeableness.

This interpretation is limited by the nature of the experimental design used. On trait representative trials, participants saw both high and low agreeable faces within seconds of performing the imitation task. The purpose of pairing faces was to make the distinction between trait diagnostic features as salient as possible. Pairing of faces in this manner, however, makes the influence of positive and negative signals difficult to separate. That is, high agreeable trials could be contaminated by the influence of low agreeable faces and vice versa. To remove potential contamination, Experiment 2 clearly separates the influence of high and low trait signals on imitation.

Experiment 2

Introduction

To clearly separate the influence high and low agreeableness on imitation, three changes were made. First, faces were presented singularly instead of in pairs (Figure 2.1.C.). Second, the neutral condition was removed, thus leaving only the distinction of high and low agreeable. Third, a blocked design was used, which ensured that in each block participants saw facial cues that signalled only high or low agreeableness.

Therefore, Experiment 2 will directly test the pro-social signal sensitivity hypothesis without contamination across the high and low agreeable conditions. Following the logic of the pro-social signal sensitivity hypothesis, it is predicted that presentation of high agreeable faces will enhance interference in the imitation task, compared with presentation of a low agreeable face.

Method

Participants

Fifty-two Bangor University students participated (33 female, 19 male; M_{age} = 19.67 years, SD = 2.37). No participants were more than 3SD from the group mean of accuracy or mean RT for congruent or incongruent trials. All provided written informed consent, were right-handed and had normal or corrected-to-normal vision. Compensation for their time was awarded by way of course credit. The Research Ethics and Governance Committee of the School of Psychology at Bangor University granted ethical approval.

Task and stimuli

Face evaluation task: The face evaluation task was based on prior work (Kramer & Ward, 2010). Two composite images of faces were used: pair one from Experiment 1. Participants were presented with the two composite faces and asked to choose which best represented each of the statements from the 10 items that were relevant to agreeableness on the International Personality Item Pool (IPIP; Goldberg, 1999; found online here: http://ipip.ori.org/newQform50b5.htm).

Automatic imitation task: The automatic imitation task was the same as in Experiment 1, except for three changes (Figure 2.1.C.). First, participants saw only one example of a high and a low agreeable face and these faces were only ever presented singularly and in blocks. Second, there were no catch trials, as participants saw the same face on every trial within a block. Third, the duration of each ISI was changed to 800, 1200, or 1600 as other studies show robust congruency effects using different ISIs (Brass et al., 2000; Cook & Bird, 2012; Wang et al., 2011a).

Design and procedure

A 2 x 2 factorial design was used, with factors of congruency (congruent, incongruent) and face type (high agreeable, low agreeable). Participants first completed a 12-trial practice, before the main automatic imitation task. The main task comprised

120 trials divided into two blocks of 60. In different blocks, participants saw the high agreeable composite or the low agreeable composite. Within each block there were 30 congruent and 30 incongruent trials, which produced 30 trials per condition. The order of high agreeable and low agreeable blocks was counterbalanced across participants. The presentation of the target hand image was pseudorandomised so that no same image could appear more than four times consecutively. Following the imitation task, participants completed the face evaluation task. The protocol for this task was the same as for the 2AFC task in Experiment 1.

Data analysis

Face evaluation: The percentage of correct responses from the total of 10 trials was calculated. This was compared, using a one-sample t-test, to the percentage that participants would be expected to get if they were performing at chance (i.e., at 50% as it was a 2AFC task).

Automatic imitation: Data were processed the same way as in Experiment 1. A 2 (face type: low, high) x 2 (congruency: congruent, incongruent) ANOVA was performed on RT. If a face type by congruency interaction was found, two separate paired-samples t-tests were performed on congruent and incongruent RT to reveal on which condition faces had an influence. To support the prosocial signal hypothesis, we would expect RT on congruent trials to be facilitated by the high agreeable face compared to the low agreeable face. The same analysis was also performed for those participants who were 100% accurate on the 2AFC face evaluation task.

Results

Face evaluation

Results from the face evaluation task (see Figure 2.3.A.) again showed that participants could accurately judge trait information from the static, invariant features of the composite faces at a rate (M: 76.92%; SD: 26.76) significantly above chance ($t(51)=7.26$, $p<.001$, Cohen's $d_z=1.00$).

Figure 2.3. - Experiment 2 face evaluation and imitation task results

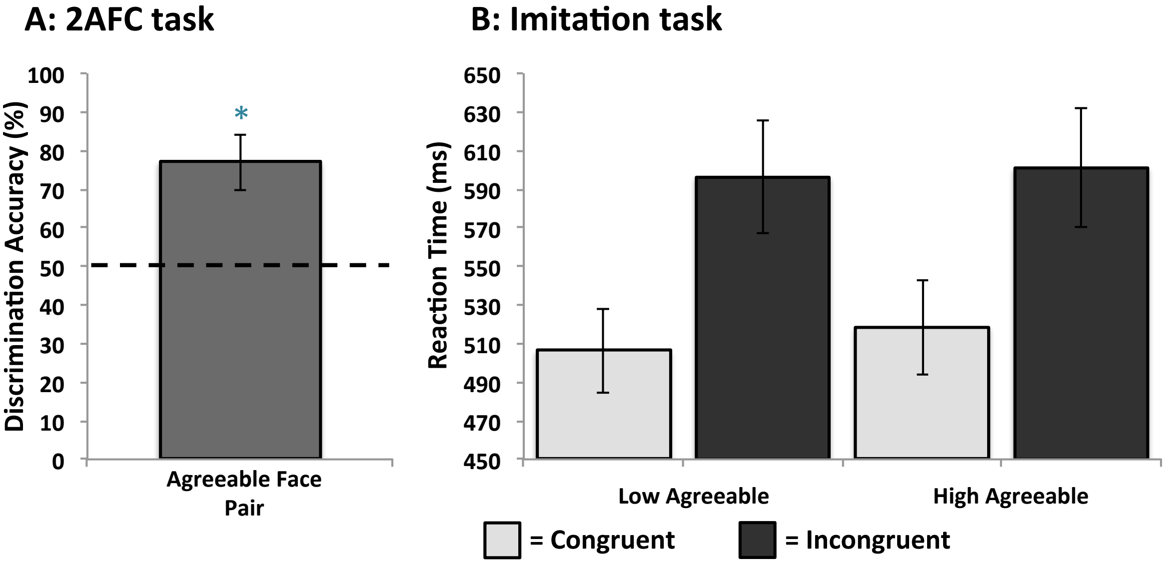

Figure 2.3. Results for Experiment 2. In a 2 alternative-forced-choice (2AFC) task, discrimination performance was again greater than chance (dashed line) for high and low agreeable face pairs **(A)**. For the imitation task reaction time (RT) for congruent and incongruent trials are compared following facial cues to low and high agreeable faces **(B)**. As shown by the trial structure in Figure 2.1.C, faces were only ever presented on their own to dissociate the influence of the high and low agreeable signals. However, in Experiment 2 facial cues to an individual's stable personality traits again do not provide an antecedent to automatic imitation. Error bars represent 95% confidence intervals. n.s. = not significant. * = <.05.

Automatic imitation

Prior to analysis, trials were removed if participants gave an incorrect response (4.45%), lifted their finger from the 'n' or the 'm' key during the ISI (0.1%), or took longer than 2000ms to respond (0.27%). Paired-samples t-tests showed that participants were significantly faster (t(51)=-13.31, p<.001, Cohen's d_z=1.84) and more accurate (t(51)=7.84, p<.001, Cohen's d_z=1.09) on congruent than incongruent trials.

A 2 x 2 ANOVA showed no main effect of face type (F(1,51)=1.57, p=.216), a main effect of congruency (F(1,51)=194.26, p<.001, η_p^2=.792), and no interaction between face type and congruency (F(1,51)=1.27, p=.265). All mean RTs and standard deviations are presented in Appendix 1. Thus, low and high agreeable faces had no dissociable influence on RT during the automatic imitation task (Figure 2.3.B.). Additionally, even if only those participants who were 100% correct on the face evaluation task (N=19) were included, there was no main effect of face type (F(1,18)=0.02, p=.891), a main effect of congruency (F(1,18)=61.21, p<.001, $\eta_p{}^2$=.773) and no interaction between face type and congruency (F(1,18)=0.11, p=.745).

Experiment 1 and 2 combined

To further examine the null results observed in Experiments 1 and 2, data from both experiments were combined and analysed in the same way as Experiment 2. As such, the neutral condition from Experiment 1 was discarded and the data for the high and low conditions from Experiments 1 and 2 were combined. As in Experiment 2, a 2 x 2 ANOVA tested the influence of low and high agreeable faces on RT for congruent and incongruent conditions. Despite slightly different stimuli and designs, this combined analysis provides a test of our hypothesis with greater statistical power than analysing the two datasets separately. This combined analysis involved 83 participants and continued to show that there was no main effect of face type (F(1,82)=0.66, p=.419), a main effect of congruency (F(1,82)=355.83, p<.001, $\eta_p{}^2$=.813) and no interaction between face type and congruency (F(1,82)=0.01, p=.980). All mean RTs and standard deviations are presented in Appendix 1.

Discussion

Despite accurate recognition of facial features that signal agreeableness, automatic imitation was no different following the presentation of a high agreeable compared to a low agreeable face. In Experiment 2, possible contamination between conditions was minimised as high and low agreeable faces were presented in separate blocks. Even with this clear separation of prosocial (high agreeable) and antisocial (low agreeable) signals we found no influence on automatic imitation of facial cues that signal stable trait characteristics. When considering the results of Experiment 1 and 2 in combination, we find no evidence that invariant features of an individual's face, which signal agreeableness, modulate imitative tendencies. As such, we find no support for the prosocial signal hypothesis or the general social sensitivity hypothesis. Even when we combine the data from Experiment's 1 and 2, we find no difference between prosocial and antisocial face signals on automatic imitation.

Prior research investigating social antecedents of imitation has focused on priming social states rather than traits (Cook & Bird, 2011, 2012; Leighton et al., 2010;

Wang & Hamilton, 2013; Wang et al., 2011a). Thus, it may be that automatic imitation is more responsive to state signals from faces, such as expressions, rather than trait signals. Research to date has focussed on investigating the role of facial imitation in the detection and recognition of expressions (Goldman & Sripada, 2005; Moody et al., 2007; Niedenthal et al., 2011; Oberman et al., 2007; Rychlowska et al., 2014; Sato et al., 2013). Less research, however, has investigated the consequence of recognising facial expressions on subsequent imitative behaviour. Thus, Experiments 3 and 4 will investigate how facial expressions of emotion impact imitation. The experimental structure will follow Experiments 1 and 2. First, Experiment 3 will pair emotional expressions together to heighten to distinction between facial signals. Then, Experiment 4 will separate the influence of emotional expressions on imitation. Across the two experiments, the prosocial signal and general social hypotheses will be tested.

Experiment 3

Introduction

To date, one study has shown that happy expressions increase the tendency to imitate compared to angry faces (Rauchbauer et al., 2015) and two studies have failed to show a reliable impact of detecting negative facial expressions on automatic imitation (Crescentini et al., 2011; Grecucci et al., 2013). No research has yet investigated the impact of positive and negative expressions compared to emotionally neutral faces, on automatic imitation. Given the prosocial, affiliative role of imitation in social interactions (Chartrand & van Baaren, 2009; van Baaren et al., 2009), it seems vital to examine the influence of social signals that are both positive and negative in valence. Additionally, prior research investigating behavioural approach tendencies has shown that facial expressions influence body movements of an observer such that the observer is more likely to approach someone who smiles (Stins et al., 2011), and avoid someone who frowns (Marsh et al., 2005). Across two experiments, we aim to clarify the influence of negative expressions by testing larger samples than prior experiments as well as investigating the role of positive expressions on automatic imitation. Experiment 3 investigates the extent to which happy and angry facial expressions influence automatic imitation compared with a neutral facial expression.

Method

Participants

Twenty-eight Bangor University students participated for course credit. One was removed from the automatic imitation part of the experiment due to equipment failure; however, their data is included in the ratings part of the experiment. Of the remaining 27 participants (22 female, 5 male; M_{age} = 19.33 years, SD = 1.33) all had normal or corrected-to-normal vision and 25 were right handed as measured by the Edinburgh Handedness Inventory. This measure showed that two participants were ambidextrous, although they were included in the sample as they reported being predominantly right-hand users. The study complied with the guidelines set by the Research Ethics and Governance Committee of the School of Psychology at Bangor University.

Task and stimuli

Face evaluation task: Stimuli were images of 12 individuals from the NimStim data set (models: 1, 2, 3, 7, 8, 9, 20, 21, 22, 23, 34, 36) with three different expressions: smiling, frowning and neutral (Tottenham et al., 2009). Closed-mouth neutral and open-mouthed smiling and frowning faces were used as these stimuli were most often correctly identified (see validation data provided by Tottenham and colleagues: http://www.macbrain.org/faq.htm). In order to avoid any influence of race, models were first excluded if they were of African- or Asian-American ethnicity. Six female and six male models whose expressions were identified with the highest accuracy across the three relevant expressions were chosen. This resulted in 36 images of faces. Participants rated each of these faces on one question “How is this person feeling?” on a scale from 1 (extremely angry) to 9 (extremely happy). Each trial began with a 500ms fixation cross and then the presentation of a face with the question and the rating scale underneath. This remained on screen until participants gave their response. The order in which the faces were presented was randomised.

Automatic imitation task: In order to emphasise the distinction between faces, the task and trial structure was the same as Experiment 1 (Figure 2.1.C.). As such, on each expressive trial, a smiling and a frowning face were initially presented together to highlight differences between them. On neutral trials, two neutral faces were paired together. After this paired presentation phase, one face would disappear leaving a single face presented centrally. On expressive trials, half of the trials a smiling face remained onscreen and half of the trials a frowning face remaining onscreen.

Design and procedure

The automatic imitation task employed a 2 x 3 factorial design, with factors of congruency (congruent, incongruent) and face type (angry, happy, neutral). Participants first completed an 8-trial practice of the automatic imitation task, before completing the main automatic imitation task. The design and procedures were the same as in Experiment 1, except for the number of trials, which changed due to the increased number of face images. There were 6 repetitions of each model presented whilst smiling, frowning, and neutral, thus the main task comprised 216 trials split into 4 equal blocks. Faces were paired so that each smiling face was paired with each frowning face, resulting in 144 trials that began with a smiling-frowning pair. Neutral faces were presented in fixed pairs, such that there were two female pairs, two male pairs and two pairs that comprised a male and a female. This resulted in 72 trials that began with a neutral pair. Thus there were 36 trials per condition (smiling congruent, smiling incongruent, frowning congruent, frowning incongruent, neutral congruent, neutral incongruent). Once the main task was completed, participants completed the face evaluation task whereby they rated each image on how angry to happy the person appeared to be feeling.

Data analysis

Face evaluation: A mean score between 1 and 9, with 1 being extremely happy and 9 being extremely angry, was calculated for each of the three face types (smiling, frowning, and neutral). A one-way ANOVA was used to assess differences in scores between the face types. Any difference was followed up with paired-samples t-tests.

Automatic imitation: Data were processed in the same way as in Experiment 1 in order to assess the hypothesis that emotionally expressive faces would influence automatic imitation compared to emotionally neutral faces. A 3 (face type: angry, happy, neutral) x 2 (congruency: congruent, incongruent) ANOVA was run on RT data. Again, the primary test of our hypothesis is the face type by congruency interaction. An interaction between face type and congruency would show that the influence of the faces on congruency differs between angry, happy, and emotionally neutral expressive faces. If there was an interaction between face type and congruency we followed up with separate ANOVAs on congruent and incongruent trials to investigate which condition, or whether both, drive the observed interaction. If either of these separate ANOVAs were significant they were followed up with paired samples t-tests to investigate which of the emotionally expressive faces drives the differences in the ANOVA. Finding that both the angry and happy faces influence differences on RT compared to the emotionally neutral face would support the general social signal hypothesis. To support the prosocial hypothesis, we would expect to see the happy face influence differences on RT in a manner dissociable from angry and emotionally neutral faces.

Results

Face evaluation

Participants rated the three face types (frowning, smiling, and neutral) significantly differently (F(2,54)=528.45, p<.001, η_p^2=.951; Figure 2.4.A.). Paired-samples t-tests showing that the frowning faces (M: 2.00; SD: 0.72) were rated as less happy than the smiling (M: 8.00; SD: 0.73; t(27)=-29.29, p<.001, Cohen's d_z=8.57) or neutral faces (M: 4.57; SD: 0.57 t(27)=-15.60, p<.001, Cohen's d_z=4.40) and the smiling faces were rated as more happy than the neutral face (t(27)=22.34, p<.001, Cohen's d_z=6.07).

Figure 2.4. - Experiment 3 face evaluation and imitation task results

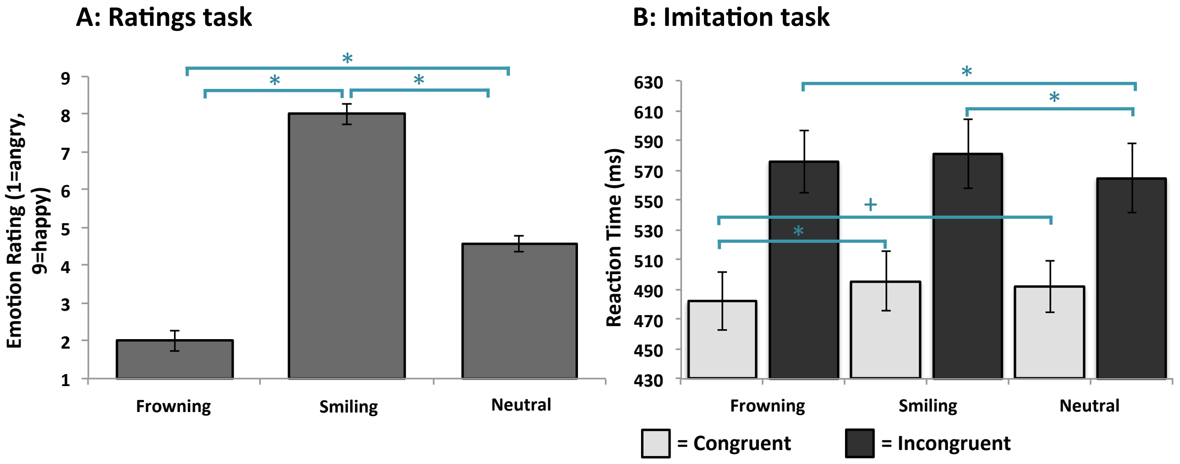

Figure 2.4. Results for Experiment 3. In a ratings task, the smiling face was rated the happiest, the frowning face as the angriest, with the neutral face rated intermediately

(A). For the imitation task reaction time (RT) for congruent and incongruent trials are compared following facial cues to angry, happy, and neutral faces **(B)**. As shown by the trial structure in Figure 2.1.C., faces were presented in pairs at the beginning of each trial in Experiment 3 to highlight the distinct state signals of the faces and then presented singularly. Results show the angry face preceded faster congruent RTs than the happy or neutral face. Additionally the angry and the happy face preceded slower incongruent RTs than the neutral face. Error bars represent 95% confidence intervals. +=0.05-0.1; * = <.05.

Automatic imitation

As in Experiment 1 and 2, prior to analysis, trials were removed if participants gave an incorrect response (2.97%), lifted their finger from the ‘n’ or the ‘m’ key during the ISI (0.02%), or took longer than 2000ms to respond (0.14%). Participants were significantly faster (t(26)=-12.89, p<.001, Cohen’s d_z=2.48) and more accurate (t(26)=5.57, p<.001, Cohen’s d_z=1.07) on congruent than incongruent trials. Accuracy on catch trials was 83.67% (SD: 10.80) and significantly greater than chance (t(27)=16.49, p<.001, Cohen’s d_z=3.12).

A 3 x 2 ANOVA showed a main effect of face type (F(2,52)=4.51, p=.016, η_p^2=.148), a main effect of congruency (F(1,26)=166.02, p<.001, η_p^2=.865), and a marginal face type by congruency interaction (F(2,52)=2.97, p=.060, η_p^2=.102). All mean RTs and standard deviations are presented in Appendix 1.

Separate ANOVAs on congruent and incongruent RT showed a marginal difference by face type on congruent trials (F(2,52)=2.80, p=.070, η_p^2=.097). As illustrated in Figure 2.4.B., follow up paired-samples t-tests showed that following presentation of an angry face congruent RTs were faster than when preceded by a happy face (t(26)=-2.06, p=.050, Cohen’s d_z=0.40), marginally faster than when preceded by a neutral face (t(26)=-1.90, p=.068, Cohen’s d_z=0.37), with no difference on congruent RTs between the happy and the neutral face (t(26)=0.6, p=.554).

A significant difference between face types was observed for RT on incongruent trials (F(2,52)=4.46, p=.016, η_p^2=.147). As illustrated in Figure 2.4.B., follow up paired-samples t-tests showed that RT on incongruent trials was significantly slower following presentation of both an angry face (t(26)=2.14, p=.042, Cohen’s d_z=0.41) and a happy face (t(26)=2.69, p=.012, Cohen’s d_z=0.52) compared to presentation of the emotionally neutral face, with no difference on RT for incongruent trials between angry and happy faces (t(26)=-0.95, p=.353).

Given that there is a main effect of face type that might bias interpretation of simple effects of face type on only congruent or only incongruent trials, I also present analyses of the congruency effects (incongruent RT minus congruent RT) for each face type. A repeated-measures ANOVA shows there is a marginally significant difference on congruency effect (F(2,52)=2.97, p=.060, , η_p^2=.102; means and standard deviations presented in Appendix 1), whereby the congruency effect following presentation of an angry face is significantly greater than following a neutral face (t(26)=2.48, p=.020, Cohen's d_z=0.48), with no other comparisons reaching significance (all p's > .14).

These results suggest that observation of an angry face has a facilitatory effect on congruent RTs compared to happy and emotionally neutral faces, and both expressive faces have a slowing influence on incongruent RTs compared to an emotionally neutral face. This results in a larger congruency effect following presentation of an angry face compared with a happy or a neutral face, although some caveats to interpreting this result are discussed below.

Discussion

Experiment 3 shows that automatic imitation is modulated by the expressivity of a viewed face. Analysis of RT differences showed that this effect was driven by longer RTs on incongruent trials for expressive faces compared to neutral faces, with a marginal difference on RTs for congruent trials, such that angry faces had a facilitatory effect compared to happy and emotionally neutral faces. As such, following angry expressions, participants are faster to perform imitative actions and thus demonstrate increased automatic imitation as measured by the congruency effect. This is similar to the results of Grecucci et al. (2011) who found that negative images sped RT on congruent trials compared to positive or neutral images. The authors suggest that negative images prime a fight-or-flight response that increases the tendency to imitate. However, this kind of influence might be expected to influence RTs generally (on both congruent and incongruent trials) following angry faces compared to other facial signals. In contrast, we show that following both happy and angry expressions, participants find it more difficult to resist the spontaneous tendency to imitate other people. One interpretation of these results is consistent with the general social signal hypothesis: perceived emotional states (happy and angry) are both antecedents to automatic imitation compared to emotionally neutral faces.

The results from Experiment 3, however, do not clearly demonstrate whether the influence of facial signal on imitation is tied to happy, angry, or both expressions. On expressive trials, participants saw both smiling and angry expressions within seconds of performing the imitation task, which makes it difficult to separate the influence of positive and negative facial signals on imitation. To separate the influence of happy and angry expressions and distinguish between the general social signal and the prosocial signal hypotheses, only one face will be presented prior to the imitation task in Experiment 4.

In addition, the results from Experiment 3 do not demonstrate if the influence of expression on imitation is tied to emotional state signals from faces per se, or if it indexes a more general-purpose mechanism. For instance, according to a general-purpose mechanism, expressive signals may capture attentional resources more than neutral facial signals, which could contribute to stronger interference in the incongruent condition. To further test the specificity of this effect, Experiment 4 includes an additional neutral condition.

Experiment 4

Introduction

Experiment 4 separates the influence of smiling and frowning faces by presenting faces singularly on every trial. In this way, it will be more similar in design to Experiment 2 where high and low agreeable faces were presented separately. However, presentation of expressive faces will be mixed, rather than blocked, due to observation of order effects in Experiment 2[2]. In this way signals from the face will be dissociable at a trial-

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[2] Trials in Experiment 2 were split into 10 miniblocks with 24 trials per miniblock. The average congruent RT, incongruent RT and congruency effect was the calculated for each miniblock and correlated with the miniblock number. We found a significant

by-trial level. Additionally, in Experiment 4 an extra neutral condition will be added, which has a salient facial feature (non-biological skin colour), but remains emotionally neutral (Figure 2.1.A.).

Experiment 4 will distinguish whether the influence of expressive faces on automatic imitation is the result of sensitivity to prosocial signals specifically, or whether imitative tendencies are sensitive to a wider class of social signal such that imitation is sensitive to any signal that is socially informative. To support the general social signal hypothesis, both smiling and frowning expressions would influence imitation compared to a neutral expression in a similar manner. By contrast, to support the prosocial signal hypothesis, happy and angry expressions should have dissociable influences on the imitation task.

Experiment 4 will also distinguish whether the influence of expressive faces is due to the social signals they convey or whether the influence is indicative of a more general-purpose mechanism. If the influence of expression is due to social signals from the face per se, it is expected that expressive faces will elicit greater imitation behaviour than the new salient neutral condition. By contrast, if the influence of facial expression operates through a more general-purpose mechanism, one that is not specifically tied to emotional states, then RT patterns following expressive faces should be similar to the new neutral condition.

Method

Participants

Forty-nine Bangor University students participated for course credit. Four participants were removed from the sample as their accuracy on congruent (n=2) or incongruent (n=2) trials was >3SD from the group mean. Of the remaining 45 (34 female, 11 male; M_{age} = 19.33 years, SD = 2.09) all had normal or corrected-to-normal

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negative correlation between miniblock number and congruency effect (r=-.88, p=.001), a marginal correlation between miniblock number and congruent RT (r=.63, p=.051) and a significant correlation between miniblock number and incongruent RT (r=-.72, p=.020). These results show that participants are getting marginally slower over time on congruent trials and significantly faster over time on incongruent trials as a result of task performance.

vision and 43 were right handed as measured by the Edinburgh Handedness Inventory. This measure showed that two participants were ambidextrous, although they were included in the sample as they reported being predominantly right-hand users. The study complied with the guidelines set by the Research Ethics and Governance Committee of the School of Psychology at Bangor University.

Task and stimuli

Stimuli were the same images used in Experiment 3 with the addition of a second category of neutral images (Figure 2.1.A). The additional neutral stimuli comprised the 12 neutral face images modified so that they were more salient (non-biological skin colour), but remained emotionally neutral. Thus, there were a total of 48 face images, four variations of 12 models that were frowning, smiling, neutral and salient neutral.

The task and trial structure was the same as in Experiment 3 without presentation of face pairs (see Figure 2.1.C.). Instead, faces were presented singularly during each trial. There were 192 total trials and 8 trial types (congruent and incongruent, for each of the four face types), thus there were 24 trials per trial type. Randomisation and ISI were the same as in Experiments 1 and 3.

Design and procedure

The automatic imitation task employed a 2 x 4 factorial design, with factors of congruency (congruent, incongruent) and face type (smiling, frowning, neutral, salient neutral). Participants first completed an 8-trial practice of the automatic imitation task, before completing the main automatic imitation task following the same procedure as Experiment 3.

Data analysis

Data were processed in the same way as in the previous experiments. The influence of angry, happy, neutral, and salient neutral was compared using a 4 (face-type: angry, happy, neutral, salient neutral) x 2 (congruency: congruent, incongruent) factorial ANOVA. As in Experiment 3, if there was a face type by congruency interaction, it was investigated using ANOVAs separately for congruent and incongruent trials and then followed up with paired-samples t-tests to examine which faces are driving any differences. Unpacking the interaction is crucial to distinguish between several hypotheses. The general social signal hypothesis predicts comparable influences on automatic imitation task performance following happy and angry faces, but different from salient neutral. The prosocial signal hypothesis predicts an influence of happy faces that is dissociable from both angry and salient neutral faces. If the result indexes a domain-general mechanism, there should be no difference between salient neutral, happy, and angry.

Results

Automatic imitation

As in Experiments 1-3, prior to analysis, trials were removed if participants gave an incorrect response (4.53%), lifted their finger from the 'n' or the 'm' key during the ISI (0.06%), or took longer than 2000ms to respond (0.24%). Participants were significantly faster (t(44)=-11.33, p<.001, Cohen's d_z=1.69) and more accurate (t(44)=7.91, p<.001, Cohen's d_z=1.18) on congruent than incongruent trials. Accuracy on catch trials was 84.56% (SD: 12.70) and this was significantly greater than chance (t(44)=18.26, p<.001, Cohen's d_z=2.72).

Figure 2.5. - Experiment 4 imitation task results

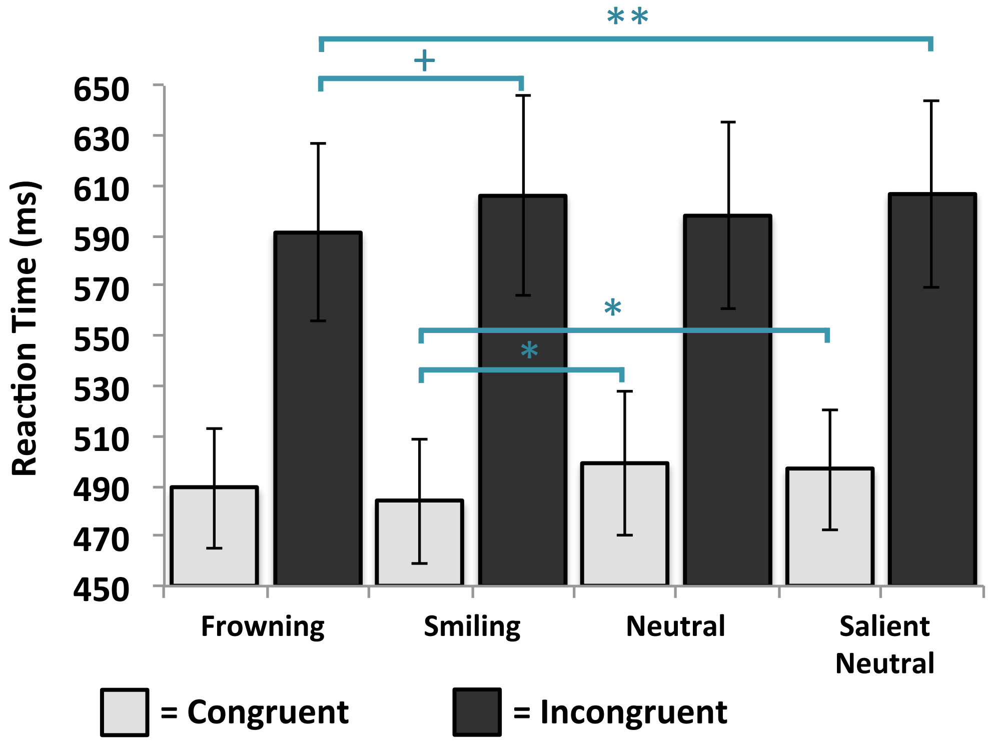

Figure 2.5. Results for Experiment 4. Reaction time (RT) for congruent and incongruent trials are compared following facial cues to angry, happy, and neutral faces, as well as emotionally neutral but salient faces. As shown by the trial structure in Figure 2.1.C., faces were only presented singularly to clearly separate the influence of happy and angry signals. In terms of congruent RTs, happy expressions facilitated responses compared to both neutral and salient but emotionally neutral faces. In terms of incongruent RTs, both happy and salient neutral conditions were interfered more than the angry condition. Error bars represent 95% confidence intervals. +=0.05-0.1; * = <.05; ** = <.01.

A 4 x 2 ANOVA showed a marginal main effect of face type (F(3,132)=2.33, p=.077, η_p^2=.050), a main effect of congruency (F(1,44)=129.49, p<.001, η_p^2=.746), and a marginal face type by congruency interaction (F(3,132)=2.55, p=.058, η_p^2=.055). All mean RTs and standard deviations are presented in Appendix 1.

Separate ANOVAs on congruent and incongruent RT showed a significant difference by face type on congruent trials (F(3,132)=-2.7, p=.048, η_p^2=.058). As illustrated in Figure 2.5., follow up paired-samples t-tests showed that congruent RTs were significantly faster following a happy face than when the preceding face was neutral (t(44)=-2.03, p=.048, Cohen's d_z=0.30) or salient neutral (t(44)=-2.69, p=.010, Cohen's d_z=0.40). All other comparisons showed no difference on congruent RTs (all p's > .1).

A marginal difference between face types was observed for RT on incongruent trials (F(3,132)=2.25, p=.086, η_p^2=.049). As illustrated in Figure 2.5., RT on incongruent trials following angry faces was significantly faster than salient neutral faces (t(44)=-2.83, p=.007, Cohen's d_z=0.42) and marginally faster compared to incongruent RT following presentation of happy faces (t(44)=-1.92, p=.061, Cohen's d_z=0.29). All other comparisons showed no difference on incongruent RTs (all p's > .1).

Given that interpretation of simple effects of face type across only congruent or only incongruent trials when there is a marginal main effect of face type that might bias results requires caution, I also present analyses on the congruency effects for each face type. A repeated-measures ANOVA shows there is a marginally significant difference on congruency effect (F(3,132)=2.55, p=.058, η_p^2=.055; means and standard deviations presented in Appendix 1), whereby the congruency effect following presentation of an happy face is significantly greater than following a neutral face (t(44)=2.49, p=.016, Cohen's d_z=0.31) or an angry face (t(44)=2.05, p=.046, Cohen's d_z=0.37), with no other comparisons reaching significance (all p's > .15).

In summary, these results show that the influence of the angry expression is not dissociable from the neutral expression whereas the happy expression is dissociable from the effects of the neutral, salient neutral and the angry expressions. The dissociation from neutral and salient neutral faces occurs on congruent trials where a happy expression is speeding responses compared to both neutral and salient neutral faces. By contrast, the dissociation of happy and angry expressions occurs on the incongruent trials where happy (and salient neutral) faces slow responses compared to the angry expression. Congruency effect analyses further support the dissociation of the influence of the happy face from the influences of angry and neutral faces.

Discussion

The aim of Experiment 4 was twofold. The first aim was to distinguish whether automatic imitation is specifically sensitive to prosocial signals, or whether it also responds to a more general class of social signal including positive and negative stimuli. Experiment 4 shows that a happy expression influences automatic imitation in a distinct manner to an angry expression. While no differences were observed on congruent trials, a greater congruency effect was observed as a result of happy faces interfering more on incongruent trials than angry faces. This suggests that resisting interference in the automatic imitation task is more difficult following the detection of a happy expression than an angry expression.

It is notable that the pattern of results for happy and angry expressions is different between Experiments 3 and 4. In Experiment 3, both angry and happy expressions slowed RT on incongruent trials, whereas in Experiment 4, happy expressions slowed RT on incongruent trials more than angry expressions. The different pattern of results is likely to reflect differences in experimental design between the two experiments. In Experiment 3, faces were presented in pairs at the beginning of each trial, whereas in Experiment 4, faces were presented singularly throughout the trial. Therefore, in Experiment 3, conflicting expressions were presented concurrently. It is possible that detection of such conflicting emotional states interfered with the processing of prosocial and antisocial expressions that would typically occur if each expression were presented alone. Such conflicting signals may have resulted in general interference and a non-dissociable impact on imitation. In Experiment 4, however, when conflict was removed, results suggest that pro- and anti-social expressions have somewhat dissociable impacts on imitation.

The second aim was to delineate whether expressive influences on imitation are specifically due to the emotion conveyed by the stimulus or a more general-purpose influence, which is not restricted to facial expressions. A happy expression produced a dissociable influence on imitation compared to an emotionally neutral, and a salient but emotionally neutral facial expression. While there were no differences on incongruent trials, happy facial signals produced a greater congruency effect than an emotionally neutral face, and facilitation on congruent trials more than both emotionally neutral facial signals. This demonstrates that it is easier to perform a congruent movement following a smile than a neutral expression, even if the neutral face stimulus had a salient feature that would capture attentional resources.

General Discussion

Imitation and facial signals underpin and guide social interactions, but little is known regarding the relationship between mechanisms for face perception and imitation. The current study provides evidence that automatic imitation is modulated by facial cues that signal emotional states more than enduring personality traits. Moreover, the impact of prosocial state signals, such as a smiling expression, was dissociable from antisocial and neutral signals. These findings show that facial signals that convey "in the moment" prosocial information are an input to the systems that guide affiliative non-verbal behaviour during social interactions.

Prior research has suggested that facial imitation *during* expression detection contributes towards understanding another's emotional state (Goldman & Sripada, 2005; Niedenthal et al., 2011). The current study furthers understanding of links between facial signals and imitation, by providing evidence that imitation of hand actions is influenced as a *consequence* of expression detection. Therefore, we show that facial expressions are an input signal to the control of imitation that extends beyond facial imitation. Taken together, these data suggest that the perception of smiling prompts multiple forms of imitation, each of which may serve different functions. First, during expression detection, facial muscles are engaged that would be used to produce the expression and contribute to understanding emotional states (Goldman & Sripada, 2005). Subsequently, detection of smiling compared to detection of a neutral face impacts imitation of actions that involve distal muscle groups. The latter form of imitation is likely to contribute to facilitating interactions between individuals, such as building rapport and affiliation (Chartrand & van Baaren, 2009; van Baaren et al., 2009).

The specificity of influence between facial signals and imitation informs the understanding of links between face perception and imitation. First, the results support a prosocial bias, rather than a general sensitivity to pro- and anti-social signals from faces. Prosocial sensitivity is consistent with research showing that observing smiles lead to approach tendencies (Stins et al., 2011) and increased automatic imitation compared to observing angry faces (Rauchbauer et al., 2015), and that priming a pro-social state increases automatic imitation (Chartrand & Lakin, 2013; Cook & Bird, 2011, 2012; Leighton et al., 2010; Wang & Hamilton, 2013). In addition, two previous studies showed that recognising negative facial expressions had little or no impact on automatic imitation (Crescentini et al., 2011; Grecucci et al., 2013). Overall, these results support the view that links between expression perception and imitation subserve an affiliative function in social interactions (Chartrand & van Baaren, 2009; van Baaren et al., 2009). Given recent evidence that physical, non-social contextual cues can also modulate automatic imitation (Cook et al., 2012b), future research may investigate the relationship between social factors and non-social factors, such as environmental context, during imitation.

The current study also demonstrates a second form of specificity: automatic imitation is sensitive to facial cues that signal a prosocial state (smiling expressions) more than a prosocial trait (agreeableness). As such, we show a stronger influence of “in the moment” signals on imitation in comparison to perception of stable prosocial tendencies. One caveat to this interpretation is that signals from trait representative faces are subtler than emotionally expressive facial cues. Indeed, trait representative facial signals are less striking and participants were less accurate detecting facial trait cues than emotional expressions. However, when analyses included only participants who accurately identified trait faces at 100% there was no modulation of automatic imitation by trait representative faces. Additionally, from an ecological validity standpoint, facial expressions are a stronger visual cue than invariant trait features in day-to-day life, so expressions may impact automatic imitation more than stable trait cues. Thus, the observed specificity of automatic imitation to modulation by emotional expressions could be the result of a more intense social signal albeit one that reflects authentic social exchanges. Future work could address this question further by showing less intense versions of emotional expressions to investigate whether there is a relationship between the intensity of the facial signal and automatic imitation.

This result informs current theories of imitation and mechanisms of social interaction. Several other lines of research that have started to uncover antecedents to imitation also typically focus on transient state signals (for reviews, see Chartrand & Lakin, 2013; Heyes, 2011). Taken together, it is clear that transient state signals, including facial expressions, are inputs to systems controlling imitation. On a neurobiological level, the mirror neuron system has been implicated in controlling imitative behaviour (Iacoboni, 2009). In addition, it has been proposed that activity in the mirror system is mediated by social cues, such as person evaluation, priming, and context (Cook & Bird, 2012; Heyes, 2011; Wang & Hamilton, 2012). Our findings provide further support that the control of imitation is not restricted to the mirror system alone (Brass et al., 2009), but instead reflects the workings of a distributed neural network, which includes the detection and recognition of facial expressions.

Limitations and future directions

Whilst it is becoming clear that a range of social factors impact imitation (Chartrand & Lakin, 2013; Heyes, 2011), the mechanisms by which they operate are largely unknown. For example, it is unclear whether the influence of social cues on imitation is anchored to the self, the target or a combination of both. If the mechanism were anchored to the self, through an elevation in mood or a general desire to affiliate for instance, imitation would increase with their interaction partner as well as with anyone else with whom they might interact. By contrast, if the mechanism were anchored to the social target in an attempt to build social connections with a particular individual, imitation would not generalise to other interaction partners. Future research might try to disentangle these possible factors to further understand the mechanisms by which imitation is controlled.

CHAPTER 3

Investigating the Relationship Between Stable Personality Characteristics and Automatic Imitation

This chapter investigates the relationship between automatic imitation and individual differences in a range of stable personality and subclinical traits in a large behavioural study (n=230), whilst controlling for potentially confounding variables such as mean RT or participant sex. This approach provides methodological strengths that allow closer estimation of population parameters in an attempt to address replication concerns within the field

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3. INDIVIDUAL DIFFERENCES AND AUTOMATIC IMITATION

Abstract

Automatic imitation is a cornerstone of nonverbal communication that fosters rapport between interaction partners. Recent research has suggested that stable dimensions of personality are antecedents to automatic imitation, but the empirical evidence linking imitation with personality traits is restricted to a few studies with modest sample sizes. Additionally, atypical imitation has been documented in autism spectrum disorders and schizophrenia, but the mechanisms underpinning these behavioural profiles remain unclear. Using a larger sample than prior studies (N=243), the current study tested whether performance on a computer-based automatic imitation task could be predicted by personality traits associated with social behaviour (extraversion and agreeableness) and with disorders of social cognition (autistic-like and schizotypal traits). Further personality traits (narcissism and empathy) were assessed in a subsample of participants (N=57). Multiple regression analyses showed that personality measures did not predict automatic imitation. In addition, using a similar analytical approach to prior studies, no differences in imitation performance emerged when only the highest and lowest 20 participants on each trait variable were compared. These data weaken support for the view that stable personality traits are antecedents to automatic imitation and that neural mechanisms thought to support automatic imitation, such as the mirror neuron system, are dysfunctional in autism spectrum disorders or schizophrenia. In sum, the impact that personality variables have on automatic imitation is less universal than initial reports suggest.

Keywords: imitation, individual differences, personality, subclinical

Introduction

People automatically imitate the actions of those around them, a process that increases feelings of affiliation and rapport between interaction partners (Chartrand & Van Baaren, 2009). Although contextual or situational antecedents of imitation are becoming clearer (Chartrand & Lakin, 2013), the underlying mechanisms remain poorly understood. It has been proposed that the mirror neuron system (MNS), a brain system that responds to performed and observed actions (Rizzolatti & Craighero, 2004), is a key biological substrate for imitation (Iacoboni, 2009). Indeed, although contentious (J. Cook et al., 2012; Hamilton, 2013; Southgate & Hamilton, 2008; Wang & Hamilton, 2012), a dysfunctional MNS has been implicated in atypical imitation abilities in autism spectrum disorders (ASD) and schizophrenia (Enticott et al., 2008; Williams et al. 2004). In addition, it has been suggested that enduring personality variables, such as empathy and narcissism, are antecedents to imitation (Chartrand & Bargh, 1999; Obhi et al., 2013). However, there is limited evidence that demonstrates how personality influences automatic imitation. The aim of the current study is to investigate the relationship between automatic imitation and individual differences in stable personality and subclinical traits.

Different forms of imitation can be conceptually distinguished. Intentional imitation involves deliberately copying an observed movement, whereas automatic imitation refers to unintended copying behaviours (Heyes 2011; Tomasello, 1996). In recent years, automatic imitation, which is also referred to as mimicry (e.g., Chartrand & Van Baaren, 2009), has been studied through two main methodological approaches. The first approach typically involves a primary task, such as describing photographs, which is performed by a participant and a confederate. Whilst the primary task is performed, copying behaviours of the participant are covertly recorded. Using this approach, automatic imitation has been documented for a variety of behaviours, including foot shaking and facial expressions (Chartrand & Bargh, 1999; Stel & Vonk, 2010).

The second measure of automatic imitation is computer-based and uses a reaction time paradigm (Brass & Heyes, 2005; Heyes 2011). Similar to the first method, the measure of copying behaviour is incidental to the primary task. For example, the task may involve making a finger movement in response to a visual cue, whilst simultaneously observing another person's finger movement (Brass et al., 2000). If the observed finger movement is incongruent to the intended finger movement, a reaction time cost or interference is incurred. Such interference has been demonstrated to be a product of spatial and imitative components of the task (Catmur & Heyes, 2011). Thus, interference reflects, in part, an urge to automatically copy an observed action, which must be inhibited when it is inconsistent with a motor intention (Brass & Heyes, 2005). Using these measures of automatic imitation, aspects of social context, such as pre-existing rapport, a goal to affiliate, mood, and emotional state have been shown to be antecedents of automatic imitation (Chartrand & Lakin, 2013; Heyes, 2011).

Insight into the antecedents of automatic imitation has also emerged by investigating how stable components of personality, rather than social context, may predispose some more than others to imitate more. Despite the wealth of knowledge regarding individual differences in personality (Durrett & Trull, 2005; Lim & Ployhart, 2004; Shaver & Brennan, 1992), as yet, only a few studies have investigated how stable personality characteristics influence automatic imitation. For example, empathy, which includes emotional components such as emotional regulation, as well as cognitive components such as the ability to understand another person's perspective and emotions (Lietz et al., 2011), has been previously linked to automatic imitation using covert recording of copying behaviours (Chartrand & Bargh, 1999). More empathic individuals, as measured by a perspective-taking subscale, exhibited more copying behaviours than less empathic individuals. Additionally, narcissism, which is characterised by several behaviours including self-centeredness and a lack of empathy (Morf et al., 2001; Wai & Tiliopoulos 2012), has been linked with automatic imitation using the RT paradigm described above (Hogeveen & Obhi, 2013; Obhi et al., 2013). Participants with more narcissistic personality traits showed less interference from observing concurrent actions than participants with fewer narcissistic traits. Taken together, these results suggest that more self-interested individuals imitate less compared to those who are more interested in others.

While these studies provide tentative support for a relationship between stable personality traits and imitation, the evidence is not yet convincing. These studies had relatively small sample sizes (empathy sample: n=50; narcissism samples: n=18, n=24), which represent the population mean less accurately than larger samples (Maxwell et al., 2008). Furthermore, variables that may vary with narcissism or empathy and explain variance in imitative tendencies, such as overall latency in RT paradigms, age and sex, were not taken into account (McNamee, 2005; Vik, 2013). More generally, given recent failures to replicate landmark results in psychology (Pashler et al., 2012; Shanks et al., 2013), it is timely to investigate these initial findings more rigorously with larger sample sizes and by controlling for confounding variables (Cumming, 2014).

Furthermore, as yet untested personality factors may also determine one's tendency to imitate others. For example, using the reaction time measure of automatic imitation, simple sentences that prime a prosocial "state" have been shown to increase automatic imitation (Cook & Bird, 2011, 2012; Leighton et al., 2010; Wang & Hamilton, 2013). Consequently, stable traits that are associated with prosocial behaviours may also modulate the tendency to imitate others. Two of the Big-Five factors of personality, agreeableness and extraversion, have been associated with prosocial behaviours, including empathy (Barrio et al., 2004), cooperative behaviour (LePine & van Dyne, 2001) and altruism (Ashton et al., 1998). In sum, due to a lack of evidence, the relationship between automatic imitation and stable personality characteristics is unclear.

Systematic variation in imitation abilities has also been discovered in atypical populations, such as ASD and schizophrenia, and many have argued that atypical imitation in these populations is underpinned by a dysfunctional MNS (Enticott et al., 2008; Oberman & Ramachandran, 2007; Thakkar et al., 2014; Williams et al., 2001). While differences in intentional imitation may occur in ASD and schizophrenia (Park et al., 2008; Williams et al. 2004), other research suggests that automatic imitation is intact, at least in individuals with ASD (Bird et al., 2007; Press et al., 2010). As such, the mechanisms that underpin differences in imitation abilities between typical and atypical groups are far from clear (Hamilton, 2013; Southgate & Hamilton, 2008). One way to gain insight into the cognitive mechanisms underpinning ASD and schizophrenia is by testing autistic-like and schizotypal traits in the typical population. It has been proposed that healthy participants show the same traits as those diagnosed with the disorder, but to a lesser extent (Nelson et al., 2013). Indeed, if autistic-like and schizotypal traits lie on a continuum from subclinical to clinical populations, and the workings of the MNS contribute to imitation difficulties present in ASD and schizophrenia, then a relationship between autistic-like or schizotypal traits and automatic imitation might be expected in the typical population.

The aim of the current study is to investigate the relationship between automatic imitation and individual differences in stable trait-based personality and subclinical traits. By doing so, we will provide deeper insights into the antecedents of automatic imitation. To assess automatic imitation, we use an established reaction time paradigm that provides an index of automatic imitative tendencies (Brass et al., 2000). In addition, a series of questionnaires measure individual differences in personality (narcissism, empathy, and Big-Five factors) and subclinical (autistic-like and schizotypal) traits. In comparison to prior studies, by using a large sample, the data will reflect the population mean more accurately (Maxwell et al., 2008) and by using multiple regression analyses, we can control for variance in imitative tendencies explained by factors aside from our predictions (McNamee, 2005; Vik, 2013), such as mean reaction time, sex, or age.

Two hypotheses can be distinguished. First, if stable personality factors are robust antecedents of automatic imitation, then relationships between imitation performance and personality variables should be observed (Chartrand & Bargh, 1999; Obhi et al., 2013; Hogeveen & Obhi, 2013). Alternatively, if stable traits have little or no influence on automatic imitation, the view that enduring personality characteristics are universal antecedents of automatic imitation would require revision. Second, if atypical imitation abilities in ASD and schizophrenia are due to impaired engagement of the MNS (Enticott et al., 2008; Oberman & Ramachandran, 2007; Thakkar et al., 2014; Williams et al., 2001) and a continuum exists between subclinical and clinical populations, the presence of autistic-like as well as schizotypal traits should result in reduced automatic imitation. By contrast, no relationship between automatic imitation and subclinical traits would provide evidence consistent with the view that the MNS is relatively spared in ASD and schizophrenia and other mechanisms may be responsible for atypical control of automatic imitation in these disorders (J. Cook et al., 2012; Southgate & Hamilton, 2008; Wang & Hamilton, 2012).

Method

Participants

Two hundred and forty-three participants took part in this experiment for monetary compensation. All participants had normal or corrected-to-normal vision and provided written informed consent prior to data collection. Participants were excluded from the sample if accuracy (n=8) or mean RT (n=5) on the automatic imitation task was >3SD from the group mean. The final sample comprised 230 participants (133 female, 97 male; M_{age} = 21.62 years, SD = 5.41) who completed the personality, autism spectrum quotient, and schizotypy questionnaires described below. Fifty-seven of these participants (36 female, 21 male; M_{age} = 22.04 years, SD = 5.46) also completed a further two questionnaires, which measured empathy and narcissism (see below for details). The data reported here were obtained from human participants under approval from the Research Ethics and Governance Committee of the School of Psychology at Bangor University. This approval does not include making the data available on a public repository. However, anonymised data used in this study can be requested from the corresponding authors.

Materials and measures

Mini International Personality Item Pool (mini-IPIP)

The mini-IPIP (Donnellan et al., 2006) is a 20-item version of the International Personality Item Pool (Goldberg, 1999), which measures stable Big-Five personality traits. Particpants responded to statements that assess trait levels of extraversion (e.g., Talk to a lot of different people at parties), agreeableness (e.g., Sympathize with others' feelings), conscientiousness (e.g., Get chores done right away), neuroticism (e.g., Have frequent mood swings) and intellect/imagination (e.g., Have a vivid imagination). Participants indicated on a 5-point scale, from very accurate to very inaccurate, how well each of the items describes them. This measure results in an average score between zero and five for each trait, with a score of five indicating high levels of the particular trait for each participant.

Short Autism Spectrum Quotient (AQ-10 Adult)

The AQ-10 (Allison et al., 2012) is a 10-item measure of autistic-like traits. Participants used a 4-point scale from definitely agree to definitely disagree to indicate how true each item is for them. Example items are “I find it difficult to work out people’s intentions” and “I often notice small sounds when others do not”. Participants scored one point per autistic-trait consistent answer, thus each participant scored between zero and ten, with 10 indicating high levels of autistic-like traits.

Brief Schizotypal Personality Questionnaire (SPQ-B)

The SPQ-B (Raine & Benishay, 1995) is a 22-item questionnaire that assesses schizotypal personality disorder. A yes or no response is required to each statement or question. An example item is “Have you ever had the sense that some person or force is around you, even though you cannot see anyone?”. Participants scored one point per schizotypal consistent response and thus received a score from zero to twenty-two, with a score of twenty-two indicating a high number of schizotypal traits.

Narcissistic Personality Inventory (NPI-16)

The NPI-16 is a 16-item measure of narcissistic personality (Ames et al., 2006). Participants indicated which statement out of a choice of two fitted them best and scored a point for every narcissism consistent statement that they chose. For example, participants could be presented with the following two statements; “I know that I am good because everybody keeps telling me so” and “When people compliment me I sometimes get embarrased”. In this example, they would score one point for choosing the first statement and zero for choosing the second statement. Seventeen participants refrained from answering one or more of the items in the NPI-16. The final score for each participant was the proportion of narcissism consistent responses that they gave, out of the total items that they answered. Therefore, scores were not influenced by the number of items that participants answered and ranged from zero to one, with one being more narcissistic.

Empathy Assessment Index (EAI-22)

The EAI-22 is a 22-item measure of empathic personaility (Lietz et al., 2011). Participants responded on a 6-point scale from never to always for items such as, “When I am with someone who gets sad news, I feel sad for a moment too”. Three participants refrained from answering one or more items on this measure. The final score for the EAI was also calculated as a proportion so that each participant’s score was not influenced by the number of items that they answered. To do this we calculated the maximum they could have scored if they gave 6 on every item that they answered. We then computed the proportion that their score was out of the maximum. Scores ranged from zero to one, with one being most empathic.

Automatic imitation task

Figure 3.1. – Automatic imitation task design

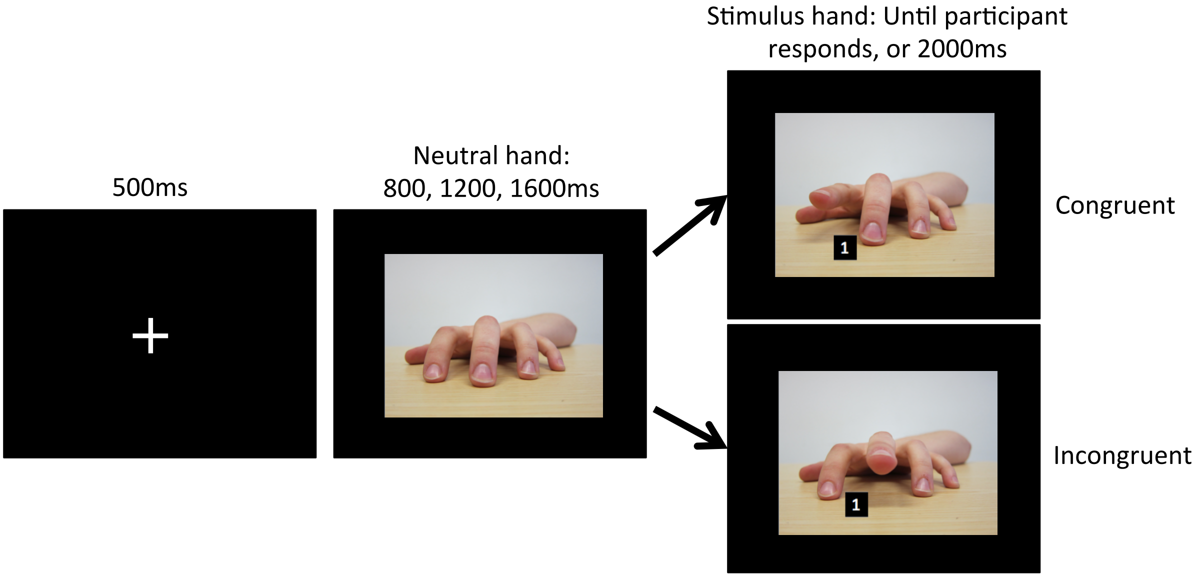

Figure 3.1. All trials for the automatic imitation task began with a fixation cross, then presentation of the neutral hand. After a variable inter-stimulus interval the stimulus hand would be presented so the participant would be simultaneously cued to make their response, and view the hand appear to move.

The automatic imitation task was based on the paradigm developed by Brass and colleagues (Brass et al., 2000). Prior to the start of the task, participants were instructed to hold down the 'n' key with the index finger of their right hand and the 'm' key with their middle finger. On each trial, upon presentation of the number target, instructions were to lift their index finger if it was a '1' and their middle finger if it was a '2', as quickly and as accurately as possible. The stimuli were images of a female left hand, viewed from the third-person so that the fingers of the hand extend towards the participants. The first image displayed the hand in a neutral position, resting on a flat surface. The other four images showed the hand with its index or middle finger lifted and a number '1' or '2' presented between its index and middle finger (Figure 3.1.). Thus, there were 4 possible target trials and two conditions arose from these, congruent and incongruent. On congruent trials, the action that participants were cued to perform matched the action observed (e.g., the participant lifted their index finger whilst observing an index finger lift, or lifted their middle finger whilst observing a middle finger lift). On incongruent trials, the action that participants were cued to perform and the action observed did not match (e.g., the participant lifted their index finger whilst observing a middle finger lift, or lifted their middle finger whilst observing an index finger lift).

As displayed in Figure 3.1. each trial consisted of the presentation of a fixation cross for 500ms, followed by the neutral hand. The neutral hand remained on screen for a random interstimulus interval (ISI) of 800, 1200, or 1600ms before the target. The sucession of hand images produced apparent motion of a finger lifting at the same time that participants were presented with the number cue. The target display remained onscreen until participants' made their response, but for no longer than 2000ms. Thus, total trial length varied, although it was never longer than 4100ms. Reaction time (RT) and error responses were recorded. RT was measured as the time from target onset to when participants lifted their finger from the 'n' or the 'm' key. Trials were considered correct if participants lifted the finger they were cued to lift. Trials were incorrect if they lifted the wrong finger, lifted a finger before target onset, or took longer than 2000ms to respond.

Trials were organised into a series of eight trials, which included two presentations of each trial-type in a random order. This eight-trial series was repeated until participants' completed 60 trials. There should have been 64 trials per participants, but due to a technical error, the last four trials for each participant were not shown. However, the majority of participants (n=147) completed 30 congruent and 30 incongruent trials. Ninety-two participants completed 30 trials per condition plus or minus one trial (e.g., 29 congruent and 31 incongruent). Four participants completed 30 trials per condition plus or minus two trials (e.g., 28 congruent and 32 incongruent). Pseudorandomisation permitted no more than 4 identical trials to occur consecutively.

Eight laptops were used to run the automatic imitation task, which was presented to participants using Psychophysics Toolbox, running in MATLAB. A 2 (congruency: congruent, incongruent) x 8 (laptop) ANOVA was used to test for differences in measured RT between the laptops. It was found that there was a main effect of congruency ($F(1,222)=1204.23$, $p<.001$, $\eta_p^2=.844$) such that participants were faster on congruent (M: 434.57, SE: 3.48) than incongruent (M: 519.59, SE: 4.65) trials. There was no main effect of laptop, ($F(7,222)=0.85$, $p=.550$), and no interaction between congruency and laptop ($F(7,222)=0.74$, $p=.641$). Therefore, for all analyses we collapsed data across the laptops used.

Design and procedure

Participants first completed three questionnaires under no time constraint and in the following order: Mini-IPIP, Autism Quotient and Schizotypal Personality Questionnaire. As described above, whilst completing these questionnaires, participants could refrain from answering certain items if they wished to. As such, for each participant the number of items that contributes to each measure varies slightly. Participants then completed the automatic imitation task, including a 12-trial practice before the main task. The task was administered in groups of up to eight participants on laptops that were arranged in two rows with space between participants that were next to each other. Participants were monitored so that no interaction took place between them while they completed the task.

In a follow-up phase of the experiment, those participants from the first part who consented to be contacted regarding further participation were asked to complete measures of empathy and narcissism in an online survey. Their data was then linked back to data collected during the first part of the study. Out of the original sample, 57 participants completed two additional questionnaires, the Narcissistic Personality Inventory (NPI-16; Ames et al., 2006) and then the Empathy Assessment Index (EAI-22; Lietz et al., 2011).

Data analysis

Questionnaire coding

Questionnaires were scored as outlined above. Apart from participant sex, which was coded as -1 for males and +1 for females, raw scores on all of the questionnaires were centred (the group mean score for each variable was subtracted from each participant's score on that variable; Kraemer & Blasey, 2004). The AQ-10, SPQ-B and

EAI-22 can all be broken down into component factors. The AQ-10 can be broken down into the factors of “attention to detail”, “attention switching”, “communication”, “imagination”, and “social”. The SPQ-B can be broken down into “cognitive-perceptual”, “interpersonal”, and “disorganised” factors. And finally, the EAI-22 can be broken down into “affective response”, “affective mentalising”, “self-other awareness”, “perspective-taking”, and “emotional regulation” factors. In all of the subsequent multiple regression analyses reported, total scores are used rather than component scores, except for the mini-IPIP as specific hypotheses regarded the subcomponents of extraversion and agreeableness. We ran these analyses with the AQ-10, SPQ-B, and EAI-22 again with component scores, but this did not change the pattern of results for any of the measures. Cronbach’s alpha for extraversion (4 items; α=.77), agreeableness (4 items; α=.62), AQ-10 (10 items; α=.38), SPQ-B (22 items; α=.84), NPI-16 (16 items; α=.77), and EAI-22 (22 items; α=.89) were generally reasonably high.

Automatic imitation

Trials were removed if participants’ gave an incorrect response (7.23% of total trials), released a key during the ISI (0.20% of total trials), or were slower than 2000ms to respond (0.11% of total trials). Participants were then removed if mean RT (n=5) or accuracy (n=8) was >3SD from the group mean. For each participant mean average RT for congruent and incongruent trials was then calculated, as well as a congruency effect (incongruent RT minus congruent RT). Furthermore, accuracy was calculated as the percentage of the total trials on which participants gave the correct response.

Multiple regression analyses

In order to test our primary hypotheses, we used multiple regression analyses. Multiple regression tests whether predictor variables explain variance in a dependent measure (i.e., the congruency effect) whilst controlling for variance explained by other related factors (Vik, 2013). As such, multiple regression can test whether or not individual differences in subclinical and/or stable personality factors predict the tendency to automatically imitate others, whilst controlling for the influence of other variables.

Before testing our predicitons, we constructed a base model. The base model was set up to account for factors that might significantly predict variance in participants' congruency effect, which were not part of our primary hypotheses. We initially included mean RT (collapsed across congruent and incongruent trials), sex, and age in the base model (Table 3.1.). Mean RT was included because we would expect participants with a faster RT to have a smaller congruency effect. In addition, research has shown that RT differs between sexes and across age groups (Der & Deary, 2006). In all subsequent tests of our hypotheses, any factors that significantly predict the congruency effect from the initial test of the base model were included.

Table 3.1. – Summary table of the multiple regression models

	Base model	Personality models			Subclinical models	
Predictors	Mean RT	Mean RT	Mean RT	Mean RT	Mean RT	Mean RT
	Participant Sex	Participant Sex	Participant Sex	Participant Sex	Participant Sex	Participant Sex
		Extraversion	Narcissism	Empathy	Autism Quotient	Schizotypy
		Agreeableness				
		Conscientiousness				
		Neuroticism				
		Intellect/Imagination				

Table 3.1. Summary of the models that will be tested using multiple regression to examine the predictive ability of each of the variables on congruency effect.

To individually test each of our predictions, participants' scores on predictor variables were added to the base model in separate hierarchical multiple regression models (Table 3.1.). By doing so, any significant predictor would explain variance in the congruency effect, which is not already explained by the base model. Although it could be argued that the base model would explain a large amount of variance in the congruency effect and thus disadvantage the possibility of finding that a stable trait characteristic predicts automatic imitation, this approach avoids the possibility of finding that a trait predicts the congruency effect but that this relationship is in fact due to a third variable. However, in order to compare if any results did change when the base model was not inlcuded, we ran each regression model without the base model included. Finally, because sex differences have been recorded on trait factors (Schmitt et al., 2008), independent-samples t-tests were used to test for sex differences on each of the trait measures. For any measures that showed a sex difference, a sex*trait interaction term was calculated and assessed in separate muliple regression models. To calculate the interaction terms, continuous predictors were centered and categorical variables were dummy coded as negative one and positive one (Blair et al., 2004; Kraemer & Blasey, 2004).

Group analyses

Comparisons between subgroups within our sample were performed in order to closely compare our results with prior work that has investigated similar questions (e.g., Obhi et al., 2013). To do so, two groups were constructed based on each variable within the base model, as well as for each predictor variable. For sex, males (n=97) and females (n=133) were compared, and for all other variables the groups consisted of the highest or lowest scoring 20 participants. Congruency effects for high and low scoring groups on each variable were compared using independent-samples t-tests.

Power analyses

For the aforementioned analyses, we calculated statistical power using G*Power 3.1 (Faul et al., 2009). The aim of these power analyses was to determine the effect sizes we had the power to detect with our samples of 230 and 57. In the primary test of our hypotheses, which involved multiple regression analyses, for the bigger sample (n =230) we had power to detect large and medium effects, whereas in the subsample (n=57) we had power to detect large effects and some medium effects.

Results

Questionnaires

Mean scores across the entire sample were calculated for each of the questionnaires. As sex differences have been found previously on trait measures of personality (Schmitt et al., 2008), independent-samples t-tests were implemented to examine whether there were sex differences on each of the stable trait characteristics in our dataset. Significant sex differences emerged on measures of agreeableness, neuroticism and intellect/imagination (all p’s <.05), such that female participants scored higher for agreeableness and neuroticism, and lower for intellect/imagination. There were marginally significant differences on conscientiousness, narcissism and schizotypy (all p’s between 0.05 and 0.1) such that female participants scored higher for conscientiousness, and lower for narcissism and schizotypy than male participants. No sex differences were found on extraversion, empathy and AQ (all p's>0.7).

Automatic imitation

As expected, participants were significantly more accurate (t(229)=16.93, p<.001) and significantly faster (t(229)=-36.09, p<.001) on congruent compared to incongruent trials (Brass et al., 2000).

Multiple regression

For transparency, simple correlations between the congruency effect and each predictor variable were calculated (Appendix 2). However, as the goal of this study is to investigate the influence of predictor variables on the congruency effect, whilst controlling for confounding factors, we focus on the results from the multiple regression analyses (summarised in Table 3.2.). Results from the first base model showed that mean RT (B=0.29, SEB=0.04, t(225)=7.79, p<.001) and sex (B=6.70, SEB=2.11, t(225)=3.18, p=.002) significantly predicted variance in the congruency effect. The positive weighting for mean RT showed that as participants' mean RT increased, their congruency effect increased. In addition, females had a larger congruency effect than males of about 13 ms. Age did not significantly predict the congruency effect (B=-0.16, SEB=0.38, t(225)=-0.43, p=.668) and was thus removed from the base model in all further analyses. As both mean RT and sex predicted congruency effect, we also tested the mean RT * sex interaction term. The interaction between mean RT and sex was a significant predictor of the congruency effect (B=0.07, SEB=0.04, t(226)=2.00, p=.047). As illustrated in Figure 3.2. (page 69), the difference in congruency effect between men and women is greater at slower than faster mean RTs. The final base model (Table 3.2., model 1) consists of mean RT, sex, and the mean RT by sex interaction.

After establishing the base model (Table 3.2., model 1), subsequent models tested our main hypotheses. For each hypothesis, we created a model that included factors from the base model plus an additional predictor variable. By doing so, we were able to test whether any of our predcitor variables could explain variance in automatic imitation in addition to the variance explained by factors within the base model.

Table 3.2. – Results from the multiple regression analysis

		Model 1 (n=230): F(3,226)=31.40, p<.001, R^2=.294				Model 2 (n=224): F(8,215)=11.33,p<.001, R^2=.296				Model 3 (n=57): F(4,52)=15.56,p<.001, R^2=.545				Model 4 (n=57): F(4,52)=15.72,p<.001, R^2=.547				Model 5 (n=220): F(4,215)=22.13,p<.001, R^2=.292				Model 6 (n=199): F(4,194)=19.83,p<.001, R^2=.290			
Predictors		B	SE B	t	p	B	SE B	t	p	B	SE B	t	p	B	SE B	t	p	B	SE B	t	p	B	SE B	t	p
Base model predictors	Constant	83.25	2.08	39.98	<.001	83.07	2.15	38.73	<.001	91.80	4.12	22.28	<.001	91.89	4.10	22.43	<.001	83.66	2.16	38.77	<.001	83.99	2.23	37.74	<.001
	Mean RT	0.27	0.04	7.45	<.001	0.27	0.04	6.83	<.001	0.50	0.07	6.81	<.001	0.50	0.07	6.88	<.001	0.27	0.04	7.15	<.001	0.27	0.04	6.73	<.001
	Participant Sex	6.98	2.08	3.35	.001	7.94	2.29	3.47	.001	-3.13	4.19	-0.75	.459	-3.06	4.09	-0.75	.458	6.91	2.16	3.20	.002	6.54	2.24	2.92	.004
	Mean RT * Sex	0.07	0.04	2.00	.047	0.08	0.04	2.07	.040	-0.05	0.07	-0.73	.470	-0.06	0.07	-0.80	.429	0.08	0.04	2.06	.040	0.08	0.04	2.15	.033
Personality characteristic predictors	Extraversion					2.46	2.44	1.01	.315																
	Agreeableness					-1.80	3.06	-0.59	.557																
	Conscientiousness					-2.79	2.41	-1.16	.249																
	Neuroticism					-1.16	2.62	-0.44	.660																
	Intellect/ Imagination					0.57	3.19	0.18	.859																
	Narcissism									-2.67	20.52	-0.13	.897												
	Empathy													19.72	35.39	0.56	.580								
Subclinical predictors	Autism Quotient																	0.80	1.25	0.64	.522				
	Schizotypy																					-0.61	0.44	-1.39	.166

Table 3.2. Model 1 includes the base model factors of mean RT, sex and the interaction between mean RT and sex. These base model factors predict the congruency effect but are not part of our personality-based predictions. Across models 2-6, an additional trait factor is added to the base model in order to assess the influence of stable personality traits on the congruency effect. By doing so, we are able to test whether personality variables influence performance on the automatic imitation task, in addition to factors within the base model.

Figure 3.2. – Sex and Mean RT difference in automatic imitation

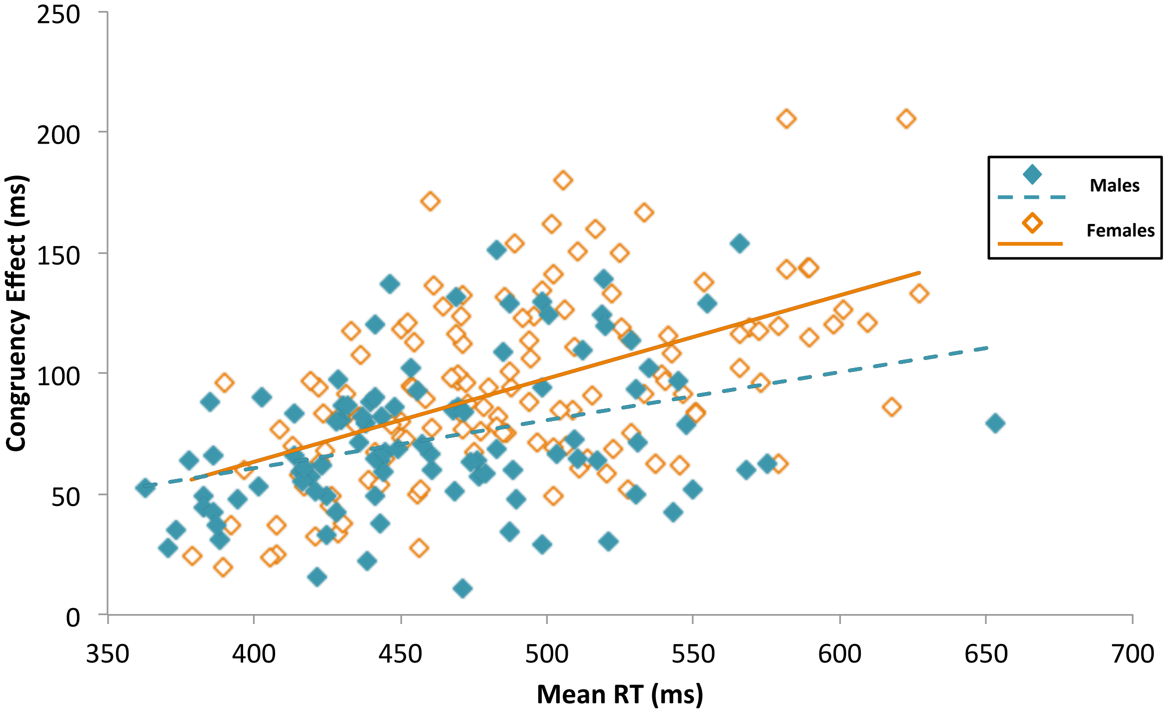

Figure 3.2. The relationship between mean RT and congruency effect as a function of participant sex. Multiple regression analyses showed that mean RT, participant sex and the interaction between these two factors significantly predict the congruency effect. Individuals with a longer mean RT had a larger congruency effect than those with a shorter mean RT. In addition, women had a larger congruency effect than men. Furthermore, the interaction indicates that the sex difference was greater for individuals with longer than shorter RTs. Stable personality characteristics, including narcissism and empathy, as well as autistic-like or schizotypal traits, showed no reliable relationship with the congruency effect.

First, stable trait personality predictors were evaluated. Model 2 (Table 3.2.), including the base model and all Big-Five factors, explained no more variance than model 1 (F(5,215)=0.59, p=.705). In addition none of the Big-Five factors was a significant predictor on its own: extraversion (B=2.46, SEB=2.44, t(215)=1.01, p=.315), agreeableness (B=-1.80, SEB=3.06, t(215)=-0.59, p=.557), conscientiousness (B=-2.79, SEB=2.41, t(215)=-1.16, p=.249), neuroticism (B=-1.16, SEB=2.62, t(215)=-0.44, p=.660) and intellect/imagination (B=0.57, SEB=3.19, t(215)=0.18, p=.859).

Two further personality measures, narcissism and empathy, were evaluated in a subsample of 57 participants. In two separate models, narcissism (Table 3.2., model 3) and empathy (Table 3.2., model 4) were added to the base model. Neither narcissism

(F(1,52)=0.02, p=.897; B=-2.67, SEB=20.52, t(52)=-0.13, p=.897) nor empathy (F(1,52)=0.31, p=.580; B=19.72, SEB=35.39, t(52)=0.56, p=.580) significantly explained variance in the congruency effect in addition to the variance explained by the base model.

Second, subclinical predictors, including autistic-like and schizotypal traits, were evaluated in our larger sample (Table 3.2., models 5 and 6). Neither autistic-like (F(1,215)=0.41, p=.522; B=0.80, SEB=1.25, t(215)=0.64, p=.522) nor schizotypal traits (F(1,194)=1.93, p=.166; B=-0.61, SEB=0.44, t(194)=-1.39, p=.166) significantly explained variance in the congruency effect in addition to variance explined by the base model.

Across models 1, 2, 5 and 6 (n = 230), mean RT and sex significantly explained variance in the congruency effect. In models 3 and 4 (n = 57) mean RT continued to predict the congruency effect, but sex did not (Table 3.2.). However, in these multiple regression analsyes, the effect size for mean RT (f^2=1.16) is considered large, whereas the effect size for sex (f^2=0.06) is considered to be between a small and medium effect (Cohen, 1992). As a consequence, it is likely that a sample of 57 may only be large enough to detect the influence of mean RT and not sex, whereas the sample of 230 was large enough to detect both effects.

Due to prior research showing sex differences in basic trait measures (Schmitt et al., 2008), we assessed the possibilty that sex*trait interactions may explain variance in automatic imitation. Having established that sex differences emerged on certain trait varibales within our sample, we tested whether the relationship between sex and trait predicted performance on the automatic imitation task more than sex or trait variables alone. For those traits that showed significant, or marginally significant sex differences, additional multiple regression models were run to assess the predictive ability of interactions between sex and each trait on the congruency effect. Separate models were constructed to assess each sex*trait interaction. Each model included factors from the base model (mean RT, sex, and the mean RT * sex interaction), plus one trait predictor as well as the sex*trait interaction term. None of the sex*trait interactions significantly predicted the congruency effect on top of variance explained by the rest of the model.

Models 2-6 were also run not including the base model. This showed that no personality characteristic significantly predicted the congruency effect (all model p's > .21), except the model including only schizotypy. As such, schizotypy did significantly predict the congruency effect (F(1,197)=8.85, p=.029; B=-1.11, SEB=0.50, t(197)=-2.20, p=.029) when factors within the base model were not controlled for.

Group analyses

The regression approach above is an effective means for testing the effects of trait variables on automatic imitation. However, we also performed group analyses, comparing the congruency effects for the highest and lowest scorers on different stable traits. Group analyses rule out the possibility that, in our regression analyses, differences at the extremes might be washed out by variability in the middle. In addition, group analyses are consistent with the analytical approach taken in prior work and therefore make it easier to compare our results with prior studies that have not used multiple regression analyses. Except for sex, which was coded categorically, for each variable of interest, congruency effects for the 20 participants who scored the highest and the 20 who scored the lowest were calculated and compared. We investaged factors within the base model first. First, an independent-samples t-test showed that mean RT was significantly faster for the low than the high RT group (t(38)=-35.64, p<.001). Subsequently, an independent-samples t-test showed that groups that differed on mean RT showed a significant difference on conguency effect (t(38)=-6.81, p<.001). The high RT group showed a larger congruency effect than the low RT group. Splitting the data into groups based on sex also revealed a significant difference (t(228)=4.51, p<.001, d=0.61), such that females had a larger congruency effect than males. The results from this group analysis is therefore in agreement with the larger regression analysis.

Next we ran similar high-low group analyses for personality measures. First, to ensure that the high and low groups scored differently on the relevant personality characteristic, independent-samples t-tests were run. For all variables (each of the Big-Five factors, empathy, narcissism, AQ and schizotypy), scores on the relevant personality and subclinical measures were significantly different between the high and low scoring groups (all p's < .001). Next, we ran the high-low group comparisons on congruency effects. We found no significant differences on congruency effects between those that scored high compared to low on each of the variables (all p's > 0.156, except from agreeableness which was 0.072). Due to the smaller sample size for the narcissism and empathy measures, we also compared the top 10 to the bottom 10 scorers, and found the same pattern of results as with groups of 20.

Discussion

Little is currently known about the relationship between automatic imitation and stable components of personality. The present study fails to support the view that inter-individual differences in stable personality and subclinical characteristics predict the extent to which individuals automatically imitate others. These findings suggest that automatic imitation is more resistant to variance in stable inter-individual differences than previously suggested (Chartrand & Bargh, 1999; Hogeveen & Obhi, 2013; Obhi et al., 2013). Moreover, these data are consistent with the view that the MNS is relatively intact in ASD and schizophrenia and other mechanisms may be repsonsible for the imitative difficulties reported in these disorders (J. Cook et al., 2012; Hamilton, 2013; Southgate & Hamilton, 2008; Wang & Hamilton, 2012). Implications for understanding the antecedents and cognitive basis of automatic imitation are discussed below.

Stable personality characteristics and automatic imitation

Contrary to our hypotheses, we found that trait personality constructs of narcissism, empathy, extraversion, and agreeableness did not predict the extent to which participants automatically imitate. The lack of relationship between narcissism and automatic imitation is contrary to previous research (Hogeveen & Obhi, 2013; Obhi et al., 2013). Given recent failures to replicate landmark results in psychology (Pashler et al., 2012; Shanks et al., 2013), such conflicting results warrant close scrutiny. Indeed, it is important to note similarities and differences between this and prior work. In terms of similarities to prior work (Hogeveen & Obhi, 2013; Obhi et al., 2013), we used the same automatic imitation task, the identical short-form measure of narcissism (NPI-16; Ames et al., 2006), and participants were comparable in age and predominantly female. Furthermore, to allow direct comparison with prior research we replicated the analytical approach used (Obhi et al., 2013). In comparison to these prior studies, the current work tested a larger sample (2-3 times larger) and used an additional analytical approach (multiple regression) that could control for potentially confounding variables (Button et al., 2013; Cumming, 2014; Maxwell et al., 2008; McNamee, 2005; Vik, 2013).

Obhi and colleagues (Obhi et al., 2013) showed that a group of high narcissists had a lower congruency effect than a group of low narcissists and the effect size was large (Cohen's d = 1.02; Cohen, 1992). Cohen's d is typically used as a measure of effect size for group differences and is equal to the mean of group one minus the mean of group two, divided by the pooled standard deviation of the two groups. In this case, values of 0.2, 0.5, and 0.8 are generally considered to be small, medium, and large respectively (Cohen, 1992). We calculated Cohen's d based on the methodological information and results provided by Obhi and colleagues (2013). Using the same analytical approach as used previously (Obhi et al., 2013), which compared those who report high and low levels of narcissism, we show no differences in imitation performance between these groups. As such, we fail to replicate Obhi and colleagues finding in a sample that is 2-3 times larger.

Furthermore, using multiple regression we are able to control for additional and potentially confounding variables. Inspection of Obhi and colleagues (2013) data shows that the high narcissism group were generally faster (mean RT=477ms) than the low narcissism group (mean RT=502ms). In the current study, regression analyses demonstrate a clear relationship between the congruency effect and mean RT, which has a large effect size (Cohen, 1992). To be consistent with the measure of effect size that we calculated for Obhi and colleagues (2013), we used our group analyses to compute Cohen's d as a measure of effect size for mean RT. We found that the difference in congruency effect between groups with low and high mean RT had a large effect size (Cohen's d = 2.15). We do not, however, show a relationship between narcissism and the congruency effect. Even if we only regress narcissism and congruency effect, we show no relationship between these variables. As a consequence, it is likely that at least part, if not all, of the previously reported relationship between congruency effect and narcissism, could be explained by differences in mean RT. Our findings, therefore, suggest that the relationship between narcissism and automatic imitation is weaker than the initial evidence suggested. Further research that tests larger samples and controls for potentially confounding variables is required to further delineate the relationship between automatic imitation and narcissism.

Prior research has also demonstrated a link between empathy and automatic imitation by measuring copying behaviours during a live interaction between two people (Chartrand & Bargh, 1999). By contrast, we did not find any influence of empathy using a computer-based RT measure of automatic imitation. Therefore, the results of the current study suggest that the influence of empathic predispositions on automatic imitation is less universal than initially conceived. Indeed, contextual factors that are integral to live human interactions, such as emotion, may be needed to reveal relationships between empathy and automatic imitation. For example, research has shown greater automatic imitation of facial expressions by individuals who are more empathic than by those who are less empathic (Sonnby-Borgström, 2002; Sonnby-Borgström et al., 2003). By contrast, in socially impoverished contexts, such as computer-based tasks, individual differences in empathy may have a reduced impact on automatic imitation. As such, future research should focus on identifying potential moderating variables in social cognition (Abbott, 2013), such as emotion, as well as comparing different measures of automatic imitation, as it may help further delineate underlying mechanisms.

Automatic imitation has been shown to be sensitive to temporary social dynamics between interaction partners (Chartrand & Lakin, 2013, Heyes, 2011). For example, priming of a prosocial state increases imitative tendencies in computer-based RT paradigms (Cook & Bird, 2011, 2012; Leighton et al., 2010; Wang & Hamilton, 2013). In the current study, we find no evidence that stable traits of extraversion and agreeableness, which are associated with prosocial tendencies (Barrio et al., 2004; LePine & van Dyne, 2001; Ashton et al., 1998), predict the tendency to imitate others. Automatic imitation may, therefore, be more sensitive to changes in temporary social dynamics than stable trait-based characteristics.

Overall, when using a computer-based task and measuring trait levels of narcissism, empathy, extraversion, and agreeableness, we do not support the view that mechanisms underpinning automatic imitation, such as the MNS, systematically vary as a function of stable predispositions to be interested in others or behave in a prosocial manner. However, further research could examine potential relationships between automatic imitation and other stable trait characteristics, which were not measured here.

Subclinical trait characteristics and automatic imitation

The current study also investigated possible links between automatic imitation and subclinical traits in the typical population. Despite the proposal that autistic-like and schizotypal traits exist on a continuum from subclinical to clinical manifestations (Nelson et al., 2013) and contrary to suggestions that a dysfunctional MNS underpins atypical imitation in ASD and schizophrenia (Enticott et al., 2008; Williams et al., 2001; Williams et al. 2004), we found no evidence for a relationship between autistic-like or schizotypal traits and automatic imitation. When we did not control for third variables, schizotypal traits negatively predicted the congruency effect. This relationship, however, was not observed when mean RT and sex were controlled for. These results highlight the methodological importance of controlling for extraneous variables whenever possible (Button et al., 2013; Cumming, 2014; Maxwell et al., 2008; McNamee, 2005; Vik, 2013). In short, these data are not consistent with the idea that imitation deficits in autism or schizophrenia are due to a dysfunctional MNS.

Two aspects of this result warrant further discussion. First, prior studies that have shown imitation deficits in ASD and schizophrenia have studied intentional rather than automatic imitation (Williams et al. 2004; Park et al., 2008; Rogers et al., 2003; Thakkar et al., 2014). Conversely, in the current task, we measured an RT index of automatic imitation. These different forms of imitation – intentional vs. automatic – are likely to rely on different neurocognitive mechanisms, at least to some extent. As such, our results do not point towards problems in the automatic system in these disorders, but leave open the possibility that some difficulties may arise from systems underpinning intentional imitation.

Second, the present results are consistent with the view that basic matching processes between vision and action may be intact in ASD and schizophrenia but other processes, such as top-down control, may be impaired (J. Cook et al., 2012; Hamilton, 2013; Southgate & Hamilton, 2008; Wang & Hamilton, 2012). Direct evidence for this proposal comes from studies of automatic imitation using an RT paradigm, which shows that individuals with ASD have an intact congruency effect (Bird et al., 2007; Press et al., 2010), but lack modulation of imitation based on social context (Cook & Bird, 2012). Further research could directly investigate whether different forms of imitation (intentional and automatic) are impaired in ASD and schizophrenia, as well as the extent that impairments rely on the MNS or other neurocognitive systems.

Sex differences in automatic imitation

Although it was not part of our *a priori* predictions, we did find that sex predicted the congruency effect, such that women had a greater tendency to automatically imitate than men. This result could not be explained by sex-differences in stable traits, as we found that no stable trait predicted performance on the imitation task and there were no sex*trait interactions. As such, any pattern of relationship between each trait and automatic imitation was the same for both male and female participants. Furthermore, we found a sex by mean RT interaction that shows that as mean RT becomes slower, the sex difference on the congruency effect becomes larger. This suggests that there is not a general sex difference across all speeds; rather, the sex difference emerges at slower speeds. Two plausible explanations of the sex difference in automatic imitation are outlined below.

First, the result may not represent a sex difference per se, but an own-sex bias. The study was not designed to test for sex differences and, as such, only a female hand was used during the automatic imitation task. Therefore, given the evidence that children copy behaviours more that are demonstrated by same gender models (Shutts et al., 2010) and the strength and ubiquity of ingroup biases even for arbitrarily assigned groups (Buttelmann & Böhm, 2014), the result could be explained by females showing more sensitivity to an ingroup member than an outgroup member. Second, the result may reflect a basic sex difference in the systems that underpin performance on the automatic imitation task. Based on performance on similar cognitive control tasks, there is currently some limited support for such sex differences. For example, women show larger interference effects than men on flanker (Clayson et al., 2011), oddball (Rubia et al., 2010), as well as gaze- and arrow-cueing tasks (Bayliss et al., 2005). All of these tasks share a similarity with the automatic imitation task: they require inhibition of a response to a task-irrelevant feature in order to enforce a task-relevant response. As such, based on sex differences in the systems that underpin such processes, women may find it more difficult than men to suppress the task-irrelevant stimulus. These proposals, however, remain speculative and further research is required to directly investigate these possibilities.

Limitations

It is possible that null results could, in part, be due to the accuracy of the underlying measures. For most of our measures, we feel this is an unlikely account of our findings. Cronbach's alpha analyses demonstrated generally good reliability of the personality measures used. Indeed, only the AQ had suboptimal reliability. Additionally, all measures used, despite being short-form versions, have been previously validated (Allison et al., 2012; Ames et al., 2006; Donnellan et al., 2006; Lietz et al., 2011; Raine & Benishay, 1995). Nevertheless, further work that aims to replicate the null effects observed here with more reliable long-form measures of personality are welcomed (e.g., the 50-item AQ).

The imitation task that we used indexes interference produced by both imitative and spatial components of the task. As such, imitation and spatial compatibility between stimulus and response could have contributed to our null findings. In order for this to occur, however, it would require assuming that automatic imitation and spatial compatibility are influenced in opposite directions by variation in personality traits (e.g. someone with more narcissistic tendencies would exhibit high levels of spatial compatibility alongside low levels of automatic imitation). As we have no reason to propose that such a negative relationship exists, we suggest it is an unlikely, yet possible, account of our null findings.

Conclusion

The present study provides novel insight into the antecedents of automatic imitation. First, we found no relationship between automatic imitation and stable components of personality including empathy and narcissism. As such, we suggest that the relationship between social components of personality and automatic imitation is less universal than initially conceived. Second, we found no relationship between automatic imitation and autistic-like and schizotypal traits, which is not consistent with the view that a dysfunctional MNS underpins atypical imitation abilities in ASD and schizophrenia. Instead, this result suggests that the systems supporting automatic imitation are intact in these disorders and other systems may be responsible for the imitation difficulties observed. More generally, we show the importance for studies of psychological processes to attempt replication experiments (Pashler et al., 2012; Shanks et al., 2013), study larger samples, and control for confounding variables (Button et al., 2013; Cumming, 2014; Maxwell et al., 2008; McNamee, 2005; Vik, 2013). By doing so, a more accurate estimate of the underlying cognitive architecure is produced.

CHAPTER 4

Sex differences in the inhibition of automatic imitation

Chapter 4 follows up on the novel finding of an unpredicted sex difference in automatic imitation that was observed in Chapter 3. The current chapter comprises a large sample behavioural experiment (n=165) and an fMRI experiment (n=28). This approach utilises the methodological strengths from Chapter 3, and extends these strengths to provide additional confidence interpreting neuroimaging findings of distal behavioural effects

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Abstract

Sex differences are apparent in a variety of cognitive control tasks requiring inhibition. For instance, greater interference to performance has been shown for women than men in social as well as non-social tasks requiring inhibition. The aim of the current study was to investigate whether common or distinct neural circuits subserve sex differences in social and non-social inhibitory control. Two brain circuits were identified as potential candidates for supporting such sex biases: 1) a dorsal frontoparietal circuit, which has been identified across a number of different inhibitory control tasks and; 2) a medial prefrontal cortex and right temporoparietal junction circuit, which has been shown to respond more specifically during the inhibition of imitation. In a behavioural study (n=165), we replicate the prior sex difference in the inhibition of automatic imitation, such that females show more interference than males. Subsequently, in an fMRI study (n=28), we demonstrate that regions in dorsal posterior frontal cortices support the sex difference in automatic imitation more than during a non-social flanker task. Therefore, we show sex- and task-specific responses in what is typically considered a domain-general neural architecture. These findings break from the idea of a neat division of labour between general and specific systems and instead add to evidence for higher complexity within domain-general and domain-specific systems.

Introduction

During social interactions we unconsciously imitate the behaviours of those around us, a process that increases affiliation and rapport between interaction partners (Chartrand & van Baaren, 2009; van Baaren et al., 2009). Thus, imitation guides social interactions. The way social interactions are regulated through imitation is proposed to vary across individuals. For instance, it has been argued that imitative tendencies operate as a function of stable individual differences, such as dimensions of personality (Chartrand & Lakin, 2013). To date, however, there is little empirical evidence that investigates individual differences in imitation. Here, across separate behavioural and fMRI experiments, we delineate how imitation varies across individuals by investigating sex differences in the propensity to automatically imitate others' actions.

Prior evidence demonstrating sex differences in imitation is sparse. Studies investigating the tendency to copy common actions or gestures, such as nose scratching, have reported no sex differences in imitation behaviour (Chartrand & Bargh, 1999; Larsen et al., 2010). By contrast, studies investigating the imitation of facial expressions have shown that women imitate expressions, such as smiling, more than men (Dimberg, 1990; Sonnby-Borgström et al., 2008). In addition, in a large sample (N=230), Butler and colleagues (2015) showed that women have greater difficulty inhibiting automatic imitation of another's actions than men. Moreover, similar sex differences have also been observed in non-social inhibitory control tasks including cueing, flanker, and oddball tasks (Table 4.1. (page 82); Bayliss et al., 2005; Clayson et al., 2011; Rubia et al., 2010; Stoet, 2010). Thus, there is good evidence that cognitive processes differ between men and women, specifically that there are sex differences in inhibitory control systems. However, the neural systems that underpin these sex differences, and whether they are the same for both social and non-social inhibitory control, remain unknown.

Much like cognitive science in general (Hirschfeld & Gelman, 1994; Kanwisher, 2010), inhibitory control research has focused on a neat division between domain-general and domain-specific mental operations. Domain-general inhibitory systems, which operate across multiple tasks, have been identified in dorsal frontoparietal cortices (Bunge et al., 2002; Hazeltine et al., 2007; Nee et al., 2007; Wager et al., 2005). In addition, a domain-specific circuit has been identified in medial prefrontal cortex (mPFC) and right temporoparietal junction (rTPJ) that operates preferentially during social contexts and specifically the inhibition of imitation (Brass et al., 2001, 2003, 2005, 2009; Klapper et al., 2014; Santiesteban et al., 2012b; Spengler et al., 2010). More recently, however, such clean divisions between domain-general and domain-specific systems have been questioned (Adolphs, 2001; Barrett & Satpute, 2013; Kanwisher, 2010). For instance, brain regions that show specialised responses for social cognition have also been shown to be responsive in non-social tasks (Baetens et al., 2014; Spunt & Adolphs, 2015). In addition, domain-general and domain-specific systems show interplay during social processing tasks (Baldauf & Desimone, 2014; Quadflieg et al., 2011; Zaki et al., 2010). Therefore, the relationship between domain-specific and domain-general networks is more nuanced and complex than previous conceptualisations have suggested.

Table 4.1. – Prior evidence of the sex difference in inhibitory control tasks

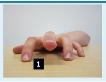
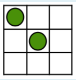
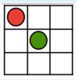
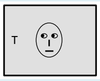
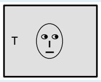
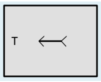
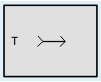
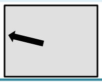
	Task	**Sample (female:male)**	**Trials per condition**	**Sex difference - interference**	**Task requirements**	**Conditions**	
						Congruent	**Incongruent**
Butler et al. (2015)	Automatic imitation	230 (133:97)	~30	Females > Males	Respond to number cue		
Stoet (2010)	Flanker	80 (40:40)	120	Females > Males	Respond to central circle		
Clayson et al. (2011)	Flanker	114 (54:60)	450	Females > Males	Respond to central arrow	< < < < <	< < > < <
Bayliss et al., 2005	Gaze-cueing	80 (40:40)	144	Females > Males	Respond to letter cue		
Bayliss et al., 2005	Arrow-cueing	40 (20:20)	144	Females > Males	Respond to letter cue		
Rubia et al. (2010)	Oddball	63 (25:38)	160 congruent 24 oddball	Females > Males	Respond to arrow direction		

Table 4.1. Sex differences in inhibitory control tasks on which females experience greater interference than male participants. NB. Images are reproduced based on figures and description in each Experiment apart from Butler et al. (2015), which are the exact images that we used. Also, in Rubia et al. (2010) the sex difference was increased interference by the oddball trials rather than the incongruent trials and this is what is represented by the images. Finally, in Butler et al. (2015) participants completed 60 trials that were 30 ± 2 trials per congruent and incongruent condition.

In the current experiments we investigate the contribution of domain-general and domain-specific systems to sex differences in the inhibition of automatic imitation. Experiment 1 uses a large behavioural sample (N=165) to compare sex differences on an automatic imitation task with a non-social inhibitory control task (a flanker task). In

Experiment 2, we use the same two tasks during fMRI with a new participant sample (N=28) to probe the neural correlates of these sex differences in inhibitory control.

Experiment One

Method

Participants

Two-hundred and two Bangor University students and staff completed both the automatic imitation and flanker tasks for monetary compensation of £15. Twenty participants were excluded as their mean RT or accuracy on either of the tasks was greater than three standard deviations from the group mean for that task. Seventeen participants did not complete the demographic questionnaire so the final sample consisted of 165 participants (56 male, 109 female; M_{age}=20.84 years, SD=3.65). Participants provided written informed consent, and ethical approval was granted by the Research Ethics and Governance Committee of the School of Psychology at Bangor University.

Automatic imitation task

The automatic imitation task was based on the paradigm developed by Brass, Bekkering, Wohlschläger and Prinz (2000). Participants were instructed to use their right hand to hold down the ‘n’ key with their index finger and the ‘m’ key with their middle finger throughout the task. Stimuli were five images of a female left hand, displayed from the third-person viewpoint. In the previous study (Chapter 3; Butler et al., 2015) one of the possible interpretations of the data was that the result may not represent a sex difference per se, but an own-sex bias. The previous study was not designed to test for sex differences and, as such, only a female hand was used during the automatic imitation task. The current study is designed to test for sex differences, as such two pilot studies were run to assess the possibility that the sex difference is the result of an own-sex bias. Pilot participants completed the automatic imitation task using stimuli that were both male and female hands, chosen for their sex-typicality. These pilot studies provided no support for an own-sex bias. In addition, participants rated the typically male hand as most masculine, the typically female hand as most feminine, and the hand used in the current and previous study was rated intermediately as neutral. As such, the same stimuli were used as in the previous study (Butler et al., 2015).

In the first image the hand was displayed resting on a flat surface. In the other four images the hand was displayed with its index or middle finger lifted, and a number '1' or '2' presented between its index and middle finger (Figure 4.1.A.; page 85). Thus, there were 4 possible target images that fell into one of two conditions, congruent and incongruent. On each trial, upon presentation of the number target, instructions were to lift their index finger for a '1' and their middle finger for a '2', as quickly and as accurately as possible. On congruent trials, the cued action matched the observed action (the participant lifted their index finger whilst observing an index finger lift, or lifted their middle finger whilst observing a middle finger lift). On incongruent trials, the cued action did not match the observed action (the participant lifted their index finger whilst observing a middle finger lift, or lifted their middle finger whilst observing an index finger lift). Each trial began with presentation of a fixation cross for 500ms, followed by the neutral hand. The neutral hand remained on screen for a random interstimulus interval (ISI) of 500, 700, or 1000ms before the target hand image. The succession of hand images produced apparent motion of a finger lifting simultaneously with presentation of the number cue. The target display remained onscreen until participants' made their response, but for no longer than 2000ms.

In this experiment, an additional, unrelated question was also addressed. As such, a face image was presented to participants for 500ms between the fixation cross and neutral hand, and remained onscreen above the neutral hand and target hand image for the duration of the trial. In the current study, we are interested in general sex differences between congruent and incongruent RTs. Additionally, there was no interaction between congruency and face image (F(4,768)=0.83, p=.508). As such, data are collasped across face presentation conditions to give an average RT measure for congruent trials and one for incongruent trials. Total trial length varied, depending on the length of the ISI, although it was never longer than 3500ms.

Pseudorandomisation permitted no more than 4 identical trials to occur consecutively. In total there were 200 trials, presented in four blocks so that participants could rest after each 50 trials. Half of the total trials were congruent and half were incongruent, which produced 100 trials per condition. Reaction time (RT) and error responses were recorded. RT was measured as the time from target onset to when participants lifted their finger. Trials were incorrect if participants lifted the wrong finger, lifted a finger before target onset, or took longer than 2000ms to respond.

Figure 4.1. – Stimuli for imitation and flanker tasks

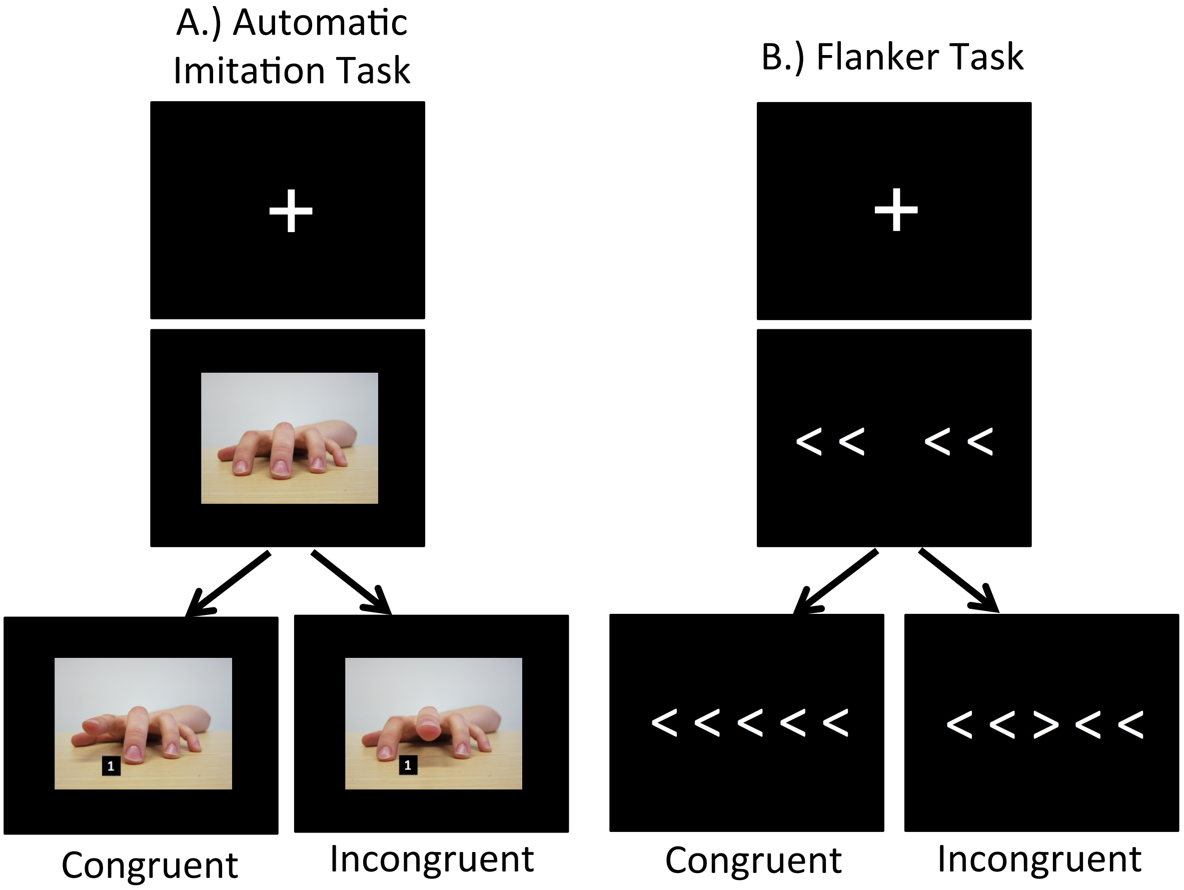


Figure 4.1. **(A)** Stimuli and trial design for the automatic imitation task. **(B)** Stimuli and trial design for the flanker task. Trials proceeded exactly like this in Experiment 2. In Experiment 1, because we were interested in additional unrelated questions, a face preceded the hand in the imitation task and on the flanker task on half of the trials, the direction of flanker arrows changed between their initial presentation and their presentation alongside the target arrow.

Flanker task

The Flanker task was a variation of the paradigm introduced by Erikson and Erikson (1974) and used a row of five white arrows presented on a black background that pointed to the left or the right (Figure 4.1.B.). Participants' task was to judge the direction of the central arrow and respond as quickly and accurately as possible by pressing the "n" key with their left index finger if they thought the central arrow pointed left and the "m" key with their right index finger if they thought the central arrow pointed right. Flanker arrow direction was congruent (<<<<< or >>>>>) or incongruent (<<><< or >><>>) with the direction of the central arrow. Therefore, there were 4 trial types, two for each condition. Each trial began with a fixation cross presented for 800ms, 1000ms, or 1200ms, followed by presentation of the flanker arrows for 100ms. The central arrow then appeared between the flanker arrows and remained onscreen until the participant responded, but for no longer than 1600ms. Total trial length varied, dependent on the length of the ISI, but was never longer than 2900ms. RT was measured as the time from target onset to when participants pressed a button. Error responses were recorded in the same way as in the automatic imitation task.

In this experiment, we addressed an additional, unrelated question. As such, on half of the congruent trials, and half of the incongruent trials, the flanker arrows changed direction during the trial between their initial presentation and presentation of the central target arrow. In the current study, we are interested in the basic congruent and incongruent RTs, irrespective of whether the flanker arrows changed direction mid-trial. Additionally, there was no interaction between congruency and flanker change ($F(1,195)<0.01$, $p=.954$). As such data are collasped across conditions where flankers change direction and those where flanker direction remains consistent to give an average RT measure for congruent trials and for incongruent trials.

In total there were 64 trials presented in one continuous block. On 32 trials the flanker and the target arrows were congruent and on 32 trials they were incongruent. Pseudorandomisation permitted no more than 4 identical trials to occur consecutively.

Procedure

Participants completed the imitation task and the flanker task. Before each task, participants completed a 10-trial practice to ensure they understood the task instructions. The tasks were administered on four desktop computers in separate rooms, or in groups of up to eight participants on laptops that were arranged in a row with space between adjacent participants. Participants were monitored so that no interaction took place between them while they completed the tasks.

Testing was conducted across twelve computers in total and both tasks were presented to participants using Psychophysics Toolbox, running in MATLAB. Based on prior work (Butler et al., 2015), we did not expect differences in RT across computers. A 2 (task: imitation, flanker) x 2 (congruency: congruent, incongruent) x 12 (computer) ANOVA showed no effect of computer, no computer*task interaction, and no computer* task*congruency interaction (all F's<1.21, all p's>.286). Therefore, all analyses were performed on data collapsed across the computers used.

Data analysis

Participants were removed if they were >3SD from the group mean accuracy or RT for congruent or incongruent trials on either task, and only correct trials were included in further analyses. For the automatic imitation and flanker tasks, separate interference effects were calculated by subtracting RT on congruent trials from RT on incongruent trials. For both tasks, first we ensured that there was a basic interference effect such that incongruent trials elicit greater RT than congruent trials. Interference effects were assessed separately for each task using paired sample t-tests on accuracy and RT to compare congruent and incongruent trials. In addition, a correlation was conducted in order to assess whether there is a relationship between interference effects on the two tasks.

We then assessed sex differences on both tasks. Sex difference analyses were conducted in a manner consistent with previous work (Butler et al., 2015). For each task, separate multiple regression analyses were set up to assess the predictive ability of mean RT, sex, and the mean RT*sex interaction on automatic imitation and flanker interference effects. Mean RT was centered by subtracting the group mean RT from each participant's mean RT, sex was coded as negative one for male participants and positive one for female participants, and the mean RT*sex interaction term was computed by multiplying each participants mean deviated mean RT with their sex. Multiple regression analyses tested whether sex predicts the level of interference experienced in each task, whilst controlling for the influence of mean RT and a mean RT*sex interaction.

Results

Interference effects

On the automatic imitation task, participants were significantly more accurate (t(181)=13.93, p<.001, Cohen's d_z=1.03)[3] on congruent trials (M: 97.48; SE: 0.41) than incongruent trials (M 89.43; SE: 0.70). Participants were also significantly faster (t(181)=-28.10, p<.001, Cohen's d_z=2.09) on congruent (M: 486.85; SE: 5.55) compared to incongruent trials (M: 579.22; SE: 7.30).

On the flanker task, participants were significantly more accurate (t(181)=8.99, p<.001, Cohen's d_z=0.67) on congruent trials (M: 97.92; SE: 0.29) than incongruent trials (M: 92.98; SE: 0.63). Participants were also faster (t(181)=-27.33, p<.001, Cohen's d_z=2.03) on congruent (M: 427.05; SE: 3.97) compared to incongruent trials(M: 491.87; SE: 4.41).

The correlation analysis showed a significant positive correlation (r(181)=.23, p=.002) showing that interference effects for both tasks are related, and that those participants who experience greater interference in one task, also experience greater interference in the other task.

Sex differences

Multiple regression analyses are displayed in Figure 4.2.. Results for the imitation task model shows that it significantly accounts for variance in interference in the automatic imitation task (F(3,161)=30.76, p<.001, R^2=.364). Additionally, mean RT (B=0.25, SEB=0.03, t(161)=7.56, p<.001, f^2=0.43), sex (B=6.84, SEB=2.91, t(161)=2.35, p=.020, f^2=0.03), and the mean RT*sex interaction (B=0.11, SEB=0.03, t(161)=3.30, p<.001, f^2=0.12) all significantly predict interference on the automatic imitation task. As illustrated in Figure 4.2., the positive beta weight for mean RT shows that interference is greater for individuals with a slower mean RT. Additionally, the positive beta weight for sex shows that women experience greater interference than men on the automatic imitation task. Finally, the interaction shows that the sex difference is greater for individuals with slower compared to faster mean RTs. Further replicating the results

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[3] Cohen's d_z is a within groups measure of effect size calculated according to procedure outlined in Lakens (2013).

from Butler et al. (2015), we find that the effect size for mean RT is considered large and the effect size for participant sex is considered small (Cohen, 1992). In addition, the effect size of the mean RT*sex interaction is considered small although nearing medium (Cohen, 1992).

Results for the flanker task model shows that it is trending towards significantly accounting for variance in interference in the flanker task (F(3,161)=2.31, p=.078, R^2=.041). Within this model, mean RT (B=0.11, SEB=0.05, t(161)=2.31, p=.022) significantly predicts interference on the flanker task. However, sex (B=1.40, SEB=2.71, t(161)=0.52, p=.605), and the mean RT*sex interaction (B=0.01, SEB=0.05, t(161)=0.18, p=.859) do not significantly predict interference on the flanker task. As illustrated in Figure 4.2., interference is greater for individuals with a slower mean RT. However, women do not show greater interference than men on the flanker task even in individuals with a slower mean RT.

Figure 4.2. – Experiment 1 multiple regression analyses

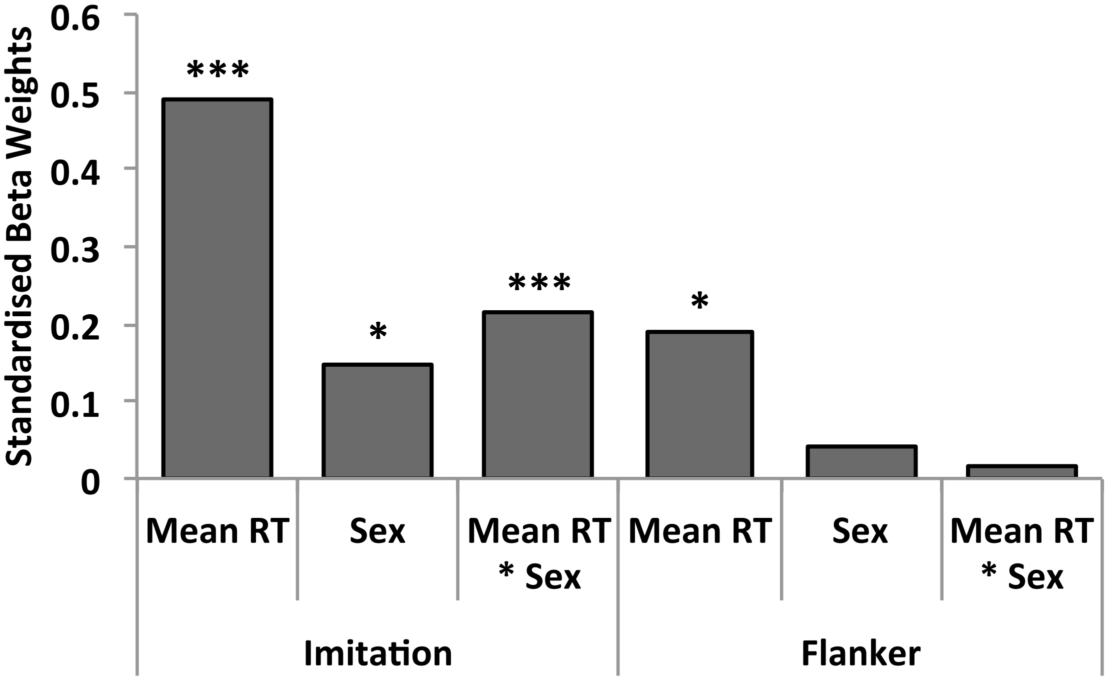


Figure 4.2. The standardised beta weights showing the predictive ability of each factor within the imitation task model and the flanker task model. In both models, task specific mean RT is a significant positive predictor of interference experienced in each task showing that as mean RT increases the interference effect increases. Sex and the mean RT*Sex interaction predict imitation interference, but not flanker interference. Sex was

coded as negative one for male and positive one for female participants. Thus the positive beta weights for sex on the imitation task shows that female participants experienced greater interference than male participants. * = p<.05, *** = p<.001.

Discussion

Results from Experiment 1 provide a replication of our previous finding that there is a sex difference in the inhibition of automatic imitation (Butler et al., 2015). Specifically, women experience greater interference to performance than men when inhibiting automatic imitation of others actions. This effect appears relatively robust: Butler and colleagues (2015) showed the effect in a sample of 230 participants whilst controlling for mean RT and a range of stable trait personality variables and here we replicate the effect in a sample of 165 participants, whilst also controlling for mean RT.

Results from the flanker task do not show the predicted sex difference, such that women would show greater interference than men (Clayson et al., 2011; Stoet, 2010). However, compared to previous work there were fewer flanker trials per condition in the current study. We had 32 congruent and 32 incongruent trials, whereas Stoet (2010) had 120 and Clayson et al. (2011) had 450 of each. Therefore, we suggest the most likely explanation for the lack of sex difference in the flanker task is a lack of precision in our estimate. As such, we are cautious to interpret this null result and may expect to replicate prior work with a greater number of trials and a more precise estimate of the effect.

Taking these findings together with prior work (Table 4.1.), there is growing evidence that aspects of inhibitory control differ between the sexes. Importantly, not all inhibitory control tasks produce the same sex differences. Stroop tasks show the opposite pattern: greater interference for men than women (Baroun & Alansari, 2006; Van der Elst et al., 2006). Thus, it is not the case that females exhibit more interference on all inhibitory control tasks. Rather, based on current evidence, females exhibit more interference than men in tasks that have a central target with a peripheral distractor (imitation, gaze-cueing, arrow-cueing, flanker), as well as in odd-ball tasks.

Although sex differences have been shown in a variety of inhibitory control tasks, the neural underpinnings of these sex differences are largely unknown. For instance, it is currently not known how brain circuits that control sex differences in the inhibition of imitation compare to nonsocial inhibitory control tasks. In Experiment 2, we use fMRI to investigate neural differences between men and women during automatic imitation and flanker tasks.

Experiment Two

Introduction

Experiment 2 uses fMRI to investigate regional brain reponses across men and women during automatic imitation and flanker tasks. Two brain networks are likely candidates to underpin sex differences in the inhibition of automatic imitation compared to inhibition of non-social conflict. First, right temporoparietal juntion (rTPJ) and medial prefrontal cortex (mPFC) have been associated with inhibiting automatic imitation across fMRI (Brass et al., 2005, 2009; Klapper et al., 2014), TMS (Santiesteban et al., 2012b) and patient studies (Brass et al., 2003; Spengler et al., 2010). Based on the dissociable roles of these two regions during the inhibition of imitation (Brass et al., 2009), a sex difference in rTPJ might suggest that female participants experience greater interference when separating self- from other- generated actions, whereas a sex difference in mPFC might suggest that female participants experience greater interference when enforcing their own action whilst observing an incongruent action.

A second brain network comprises parietal, and dorsolateral and medial frontal cortices, and has been associated with inhibiotry control across a range of tasks (Bunge et al., 2002; Hazeltine et al., 2007; Nee et al., 2007; Wager et al., 2005). In these regions, we distinguish between two possible hypotheses. First, if the sex difference in automatic imitation represents a general difference in interference control between women and men, then engagement of this network should not be dissociable from a sex difference on the flanker task. Second, if the sex difference in automatic imitation is dissociable from a sex difference on the flanker task then it would suggest that inhibition of imitation in women involves a specialised use of brain systems that are engaged in general cognitive control (Baetens et al., 2014; Spunt & Adolphs, 2015). Based on the functional roles of areas in this network, a sex difference in parietal areas might suggest that female participants recruit these areas to a greater extent in order to maintain a representation of possible responses compared to male participants during the automatic imitation task, whereas a sex difference in frontal areas might suggest that female participants recruit these areas to a greater extent when selecting among competing response alternatives and inhibiting possible incorrect responses (Bunge et al., 2002; Hazeltine et al., 2007; Nee et al., 2007; Wager et al., 2005).

As demonstrated by our effect size analyses in Experiment 1 and in Butler et al. (2015), the sex difference in automatic imitation is a small or small-to-medium effect size. Due to the high cost of scanning which typically restricts fMRI sample sizes to less than 30 participants we consequently do not expect to be able to detect behavioural sex differences during scanning. However, prior work as well as the results of Experiment 1, show that sex differences in inhibitory control are relatively robust. Sex differences in inhibitory control have been reported in relatively large sample sizes, across different laboratories and using different tasks (Table 4.1.). Ultimately, therefore, such distal behavioural effects must have a proximal neural correlate on some level of brain organisation (Yarkoni, 2014). In other words, there is good evidence that neural circuits supporting inhibitory control differ between men and women, and we aim to measure regional brain responses that support this difference with fMRI.

Method

Participants

Twenty-eight Bangor University students (14 male, 14 female; M_{age}=23.96, SD=5.52) participated for monetary compensation of £15. Due to the lower sample size in Experiment 2 compared to Experiment 1, task performance requirements were less strict and subjects were removed if their accuracy on congruent or incongruent trials for either task was <80%. Seeing as the exclusion criteria were adjusted, we reanalyzed Experiment 1 data with the new exclusion criteria (<80% accuracy) and there was minimal difference in the outcome of analyses. As such, we continued to use the <80% accuracy exclusion criteria here. Based on this exclusion criteria, four participants were removed from analyses that include the flanker task as their accuracy on this task was less than 80%. Therefore, there are twenty-four participants (12 male, 12 female; M_{age}=24.21, SD=5.91) in analyses involving the flanker task. Participants provided written informed consent, reported no history of neurological damage, and ethical approval was granted by the Research Ethics and Governance Committee of the School of Psychology at Bangor University.

Automatic imitation task

The same task was used as in Experiment 1, with two changes. First, no faces were presented. Second, the target hand image remained on screen until 2000ms irrespective of when during the 2000ms period participants made their response.

There were four trial types in an event-related design. Two trial types were congruent, whereby participants were cued to lift their index finger and simultaneously observed an index finger lift, or were cued to lift their middle finger and simultaneously observed a middle finger lift. Two trial types were incongruent, whereby participants were cued to lift their index finger and simultaneously observed a middle finger lift, or were cued to lift their middle finger and simultaneously observed an index finger lift. In event-related fMRI designs, to separately model the influence of events that are presented close together in time, jitter between trials can be introduced and events can be ordered in such a way that each condition precedes each other equally often (Josephs & Henson, 1999; Wager & Nichols, 2003). In the current experiment the four trial types were pseudorandomised in such a way that each trial type was preceded by itself and each other trial type an equal number of times. There were 17 trials per block, with the first trial of each block being used to set up the randomisation sequence. The first trial of each block was discarded because unlike all other trials it was not preceded by any other trial. The remaining 16 trials of each block were analysed, half of which were congruent and half of which were incongruent. There were five blocks within one scanning session, with a fixation cross presented for a random duration of 3, 4, or 5 seconds between each block. In total there were 80 trials of interest (40 congruent and 40 incongruent).

Flanker task

Trial structure was the same as in Experiment 1 with two changes. First, the target screen, on which the central arrow was presented, was onscreen for 2000ms irrespective of when during the 2000ms period participants made their response. Second, flanker arrows did not change direction between their initial presentation and presentation with the central arrow. Block structure and pseudorandomisation were the same as in the fMRI version of the automatic imitation task. There were five blocks of 17 trials, 16 trials of interest per block, half of which were congruent and half of which were incongruent.

Procedure

Participants completed an 8-trial practice on both tasks outside of the fMRI scanner before being taking into the scanner to complete the full automatic imitation and flanker tasks. Task order was counterbalanced across participants. Of the 24 participants that are included in analyses involving the flanker task, 13 participants did the automatic imitation task first and 11 participants did the flanker task first. The automatic imitation and flanker tasks were intersped with runs of three additional tasks that assessed questions unrelated to the current study.

Image acquisition

Images were acquired using a 3 Tesla Philips Achieva MRI scanner using a SENSE 32 channel phased-array head coil. Participants were requested to keep their heads as still as possible throughout scanning and were provided with a foam pillow and padding to help minimise head movement. Participants responded on both tasks using a button box that allowed recording of RT. Stimuli were displayed on a screen behind the scanner, viewable by participants via a mirror attached to the head-coil.

During functional scans images were collected using a T2*-weighted gradient echo planar imaging sequence with the following parameters: repetition time (TR) = 2000ms; echo time (TE) = 30ms; flip angle = 90°; number of axial slices = 35; slice thinkness = 4mm; slice gap = 0.8mm; field of view = 230 x 230 x 167mm^3. There were 174 volumes collected for the automatic imitation task, and 146 for the flanker task. Four dummy scans were run at the beginning of each task to reduce saturation effects and were excluded from analysis. For the T1-weighted anatomical scan parameters were as follows: TR = 12ms; TE = 3.5ms; flip angle = 8°; number of axial slices = 170; voxel dimensions = 1mm^3; field of view = 250 x 250 x 170 mm^3.

Data analysis

Participants were removed if they were <80% accurate on congruent or incongruent trials for either task and only correct trials were included in the analyses. Behavioural data were analysed in the same way as in Experiment 1. However, due to the small or small-to-medium effect size of the sex difference (Experiment 1; Butler et al., 2015), we do not expect to have a precise enough estimate of the behaviour in 28 participants to observe the sex difference in Experiment 2.

Head motion was examined for each participant on each task, with an exclusion criteria if displacement across either task exceeded 3 millimeters. No participant's head motion exceeded this threshold, thus no participants were removed on the basis of head motion. fMRI data were analysed with Statistical Parametric Mapping software (SPM8; Wellcome Trust Department of Cognitive Neurology, London, UK: www.fil.ion.ucl.ac.uk/spm/). Data were realigned, unwarped, corrected for slice timing, and normalised to the MNI template with a resolution of $3mm^3$. Images were then spatially smoothed (8mm). Separately for the two tasks, a design matrix was fitted for each participant with four regressors: congruent trials, incongruent trials, first trial from each block, and error trials. First trials and error trials were not analysed further, thus all analyses are performed on correct trials of interest only. Stimulus onsets were time-locked to the presentation of the number cue in the automatic imitation task, or to presentation of the central target arrow in the flanker task, with a zero second duration and convolved with a standard hemodynamic response function.

Imaging analyses were designed to achieve two primary objectives:

1) Interference effects: First, we aimed to identify clusters showing both imitation interference and flanker interference. Interference contrast images (incongruent > congruent) were calculated at the single-subject level separately for each task. Then group level contrast images were created from the single subject interference contrast images to identify clusters showing interference consistently across the sample for the automatic imitation task, and then for the flanker task. To identify brain areas of common interference in both tasks, we overlaid the group level imitation task contrast with the group level flanker task contrast on a template brain. This form of conjunction analysis identifies engagement of common voxels in two independent contrasts.

***2) Sex differences in automatic imitation*:** Second, we aimed to identify a neural signature of the sex difference in automatic imitation. These analyses would identify regions that support a sex difference that is greater in automatic imitation than a non-social inhibitory control task. Therefore, we tested the three way sex*task*congruency interaction. Given that the focus of this analysis was the measure of interference, and how this changes as a function of participant sex and task, the single subject interference contrasts (incongruent > congruent) defined in the first step of the analyses were entered into a group level sex*task ANOVA. The positive interaction of the sex*task ANOVA, [Imitation task: *Female(interference)>Male(interference*)] > [Flanker task: *Female(interference)>Male(interference*)], would show those areas where there is a three-way sex*task*congruency interaction in the direction that we predict.

To help distinguish between possible patterns of three-way interaction, we also calculated two separate congruency*sex interactions, one for the imitation task and one for the flanker task. To do so, a group-level two-sample t-test was run on automatic imitation task data using the single-subject interference contrasts (incongruent > congruent) to find where in the brain this contrast was greater for female than male participants [Imitation task: *Female(interference)* > *Male(interference)*]. The same analysis was also performed on the flanker data [Flanker task: *Female(interference)* > *Male(interference)*].

For all analyses, contrast images were taken to the group level and thresholded using a voxel-level threshold of p < .005 and a voxel-extent of 10 voxels (Lieberman & Cunningham, 2009). Correction for multiple comparisons was performed at the cluster level (Friston et al., 1994) with clusters that survive correction for multiple corrections using a family-wise error (FWE) correction (p < .05) shown in bold font in Table 4.2. and Appendices 3 and 4. Clusters of activity were identified with the SPM Anatomy toolbox (Eickhoff et al., 2005).

Results

Behavioural Results

RT data are presented for the imitation and flanker task in Appendix 3. During the automatic imitation task, participants were significantly faster (t(23)=-9.32, p<.001, Cohen's d_z=1.91) and more accurate (t(23)=2.60, p=.016, Cohen's d_z=0.53) on congruent trials (M_{RT}: 759.62, SE_{RT}: 47.06; $M_{accuracy}$: 99.38, $SE_{accuracy}$: 0.23) compared to incongruent trials (M_{RT}: 837.63, SE_{RT}: 44.51; $M_{accuracy}$: 97.92, $SE_{accuracy}$: 0.58).

During the flanker task, participants were significantly faster (t(23)=-10.04, p<.001, Cohen's d_z=2.05), but not more accurate (t(23)=1.37, p=.185, Cohen's d_z=0.28) on congruent trials (M_{RT}: 466.10, SE_{RT}: 24.31; $M_{accuracy}$: 99.38; $SE_{accuracy}$: 0.27) compared to incongruent trials (M_{RT}: 533.59, SE_{RT}: 22.45; $M_{accuracy}$: 98.44; $SE_{accuracy}$: 0.56).

Multiple regression analyses showed that mean RT, sex, and the mean RT*sex interaction do not predict interference effects in either the automatic imitation task or the flanker task (all p's for t-test of beta weights >.165). As such, in a sample of 28 participants in the fMRI experiment, we were unable to detect behavioural sex differences in imitation or flanker tasks. This was expected due to the small or small-to-medium effect size of this sex difference (Experiment 1; Butler et al., 2015). However, in studies with more precise estimates of sex differences in inhibitory control, the effect is consistently shown (Table 4.1.). As such, there is good evidence that recruitment of neural circuits involved in inhibitory control may differ between men and women, and the proximal neural correlates of this behavioural effect are still unknown.

fMRI Results

1) Interference effects: Interference effects (incongruent > congruent) were observed in dorsomedial frontal and bilaterally in dorsolateral frontal and parietal areas for the imitation task (Appendix 4.A.) and bilaterally in dorsolateral frontal and parietal cortices for the flanker task (Appendix 4.B.). When displayed on a common brain template, these interference effects overlapped bilaterally in dorsolateral frontal and parietal cortices (Figure 4.3.; page 98). This shows that both tasks do recruit common inhibitory control regions, supporting the idea that they are, at least in part, tapping into similar inhibitory control mechanisms.

2) Sex differences in automatic imitation: The sex*task*congruency interaction revealed clusters in predicted brain regions including dorsolateral and dorsomedial frontal cortices (Table 4.2.A. and Figure 4.4.; pages 99 and 100 respectively). Illustration of parameter estimates shows that the pattern of response within these regions reveals greater interference for female participants compared to male participants on the automatic imitation task more than the flanker task (Figure 4.4.).

Figure 4.3. – Overlapping brain regions for imitation and flanker interference effects

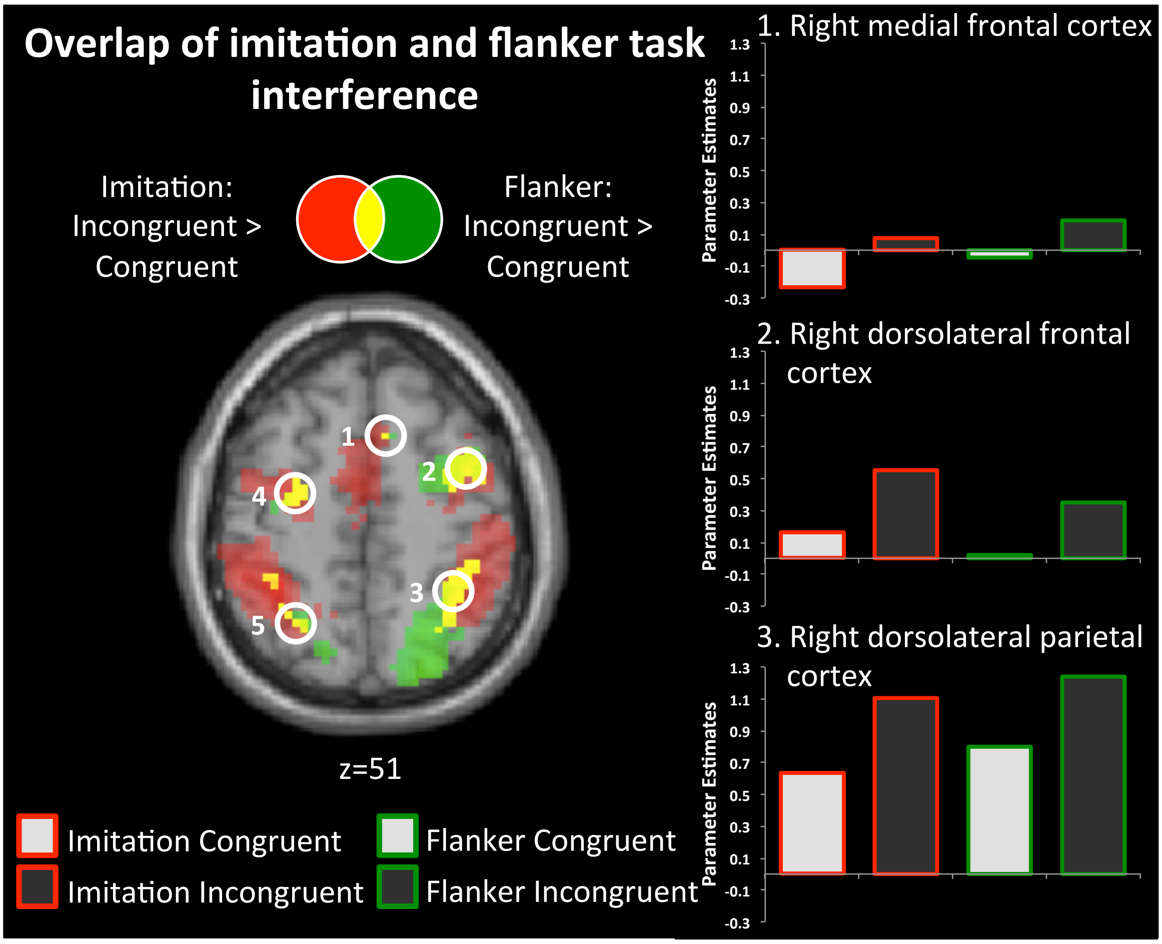


Figure 4.3. Coordinates for each region of overlap between the imitation task and flanker task are as follows: Cluster 1: Medial frontal cortex (x = 9, y = 16, z= 51); Cluster 2: Right dorsolateral frontal cortex (x = 41, y = 5, z = 51); Cluster 3: Right parietal cortex (x = 37, y = -46, z = 51); Cluster 4: Left dorsolateral frontal cortex (x = -26, y = -6, z = 51); Cluster 5: Left parietal cortex (x = -29, y = -57, z = 51). All clusters show both imitation and flanker task interference effects. For visualisation purposes parameter estimates have been extracted from a 4mm sphere from each region of overlap for medial and right hemisphere clusters.

Table 4.2. Brain regions supporting the sex*task*congruency interaction, and those that survive masking by the sex difference in automatic imitation interference

				Montreal Neurological Institute coordinates		
Region	Cluster Size	P FWE Corr	t-value	x	y	z
A) Sex*Task*Congruency interaction						
L Middle Frontal Gyrus	109	0.220	4.76	-21	8	40
L Inferior Frontal Gyrus			4.36	-30	5	31
L Postcentral Gyrus	**473**	**<0.001**	**4.47**	**-36**	**-22**	**46**
L Precentral Gyrus			**3.88**	**-30**	**-16**	**43**
R Posterior-medial Frontal			**3.85**	**9**	**-19**	**58**
R Precentral Gyrus	129	0.134	4.08	24	-13	73
R Precentral Gyrus			3.93	42	-10	52
R Precentral Gyrus			3.80	30	-16	55
R Postcentral Gyrus	23	0.991	3.59	48	-4	22
R Supramarginal Gyrus			3.50	42	-13	25
L Inferior Frontal Gyrus	22	0.993	3.52	-36	26	19
R Superior Frontal Gyrus	40	0.900	3.51	21	41	49
Cerebellar Vermis (6)	40	0.900	3.47	0	-70	-8
R Cerebellum (VI)	18	0.998	3.35	18	-55	-20
L Middle Occipital Gyrus	13	1.000	3.17	-27	-82	13
L Superior Frontal Gyrus	19	0.997	3.16	-21	35	49
L Cerebellum (IV-V)	14	0.999	3.09	-24	-31	-32
B) Sex*task*congruency interaction inclusively masked by Imitation sex difference: Female(interference) > Male(interference)						
L Postcentral Gyrus	97	0.295	4.47	-36	-22	46
L Precentral Gyrus			3.88	-30	-16	43
L Postcentral Gyrus			3.61	-24	-31	52
L Posterior-medial Frontal	19	0.997	3.73	-9	-16	55
L Middle Frontal Gyrus			3.23	-18	-16	55
R Posterior-medial Frontal	12	1.000	3.54	9	-13	58

Table 4.2. Regions surviving a voxel-level threshold of p<.005 and 10 voxels are reported for the sex*task*congruency interaction **(A)** and for the sex*task*congruency interaction masked inclusively by the automatic imitation only sex*congruency interaction **(B)**. Subclusters at least 8 mm from the main peak are listed. Bold font indicates clusters that survive correction for multiple corrections using a family-wise error (FWE) correction (p < .05).

Figure 4.4. – Brain regions supporting the sex*task*congruency interaction

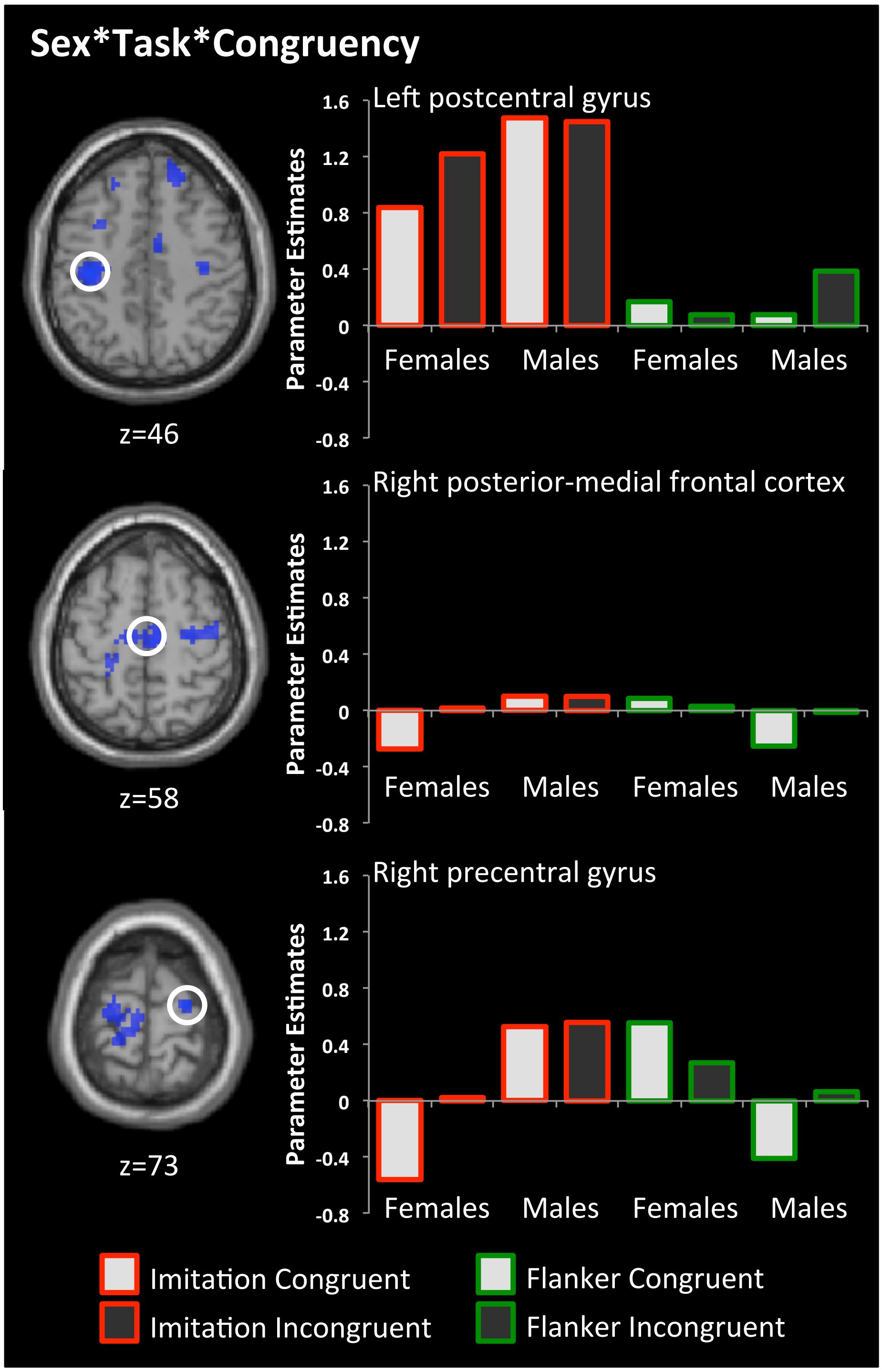


Figure 4.4. Sex*Task*Congruency contrast defined as [Imitation task: *Female(interference)* > *Male(interference)*] > [Flanker task: *Female(interference)* > *Male(interference)*] in order to identify regions that support a sex difference that is greater in automatic imitation than a non-social inhibitory control task. Left postcentral gyrus (x = -36, y = -22, z = 46); Right posterior-medial frontal cortex (x = 9, y = -19, z = 58); Right precentral gyrus (x = 24, y = -13, z = 73). To illustrate the pattern of response within regions, parameter estimates were extracted from a 4mm sphere from relevant peaks and subpeaks identified by the three-way task*sex*congruency analysis.

To help further distinguish between possible patterns of three-way interaction, we inclusively masked the three-way interaction result by the sex*congruency interaction for automatic imitation. This masking procedure ensures that clusters observed in the three-way interaction also show the predicted pattern of interaction for the sex*congruency interaction such that women show greater interference than men for the imitation task. Following this analysis, clusters emerged in left dorsolateral frontal cortex and dorsomedial frontal regions (Table 4.2.B.). To help visualise these results, we overlaid the sex*task*congruency interaction and the sex*congruency interaction for imitation (Appendix 5.A.) on a template brain (Figure 4.5.). As depicted in Figure 4.5., the location of these frontal clusters span posterior dorsolateral and dorsomedial frontal cortices, comprising posterior middle frontal gyrus around premotor cortex. In contrast, the sex*congruency interaction for the flanker task revealed no suprathreshold clusters (Appendix 5.B.). Thus, these data show that during the inhibition of automatic imitation for women more than men there is additional recruitment of a broader frontal brain network, one that extends posteriorly in frontal cortex.

Figure 4.5. – Overlap between the Sex*Task*Congruency interaction and the Sex*Congruency interaction in automatic imitation

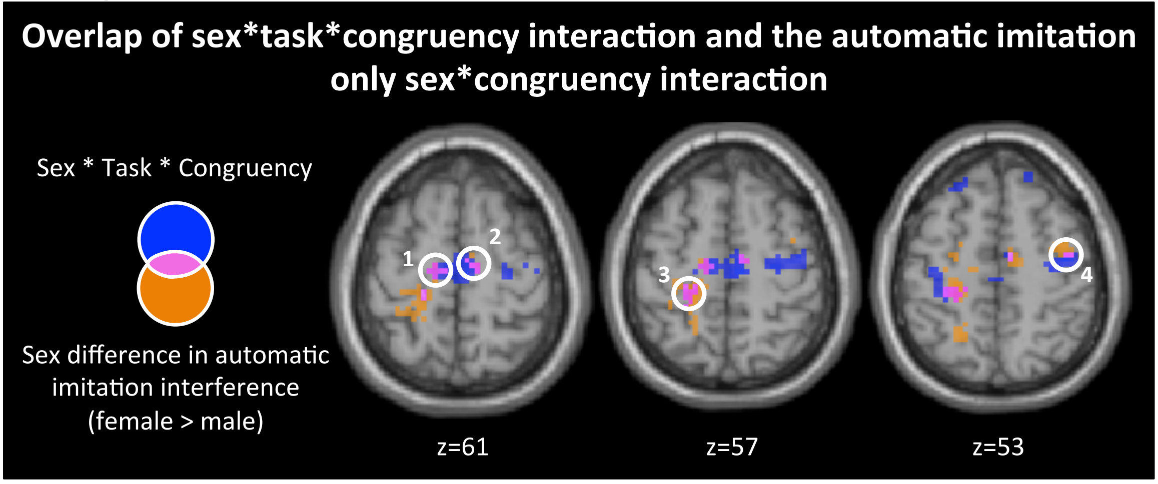


Figure 4.5. Visualisation of regions that overlap in the sex*task*congruency interaction contrast defined as [Imitation task: *Female(interference)* > *Male(interference*)] > [Flanker task: *Female(interference)* > *Male(interference*)] and the sex*congruency contrast for the automatic imitation task only defined as [Imitation task: *Female(interference)* > *Male(interference*)]. This highlights regions where the three-way interaction is also showing the predicted sex difference in automatic imitation. Coordinates for each region of overlap are as follows: Cluster 1: Left posterior-medial frontal cortex (x = -12, y = -16, z = 61); Cluster 2: Right posterior-medial frontal cortex

(x =12, y =-14, z = 61); Cluster 3: Left postcentral gyrus (x = -21, y = -32, z = 57); Cluster 4: Right precentral gyrus (x = 44, y = -8, z = 53).

Despite rTPJ showing the simple imitation interference effect (Appendix 4), which is consistent with prior work (Brass et al., 2003, 2005, 2009; Klapper et al., 2014; Santiesteban et al., 2012b; Spengler et al., 2010), there was no three-way interaction or two-way interaction in mPFC nor TPJ.

Discussion

Cognitive processing differences between men and women are well documented in the domain of inhibitory control (Bayliss et al., 2005; Butler et al., 2015; Clayson et al., 2011; Rubia et al., 2010; Stoet, 2010). However, little is currently known regarding sex differences in the neural systems that support inhibition of automatic imitation. In a previous behavioural study, we have shown that women have a greater tendency to automatically imitate than men (Butler et al., 2015). In the present study we investigate the neural signature of this sex difference and compare it to a non-social inhibitory control task. In Experiment 1 we use behavioural methods to support the idea that there are cognitive processing differences between men and women by replicating the sex difference in the inhibition of automatic imitation. In Experiment 2 we use fMRI to gain insight into the neural architecture supporting this sex difference and find that posterior dorsolateral and dorsomedial frontal cortices show a specialised response in two ways. First, women recruit these frontal areas to a greater extent when overcoming interference in the automatic imitation task compared to men. Second, this sex difference in the control of automatic imitation is greater than in the flanker task. This suggests that the sex difference in automatic imitation is not indicative of general inhibitory control differences between women and men. Rather, it suggests that these brain regions show a specialised response, one that shows a sex bias in a particular type of inhibitory control.

Sex differences in inhibitory control

The vast majority of cognitive science has focused on a neat division between domain-general and domain-specific mental operations (Hirschfeld & Gelman, 1994; Kanwisher, 2010). In a similar vein, engagement of a dorsal frontoparietal circuit has been identified across a number of different inhibitory control tasks (Bunge et al., 2002;

Hazeltine et al., 2007; Nee et al., 2007; Wager et al., 2005), whereas mPFC and rTPJ have been shown to respond more specifically during social inhibitory control (Brass et al., 2003, 2005, 2009; Klapper et al., 2014; Santiesteban et al., 2012b; Spengler et al., 2010). In the current study, we break from this neat division of labour between general and specific systems, and show specialised engagement of what is typically considered a domain-general cognitive and neural architecture. Therefore, we add to growing evidence for higher complexity within domain-general and domain-specific systems (Baetens et al., 2014; Spunt & Adolphs, 2015; Quadflieg et al., 2011; Zaki et al., 2010). Indeed, brain regions may be responsible for both social and non-social processes (Baetens et al., 2014; Spunt & Adolphs, 2015), as well as regulate functional interplay between general and specific circuits (Baldauf & Desimone, 2014; Quadflieg et al., 2011; Zaki et al., 2010).

Any account of the cognitive processes that underpin these results has to explain how inhibitory control varies between sexes (female > male) and domain (social > non-social). Indeed, general differences in inhibitory control between men and women or between tasks could not explain our results. A general sex difference in inhibitory control, for example, should operate in both tasks. Instead, based on differences between the tasks, we propose that the engagement of posterior frontal cortices is a product of differences in encoding the observed action between men and women, which leads to differences in inhibition. That is, through enhanced encoding of the social stimulus compared to a non-social stimulus, women require greater inhibitory control to resist the propensity to automatically imitate. Previous evidence provides support for this idea. Sex differences have been observed in the mirror neuron system (MNS), which comprises regions that are active during both execution and observation of actions (Rizzolatti & Craighero, 2004). Activity in MNS regions was greater in women than men (Cheng et al., 2006, 2007, 2008), and this sex difference was greater when observing a hand action than when observing a moving dot (Cheng et al., 2007, 2008). This suggests that women might indeed represent another's action, or social stimuli generally, more strongly than men. Future research is necessary to further test this proposal. Additionally, during inhibitory control tasks, many studies support the view that parietal regions represent possible responses whereas frontal regions select between response possibilities and inhibit possible incorrect responses (Bunge et al., 2002;

Hazeltine et al., 2007; Iacoboni et al., 1998; Nee et al., 2007; Praamstra et al., 1999; Wager et al., 2005). Consequently, a more salient action representation in women would result in greater difficulty selecting between competing responses on incompatible trials, which would recruit frontal cortex more. However, in order to fully understand the exact cognitive processes that are responsible for the sex difference in automatic imitation further work will be required.

Based on prior work showing functional interactions between domain-general and domain-specific brain circuits (Baldauf & Desimone, 2014; Quadflieg et al., 2011; Zaki et al., 2010), it is also possible that these results could be explained by differences in how frontal inhibitory control circuits bias responses within social processing circuits. However, future functional connectivity studies would be required to directly investigate this hypothesis.

A possible limitation to these interpretations is that the results reflect non-social rather than social differences between the tasks. As with the social interpretation of the cognitive processes that underpin these results, any non-social interpretation would also have to explain how inhibitory control varies between both the sex (female > male) and domain (social > non-social). We find no evidence for this being the case. Behavioural data collected during scanning showed that the size of interference is equivalent between the two tasks and sexes. Thus, we can rule out an account of our findings based on task difficulty and “time on task”. Additionally, prior work has shown no sex by task difficulty interaction and thus there is no suggestion that sex differences in cognitive control emerge only when processing demands are high (Gur et al., 2000; Speck et al., 2000; Wei et al., 2013). The remaining non-social difference between the two tasks is the type of spatial interference. The automatic imitation task is in the vertical orientation and the flanker is in the horizontal orientation. Although possible, there is no *a priori* reason why women more than men would engage portions of frontal cortex to resolve spatial conflict in a vertical than horizontal interference task. Moreover, females show greater interference than males when interference tasks are in the horizontal domain (e.g., gaze and arrow-cueing, oddball; Table 4.1.). Therefore, although possible, it seems unlikely that this interpretation would account for the pattern of results observed in the current study.

Methodological implications for studying individual differences in automatic imitation

Given on-going concerns over a lack of replication in psychology and neuroscience (Button et al., 2013; Pashler, et al., 2012; Shanks, et al., 2013; Simmons et al., 2011), a methodological strength of the current study is the use of a large behavioural dataset in combination with an fMRI study. This approach helps to mitigate problems of low sample size and high expense in fMRI studies of individual differences (Yarkoni, 2014), thus enhancing the use of fMRI to shed light on cognitive processes. For instance, in the present study, our fMRI result would be more speculative if it were not paired with a large sample behavioural study that shows the behavioural effect and adds weight to interpretation of neural differences revealed by fMRI. As such, we encourage future research investigating individual differences to adopt this approach when examining the neural correlates of an effect that may not be observed behaviourally in a typical fMRI sample.

CHAPTER 5

GENERAL DISCUSSION

The studies comprising this thesis have examined automatic imitation, a socially important nonverbal behaviour, using a combination of behavioural and neuroimaging approaches. In the first empirical chapter (Chapter 2) I provided characterisation of the role of facial signals from an interaction partner as antecedents to automatic imitation behaviour. In Chapters 3 and 4 I investigated the relationship between one's own stable characteristics and automatic imitation using large sample behavioural and neuroimaging (fMRI) approaches. In the following, a brief summary section will recap the main findings from each empirical chapter before I proceed to outline implications for the field of imitation research and social cognitive neuroscience more generally. Finally I will suggest methodological implications, and directions for future research.

5.1. Summary of findings

In Chapter 2, I investigated the role of facial signals as antecedents to imitation. Facial signals varied on two dimensions: cue type and valence. I showed that positive emotional expressions increased imitation behaviour relative to an emotionally neutral face. By contrast, there was no influence of facial cues to the stable personality characteristic of agreeableness on automatic imitation. This is the first study to investigate the influence on automatic imitation of facial signals to an interaction partner's stable personality characteristics. The contrast between the influence of facial cues to transient emotional state compared to stable personality characteristics suggests that automatic imitation mechanisms are more sensitive to transient facial cues that provide information regarding an interaction partners likely behaviour in the current interaction, rather than facial cues to an interaction partners likely behavioural disposition more generally.

In Chapters 3 and 4, using large sample behavioural studies and an fMRI study, I investigated the relationship between one's own stable personality characteristics and imitation behaviour. In Chapter 3 I tested the hypothesis that individual differences in stable personality or subclinical characteristics would predict variance in automatic imitation behaviour using multiple regression and a large sample (N=230). Results showed that stable personality characteristics, which were hypothesised to influence automatic imitation, were not related to variation in imitation behaviour. However, there was an unexpected sex difference such that women demonstrated greater automatic imitation than men. Following up this result in Chapter 4, I replicated the sex difference in automatic imitation behaviour in a large behavioural sample (N=165) and identified the neural architecture supporting this sex difference in imitation (N=28). I showed that a posterior part of dorsolateral and dorsomedial frontal cortices were recruited more by women than men during automatic imitation, and this sex difference was greater during automatic imitation than during a non-social inhibitory control task. The results from Chapters 3 and 4 suggest that imitation is resistant to individual differences in one's stable personality characteristics, but is different between women and men.

Taken together, the key results from my thesis suggest that imitation is sensitive to transient emotional cues from other people's faces, but resistant to signals of stable traits. In addition, automatic imitation is resistant to individual differences in one's own stable personality characteristics, such as empathy, narcissism, or agreeableness, whilst being greater in women than men. Implications of these findings will now be discussed.

5.2. Implications for imitation and social cognition

5.2.1. Is there really no relationship between imitation and stable personality trait features?

I investigated the relationship between imitation and stable personality features in two ways: in terms of facial signals from an interaction partner's face and in terms of individual differences in one's own stable personality characteristics. In both cases I found no modulating influence of stable personality characteristics on automatic imitation. This would suggest that the mechanism that is controlling automatic imitation is really sensitive only to transient "in-the-moment" cues about a current social interaction. However, given the social consequences of automatic imitation, including building affiliative bonds and rapport between interacting individuals (Chartrand & Bargh, 1999; Chartrand & Lakin, 2003; Stel & Vonk, 2010; van Baaren et al., 2009), and the assumption that one would benefit more from building links with more prosocial individuals, this requires further investigation.

Two caveats prevent the conclusion that trait features of an interaction partner do not modulate automatic imitation. First, I investigated only facial signals to agreeableness as this is robustly recognised by observers (Kramer & Ward, 2010; Penton-Voak et al., 2006) and has been associations with other prosocial behaviours (Ashton et al., 1998; Barrio et al., 2004; LePine & van Dyne, 2001). However, there are many other traits that can be accurately perceived by observers that might impact on social interaction behaviour, including facial signals to extraversion or depression (Kramer & Ward, 2010; Penton-Voak et al., 2006; Scott et al., 2013). Second, trait representative facial signals are subtler than emotional expressions; as such, these signals may influence automatic imitation but require more sensitive measures to detect. One way to test this would be to measure more subtle versions of the expressions in order to investigate whether the effect of expressions decreases as they become less potent.

In terms of individual differences in one's own characteristics, I provide a comprehensive test of many traits (Chapter 3). Previous work has only investigated a limited number of stable personality characteristics, including interoceptive awareness, empathy, narcissism, and mirror-touch synaesthesia (Ainley et al., 2014; Chartrand & Bargh, 1999; Hogeveen & Obhi, 2013; Obhi et al., 2013; Santiesteban et al., 2015). Although one of these studies provides control of potentially confounding variables (Ainley et al., 2014), in general I provide a more rigorous test of individual differences as a result of using a large sample and controlling for potentially confounding variables via multiple regression analyses (Cumming, 2014; Maxwell et al., 2008). This is an important methodological strength as it is a preventative measure against interpreting positive effects that might occur by chance as a result of small sample sizes, and we gain a closer approximation of the population parameters (Maxwell et al., 2008). As such, I am confident that individual differences in those stable characteristics that we measured do not relate to one's automatic imitation behaviour, at least not directly.

Although our results appear to point to a conclusive resistance of automatic imitation to one's own stable personality characteristics, given the complexity of social behaviour (Adolphs, 2001) it seems unlikely that individual differences in stable personality traits have absolutely no part to play in automatic imitation behaviour. One way in which individual differences in stable personality characteristics could still impact on automatic imitation is through moderating the impact of other social signals on imitation. For instance, research has shown that individual differences in neuroticism were related to differences in neural connectivity whilst viewing negative compared to neutral valence faces (Cremers et al., 2010). Additionally, increased trait anxiety has been linked to an increased influence of subliminal affective priming by fearful faces when viewing surprise expressions behaviourally and as measured by event-related potentials (Li et al., 2008). These studies indicate that individual differences do indeed moderate the influence of perception of social signals on both behaviour and neural function. It would be interesting to see whether the same moderating effect of one's stable traits exists for the impact of perception of socially important signals on imitation behaviour. One study has recently investigated the extent to which individuals copy the behaviours of a high- or low-status interaction partner and how this is moderated by the individual's level of narcissism (Ashton-James & Levordashka, 2013). Interestingly they report no influence of narcissism on copying behaviour overall, however, narcissism had a moderating effect such that high narcissists copied behaviour of a high-status interaction partner more so than a low-status interaction partner. Therefore it would be interesting to investigate whether, for example, individual differences in anxiety or neuroticism predict modulation of imitation behaviour when facial expression signals are ambiguous. Or whether individual differences in one's autistic-like traits interact with the facilitatory influence of direct eye gaze on automatic imitation.

In sum, our findings indicate no direct relationship between stable personality characteristics and automatic imitation. Despite being a null result, I am confident in these findings given the methodological strengths of our approach. Additionally, there are exciting and interesting avenues still open to explore the impact of facial cues to an interaction partners stable personality characteristics, as well as any potential moderating relationships between one's own stable characteristics and sensitivity of automatic imitation behaviour to external social cues.

5.2.2. What does the sex difference in automatic imitation mean?

One stable characteristic that was related to automatic imitation was not a personality or subclinical factor, but the sex of the participant. The sex difference in automatic imitation appears robust as it replicates across Chapters 3 and 4, with a combined total of 395 participants. Evidence suggests that the sex difference does not impact on automatic imitation via an interaction with any of the stable personality traits that I measured (Chapter 3). Additionally, although the same sex difference is observed across a range of inhibitory control tasks (Chapter 4, Table 4.1.), engagement of posterior frontal cortices is greater for women than men in the inhibition of imitation, and this is greater than in a non-social inhibitory control task. This indicates a sex difference in a specialised response for inhibition of imitation or inhibition in social contexts more generally compared with non-social inhibition (Chapter 4). As with any new finding, the current interpretation remains speculative. However, I will outline several possible interpretations, which future research will have to purse for a more complete understanding.

In Chapter 4 I suggested that if the sex difference is not indicative of a general sex difference in inhibitory control, that women might encode the social stimulus more strongly than the non-social stimulus relative to men. Thus women would require greater inhibitory engagement in the social task in order to resist the tendency to imitate the observed action. In order to evaluate this hypothesis and gain further insight into this sex difference we can ask two questions. First, are there sex differences reported that would support a sex difference in encoding others' actions, for example, do we see a sex difference in brain regions associated with action representation? Second, is this a sex difference in the encoding of social stimuli compared to non-social stimuli more broadly, for example, do women encode more strongly bodies compared to cars, or text describing another's thoughts, intentions, or desires compared to a description of a non-social topic? I evaluate these questions below.

The mirror neuron system (MNS) comprises neural regions that are active when an individual performs an action, but also when they observe an action (Rizzolatti & Craighero, 2004). Greater recruitment of these areas by women compared to men might support the idea that women represent another's action more strongly than men. Indeed, sex differences have been found in these regions during action observation (Cheng et al., 2006, 2007, 2008; Schulte-Rüther et al., 2008). MNS activity was greater in women compared to men when observing bipedal step (Cheng et al., 2007) and when observing hand movements compared to a moving dot, as measured by magnetoencephalography (Cheng et al., 2007) and mu suppression (Cheng et al., 2008). Schulte-Rüther and colleagues (2008) showed that women recruit MNS regions to a greater extent than men when observing emotional facial expressions and evaluating their own or the observed emotion. Taken together, these studies suggest that there are sex differences in brain regions associated with action representation. This provides some support for the idea that women might encode another's actions more strongly than men. Additionally, Cheng et al., (2007, 2008) showed that this sex difference in MNS activation occurred only when viewing hand actions, and not a moving dot condition. This supports our suggestion that that possible encoding differences do not extend to non-social stimuli.

Regarding whether the sex difference in encoding could extend from actions to encoding social stimuli, or social-cognitive abilities more broadly, it has been suggested that women excel across a range of social processes (Baron-Cohen, 2002). However, the investigation of sex differences has long been considered a controversial topic for arguably being based on gender stereotyping rather than empirical evidence (Miller & Halpern, 2014; Russell et al., 2007) and perpetuating the idea that men and women are fundamentally different leading to educational and societal gender biases (Halpern, 2012; Miller & Halpern, 2014). In addition, evidence for sex differences comes primarily from research in children and is mixed in studies with adults (Miller & Halpern, 2014; Russell et al., 2007). For example, in studies of the perception of facial affect, sometimes women are reported to be more accurate generally, whereas other times women are more accurate only for male faces, and sometimes no sex differences are apparent (Campbell et al., 2002; Thayer & Johnsen, 2000; Rahman et al., 2004). These mixed findings may be related to differences in task demands (Miller & Halpern, 2014; Russell et al., 2007). Finding the sex difference in one measure, but not another would provide a way of characterising the sex difference through analyses of task similarities and differences. As such, it would be interesting to investigate the sex difference in automatic imitation using other measures of imitation behaviour, for example measuring copying behaviours in a naturalistic social setting. Additionally, the sex difference in automatic imitation could be assessed in children to investigate whether it is present early in development, or whether it develops at later stages.

In conclusion, further work using a range of tasks is necessary to elucidate the underlying causes and mechanisms of the sex difference in automatic imitation in order more fully understand this sex difference. And even then, what these sex differences "mean" requires careful thought.

> *"Thus, while we can talk about sex differences on various tests, we cannot always interpret what these differences mean"*
>
> (Halpern, 2012)

5.2.3. Domain-general vs. domain-specific division in cognitive neuroscience

The debate regarding the organisation and structure of the brain and its relation to cognitive processes has long been waged (Kanwisher, 2010). Although a consensus was reached that basic sensory and motor functions rely on specific neural regions, the same debate continues regarding how distinct are specific modules for higher-level cognitive processes (Kanwisher, 2010) and for social compared to non-social processing (Adolphs, 2001).

It has been found that specific areas of the brain are preferentially engaged when processing faces (Haxby et al., 2000; Kanwisher et al., 1997; Liu, 2010; Pitcher et al., 2011; Winston et al., 2004), places (Epstein & Kanwisher, 1998), bodies (Downing et al., 2001; Peelen & Downing, 2007), objects (Grill-Spector et al., 2001; Malach et al., 1995), and even thinking about other people's beliefs, intentions, and desires (Ma et al., 2011; Saxe & Kanwisher, 2003). This adds support to the modular view that regions of the brain are specialised for specific processes (Downing et al., 2006; Pitcher et al., 2009;

Yovel & Kanwisher, 2004) and that there is a clear division between domain-specific and domain-general processing (Hirschfeld & Gelman, 1994; Kanwisher, 2010). With particular pertinence to my PhD, within the domain of inhibitory control, medial prefrontal cortex (mPFC) and right temporoparietal junction (rTPJ) have been shown to respond specifically during social inhibitory control (Brass et al., 2003, 2005, 2009; Klapper et al., 2014; Santiesteban et al., 2012b; Spengler et al., 2010) whereas a more general dorsal frontoparietal network shows engagement across a number of inhibitory control tasks (Bunge et al., 2002; Hazeltine et al., 2007; Nee et al., 2007; Wager et al., 2005). As such, it seems that there is a clear division between domain-general non-social and domain-specific social inhibitory control mechanisms.

However, since the first proposal of neural specialisation, opponents have argued against this view (Kanwisher, 2010) and more recently neuroscientists are challenging the strong interpretation of functional specialisation (Adolphs, 2001; Barrett & Satpute, 2013; Kanwisher, 2010; Ochsner & Lieberman, 2001). Questions arise regarding whether the information processing demands for social processes are similar and rely on the same underlying cognitive and neural mechanisms as more general non-social processing (Adolphs, 2001; Frith, 2007; Frith & Frith, 2012). Indeed, recent empirical work suggests higher complexity within, and interactions between, purportedly domain-general and domain-specific neural mechanisms (Baetens et al., 2014; Baldauf & Desimone, 2014; Quadflieg et al., 2011; Spunt & Adolphs, 2015; Zaki et al., 2010). Regions that are considered as specialised for social cognition have been shown to be responsive in non-social tasks (Baetens et al., 2014; Spunt & Adolphs, 2015) and regions involved in more general processes have been suggested to functionally interact with more specialised social processing regions in order to direct processing to the appropriate specialised system (Baldauf & Desimone, 2014; Quadflieg et al., 2011; Zaki et al., 2010).

If taking a strict view of specialisation, it seems that the neat division between domain-general and domain-specific processing is over. However, I think it does not need to be as black and white as “there is” or “there is not” a neat division between domain-general and domain-specific processing. I take these findings to show that the relationship between domain-specific and domain-general networks is more nuanced and complex than previous conceptualisations have suggested. In some cases it may be that the distinction is clear-cut, and in others it may be less clear. However, characterising where there is a clear division between domains, and where the process is more important for engaging a region than the domain, gives interesting insight into the structure and function of the brain. Although there are clearly regions with specialised roles in cognitive processes (Kanwisher, 2010), there is argument that there are fewer of these specialised regions than one might think (Downing et al., 2006; Kanwisher, 2010). Additionally, in some cases these regions are also engaged across different domains (Baetens et al., 2014; Spunt & Adolphs, 2015), and do not stand alone but work in concert with other brain regions and networks (Baldauf & Desimone, 2014; Quadflieg et al., 2011; Zaki et al., 2010). The results from Chapter 4 provide an interesting insight into this debate. I found that the sex difference in automatic imitation recruits putative domain-general neural regions, but that these regions show a specialised response in order to support the sex difference in automatic imitation, more so than in a non-social inhibitory control task. This suggests support for the idea that conceptualisations of brain function are more complicated than previously accounted for. However, it does not provide insight into the characterisation of this complication, whether or not these regions are engaged across different domains and whether or not they show interplay with regions involved in the control of social processes.

Fortunately, methodological developments are leading to more sensitive and nuanced measures of brain function that are able to assess the complexity that is more true to how the brain is structured and functions. These developments include multi-voxel pattern analysis (MVPA) or repetition suppression analyses in order to more fully understand the representation of information within a region and connectivity analyses in order to characterise interplay between regions and networks.

5.3. Methodological implications: Large samples and combining approaches

A methodological strength of the work in my PhD is the use of large behavioural samples. Although I used this approach to investigate individual differences, this offers a benefit to psychological research more broadly in both purely behavioural as well as in combination with neuroimaging work. A “crisis” of replication failure in psychology research has recently risen to the forefront of conversation. Reproducibility is considered a defining feature of science, and key to assuring its credibility and yet the focus on producing novel work means that the importance of replication experiments is often overlooked (Open Science, 2015). As such, throughout the field of psychology and neuroscience there are on-going concerns over the reproducibility of landmark research findings (Button et al., 2013; Open Science, 2015; Pashler, et al., 2012; Shanks, et al., 2013; Simmons et al., 2011).

By using large samples in behavioural work we increase the likelihood of replication, as large samples represent the population more accurately than smaller samples (Maxwell et al., 2008) and additionally have more power to control for confounding variables that may influence our results (Cumming, 2014; McNamee, 2005). This combination of controlling for confounding variables and approximating the population more accurately should help to ensure that replication experiments reproduce original findings as they are reducing the amount of error measured and therefore become closer to measuring the true phenomena of interest. In Chapter 3 the main findings are null results, including a failure to replicate prior work that showed automatic imitation was related to individual differences in narcissism (Obhi et al., 2013). With a smaller sample one might conclude that these results are the result of low power to detect these effects. However, with a large sample, we can be more confident in the null result, especially seeing as I demonstrated that I had sufficiently sensitive methods to detect a sex difference with a small or small-to-medium effect size (Chapters 3 and 4).

In terms of neuroimaging work, the high expense of this approach leads to low sample sizes as standard, and therefore to the associated low power and difficulty approximating the population accurately. In addition, due to low power resulting from the sample size, neuroimaging samples may not display the behavioural effect which one is investigating the neural bases of (Yarkoni, 2014). However, by combining a large behavioural sample in order to observe the behavioural effect with a neuroimaging sample to investigate the neural bases of the effect, we can increase confidence in interpreting proximal neural correlates in the absence of a more distal behavioural effect in the neuroimaging sample. Indeed, in Chapter 4 I did not observe the sex difference in the behavioural data from the fMRI sample (Experiment 2) however, the effect size meant that this was predicted considering the size of the sample. Additionally, by combining with a large sample study (Experiment 1) we replicated this effect behaviourally. This suggested that despite being small, the sex difference was a robust effect. As such, combination with the large behavioural sample was essential to add confidence to the interpretation of neural sex differences as underlying the behavioural effect, despite not being apparent in our fMRI sample behaviourally.

In conclusion, the use of large sample behavioural approaches and particularly integration with neuroimaging approaches in cognitive neuroscience is useful for mitigating problems of low sample size and high expense of fMRI studies (Yarkoni, 2014), thus enhancing the use of fMRI to shed light on cognitive processes. As such, I believe this is a strong approach and encourage researchers in the domain of cognitive neuroscience to adopt this approach where possible but especially when examining the neural correlates of an effect that may not be observed behaviourally in a typical fMRI sample.

5.4. Future research

Throughout this discussion I have mentioned several future directions following on from this work, including investigation of stable characteristics of an interaction partner's face in addition to agreeableness, and investigation of possible interactions between one's own traits and modulation of imitation by other cues. As such, in the current section I will focus on future directions to investigate the sex difference in automatic imitation that I find particularly interesting and includes consideration of higher complexity within and between neural regions during a cognitive process. Above, I discuss what this sex difference might mean, however, we really need more data on this phenomenon before we can say with more confidence what it might mean. There are two avenues by which the sex difference in this social cognitive process could be further investigated that take into account the complexity of neural systems. First, one could use multi-voxel pattern analysis (MVPA) to investigate whether women represent the action of another more strongly than men. Second, one could use functional connectivity analyses so examine interplay between those regions identified in Chapter 4 and regions specific to the control of automatic imitation. I will now elaborate on those possibilities.

MVPA is increasingly being used to examine how information is represented within the brain and affords researchers greater sensitivity than more conventional univariate analyses (Norman et al., 2006). Using a subset of the data in MVPA a classifier can be trained to find regions than show a certain pattern of local activation, that differs amongst categories of stimuli. You can then test this classifier on the remaining data and the classifier should most accurately explain the pattern of data within a region when that region is representing information pertaining to the category on which the classifier was trained. Therefore, one way to interrogate the encoding actions interpretation of the sex difference in automatic imitation would be to use MVPA to compare classifier accuracy across a range of stimulus categories. You would look for regions whereby the classifier would show greater discrimination accuracy for action stimuli compared to non-action stimuli and that this difference in discrimination accuracy would be stronger in women than in men. This finding would suggest that within that region women represent the actions of others more so that non-actions and that this encoding difference is greater for women than men. You could also use a wider category of social compared to non-social stimuli to investigate whether women encode not only actions but also social information more generally greater than non-social cues compared to men.

Functional connectivity analyses are also being increasingly used to examine the task-based interplay between neural regions (Friston et al., 1997; Rogers et al., 2007). This could be a useful method to investigate the sex difference in automatic imitation and also take into account the complexity of the brain by examining differences between men and women in functional connectivity between domain-general and domain-specific regions during the inhibition of automatic imitation compared to non-social inhibitory control. It is possible that dorsolateral and dorsomedial frontal regions identified in Chapter 4 show increased functional coupling with regions specifically recruited during the control of automatic imitation in women compared to men. This might suggest that women encode the observed action more strongly than men do, leading to greater interplay with those regions involved in separating the self from the other, or enforcing one's own action over representation of an observed action. This is particularly interesting as research has shown that regions that do not show direct engagement in a task can show task-dependent connectivity with regions that are directly engaged in the task (Burnett & Blakemore, 2009). This suggests that these regions do not provide a direct influence in the cognitive process of interest, but instead provide a regulatory influence on those regions that are directly engaged (Burnett & Blakemore, 2009). In Chapter 4 I showed no sex difference in TPJ or mPFC, however, that does not rule out the possibility that one or both of them might functionally connect to regions that do show a sex difference more so in imitation than non-social inhibitory control. This would suggest a sex difference in the regulatory role of these regions, rather than direct engagement in the sex difference in inhibitory control of automatic imitation.

5.5. Conclusions

In summary, this thesis provides novel insight into automatic imitation in terms of antecedents and individual differences in stable characteristics. Overall, results suggest that imitation is sensitive to transient cues from an interaction partner rather than stable characteristics of the interaction partner or one's own stable characteristics. This suggests that imitation is flexibly modulated by social cues that predict the outcome of the current interaction rather than those that would predict the outcome of interactions more generally. However, the full extent of the relationship between automatic imitation and stable characteristics has not been exhausted and many interesting questions remain. In addition, a novel finding revealed an unpredicted sex difference in automatic imitation that recruits generally considered domain-general neural circuitry, despite showing a sex difference that was greater for automatic imitation than in a non-social inhibitory control task. Thus, this work provides insight into broader methodological and theoretical debate by providing support for greater neural complexity than has been initially conceived as well as demonstrating the benefits of integrating a large sample behavioural approach with an fMRI approach. This method has the potential to increase reproducibility in the field, as well as increasing confidence in interpreting neural correlates of a behavioural effect that might not be observed in a typical fMRI sample size.

REFERENCES

Abbott, A. (2013). Disputed results a fresh blow for social psychology. *Nature, 497(7447),* 16.

Adolphs, R. (2001). The neurobiology of social cognition. *Current Opinion in Neurobiology, 11 (2),* 231–239.

Ainley, V., Brass, M. & Tsakiris, M. (2014). Heartfelt imitation: High interoceptive awareness is linked to greater automatic imitation. *Neuropsychologia, 60,* 21–28.

Allison, C., Auyeung, B., & Baron-Cohen, S. (2012). Toward brief "red flags" for autism screening: The short autism spectrum quotient and the short quantitative checklist in 1,000 cases and 3,000 controls. *Journal of the American Academy of Child & Adolescent Psychiatry, 51(2),* 202-212.

Ames, D. R., Rose, P., & Anderson, C. P. (2006). The NPI-16 as a short measure of narcissism. *Journal of Research in Personality, 40,* 440-350. doi:10.1016/j.jrp.2005.03.002

Ashton-James, C. E., & Levordashka, A. (2013). When the wolf wears sheep's clothing: Individual differences in the desire to be liked influence nonconscious behavioral mimicry. *Social Psychological and Personality Science, 4,* 643-648. DOI: 10.1177/1948550613476097

Ashton, M. C., Paunonen, S. V., Helmes, E., & Jackson, D. N. (1998). Kin altruism, reciprocal altruism, and the big five personality factors. *Evolution and Human Behaviour, 19,* 243-255.

Baetens, K., Ma, N., Steen, J., & Van Overwalle, F. (2014). Involvement of the mentalizing network in social and non-social high construal. *Social Cognitive Affective Neuroscience, 9(6)*, 817-824, doi: 10.1093/scan/nst048

Bailenson, J. N., & Yee, N. (2005). Digital chameleons: automatic assimilation of nonverbal gestures in immersive virtual environments. *Psychological Science, 16(10),* 814-819.

Baldauf, D., & Desimone, R. (2014). Neural Mechanisms of Object-Based Attention. *Science, 344,* 424–427.

Bardi, L., Bundt, C., Notebaert, W., & Brass, M. (2015). Eliminating mirror responses by instructions. *Cortex, 70,* 128e136. doi:10.1016/j.cortex.2015.04.018

Baron-Cohen, S. (2002). The extreme male brain theory of autism. *Trends in Cognitive Sciences, 6,* 248–254

REFERENCES

Baroun, K., & Alansari, B. M. (2006). Gender differences in performance on the Stroop Test. *Social Behaviour and Personality, 34 (3),* 309-318.

Barrett, L. F. & Satpute, A. (2013). Large-scale brain networks in affective and social neuroscience: Towards an integrative functional architecture of the brain. *Current Opinion in Neurobiology, 23(3),* 361–372. doi:10.1016/j.conb.2012.12.012

Barrio, V., Aluja, A., & García, L. F. (2004). Relationship between empathy and the big five personality traits in a sample of Spanish adolescents. *Social Behaviour and personality, 32(7)*, 677-682.

Bayliss, A. P., di Pellegrino, G., & Tipper, S. P. (2005). Sex differences in eye gaze and symbolic cueing of attention. *The Quarterly Journal of Experimental Psychology, 58A(4),* 631-650. doi:10.1080/02724980443000124

Bird, G., Leighton, J., Press, C., & Heyes, C. (2007). Intact automatic imitation of human and robot actions in autism spectrum disorders. *Proceedings of the Royal Society B, 274(1628),* 3027-3031. doi: 10.1098/rspb.2007.1019

Blair, I. V., Judd, C. M., & Chapleau, K. M. (2004). The influence of afrocentric facial features in criminal sentencing. *Psychological Science, 15(10),* 674-679.

Blakemore, S.-J., Winston, J., & Frith, U. (2004). Social cognitive neuroscience: where are we heading? *Trends in Cognitive Sciences, 8(5),* 216-222. doi: 10.1016/j.tics.2004.03.012

Brass, M., & Heyes, C. (2005). Imitation: is cognitive neuroscience solving the correspondence problem? *Trends in Cognitive Sciences, 9(10),* 489-495. doi:10.1016/j.tics.2005.08.007

Brass, M., Bekkering, H., Wohlschlager, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: comparing symbolic, spatial, and imitative cues. *Brain and Cognition, 44(2),* 124-143. doi: 10.1006/brcg.2000.1225

Brass, M., Derrfuss, J., & von Cramon, D. Y. (2005). The inhibition of imitative and overlearned responses: a functional double dissociation. *Neuropsychologia, 43(1),* 89-98.

Brass, M., Derrfuss, J., Matthes-von Cramon, G., & von Cramon, D. Y. (2003). Imitative response tendencies in patients with frontal brain lesions. *Neuropsychology, 17(2),* 265-271.

Brass, M., Ruby, P., & Spengler, S. (2009). Inhibition of imitative behaviour and social cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364(1528),* 2359-2367. doi: 10.1098/rstb.2009.0066

Brass, M., Zysset, S., & von Cramon, D. Y. (2001). The inhibition of imitative response tendencies. *NeuroImage, 14(6),* 1416-1423.

Bunge, S. A., Hazeltine, E., Scanlon, M. D., Rosen, A. C., & Gabrieli, J. D. E. (2002). Dissociable contributions of prefrontal and parietal cortices to response selection. *NeuroImage, 17,* 1562-1571. doi: 10.1006/nimg.2002.1252

Burnett, S., & Blakemore, S.-J. (2009). Functional connectivity during a social emotion task in adolescents and in adults. *European Journal of Neuroscience, 29 (6),* 1294–301. DOI: 10.1111/j.1460-9568.2009.06674.x

Butler, E. E., Ward, R., & Ramsey, R. (2015). Investigating the Relationship between Stable Personality Characteristics and Automatic Imitation. *PLoS ONE, 10(6),* e0129651. doi:10.1371/journal. pone.012965

Buttelmann, D., & Böhm, R. (2014). The ontogeny of the motivation that underlies in-group bias. *Psychological Science, 25(4),* 921-927. doi: 10.1177/0956797613516802

Button, K. S., Ioannidis, J. P. A., Mokrysz, C., Nosek, B. A., Flint, J., Robinson, E. S. J., & Munafò, M. R. (2013). Power failure: why small sample size undermines the reliability of neuroscience. *Nature Reviews Neuroscience, 14,* 365-376. doi:10.1038/nrn3475

Campbell, R., Elgar, K., Kuntsi, J., Akers, R., Terstegge, J., Coleman, M., & Skuse, D. (2002). The classification of "fear" from faces is associated with face recognition skill in females. *Neuropsychologia, 40 (6),* 575–584. doi:10.1016/S0028-3932(01)00164-6

Carr, L., Iacoboni, M., Dubeau, M.C., Mazziotta, J.C., and Lenzi, G.L. (2003). Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proceedings of the National Academy Sciences USA, 100(9),* 5497–5502. doi: 10.1073/pnas.0935845100

Catmur, C., Walsh, V., Heyes, C.M., 2007. Sensorimotor learning configures the human mirror system. *Current Biology, 17 (17),* 1527–1531. doi:10.1016/j.cub.2007.08.006

REFERENCES

Catmur, C., & Heyes, C. (2011). Time course analyses confirm independence of imitative and spatial compatibility. *Journal of Experimental Psychology: Human Perception and Performance, 37(2),* 409-421Chartrand, T. L., & Bargh, J. A. (1999). The chameleon effect: The perception-behavior link and social interaction. *Journal of personality and Social Psychology, 76(6),* 893-910.

Chartrand, T. L., & Lakin, J. L. (2013). The Antecedents and Consequences of Human Behavioral Mimicry. *Annual Review of Psychology, 64(1),* 285-308. doi:10.1146/annurev-psych-113011-143754

Chartrand, T. L., & Van Baaren, R. (2009). Human mimicry. *Advances in Experimental Social Psychology, 41*, 219–274. doi:10.1016/S0065-2601(08)00405-X

Cheng, Y., Decety, J., Lin, C.-P., Hsieh, J.-C., Hung, D., & Tzeng, O.J.L. (2007). Sex differences in spinal excitability during observation of bipedal locomotion. *NeuroReport, 18(9),* 887–890.

Cheng, Y., Lee, P.-L., Yang, C.-Y., Lin, C.-P., Hung, D., & Decety, J. (2008). Gender differences in the mu rhythm of the human mirror-neuron system. *PLoS ONE, 3(5),* e2113. doi: 10.1371/journalpone.0002113

Cheng, Y., Tzeng, O.J.L., Decety, J., Imada, T., Hsieh, J.-C. (2006). Gender differences in the human mirror system: a magnetoencephalography study. *NeuroReport, 17(2),* 1115–1119.

Clayson, P. E., Clawson, A., & Larson, M. J. (2011). Sex differences in electrophysiological indices of conflict monitoring. *Biological Psychology, 87,* 282-289. doi:10.1016/j.biopsycho.2011.03.011

Cohen, J. (1992). A power primer. *Quantitative Methods in Psychology, 112(1),* 155-159.

Cook, J., & Bird, G. (2011). Social attitudes differentially modulate imitation in adolescents and adults. *Experimental Brain Research, 211,* 601-612. doi:10.1007/s00221-011-2584-4

Cook, J., & Bird, G. (2012). Atypical Social Modulation of Imitation in Autism Spectrum Conditions*. Journal of Autism and Developmental Disorders, 42(6),* 1045-1051. doi: 10.1007/s10803-011-1341-7

Cook, J., Barbalat, G., & Blakemore, S. (2012). Top-down modulation of the perception of other people in schizophrenia and autism. *Frontiers in Human Neuroscience, 6(175),* 1-10. doi: 10.3389/fnhum.2012.00175

Cook, R., Bird, G., Lünser, G., Huck, S., and Heyes, C. (2012a). Automatic imitation in a strategic context: players of rock-paper-scissors imitate opponents' gestures. *Proceedings of the Royal Society B, 279,* 780–786. doi: 10.1098/rspb.2011.1024

Cook, R., Dickinson, A., & Heyes, C. (2012b). Contextual modulation of mirror and counter-mirror sensorimotor associations. *Journal of Experimental Psychology: General, 141(4),* 774-87. doi: 10.1037/a0027561

Cremers, H. R., Demenescu, L. R., Aleman, A., Renken, R., van Tol, M. J., van der Wee, N. J., Veltman, D. J., & Roelofs, K. (2010). Neuroticism modulates amygdala-prefrontal connectivity in response to negative emotional facial expressions. *NeuroImage, 49,* 963–70. doi:10.1016/j.neuroimage.2009.08.023

Crescentini, C., Mengotti, P., Grecucci, A., & Rumiati, R. I. (2011). The effect of observed biological and non biological movements on action imitation: an fMRI study. *Brain Research, 1420,* 80-92. doi:10.1016/j.brainres.2011.08.077

Cross, K.A., Iacoboni, M., (2013). Optimized neural coding? Control mechanisms in large cortical networks implemented by connectivity changes. *Human Brain Mapping, 34,* 213–225.

Cumming, G. (2014). The new statistics: Why and how. *Psychological Science, 25,* 7-29. doi:10.1177/0956797613504966

De Coster, L., Mueller, S. C. , T'Sjoen, G., De Saedeleer, L., Brass, M. (2014). The influence of oxytocin on automatic motor simulation. *Psychoneuroendocrinology, 50,* 220-226. doi: 10.1016/j.psyneuen.2014.08.021

Der, G., & Deary, I. J. (2006). Age and sex differences in reaction time in adulthood: Results from the United Kingdom health and lifestyle survey. *Psychology and Aging, 21(1),* 62-73. doi: 10.1037/0882-7974.21.1.62

Dimberg, U. (1990). Gender differences in facial reactions to facial expressions. *Biological Psychology, 30,* 151–159.

Donnellan, M. B., Oswald, F. L., Baird, B. M., & Lucas, R. E. (2006). The Mini-IPIP scales: Tiny-yet-effective measures of the big five factors of personality. *Psychological Assessment, 18(2),* 192-203. DOI: 10.1037/1040-3590.18.2.192

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science, 293,* 2470–2473

Downing, P. E., Chan, A. W., Peelen, M. V., Dodds, C. M., & Kanwisher, N. (2006). Domain specificity in visual cortex. *Cerebral Cortex 16,* 1453–1461.

Durrett, C., & Trull, T. J. (2005). An evaluation of evaluative personality terms: A comparison of the big seven and five-factor model in predicting psychopathology. *Psychological Assessment, 17(3),* 359-368. doi: 10.1037/1040-3590.17.3.359

Eickhoff, S. B., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K,. & Zilles, K. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *NeuroImage, 25,* 1325–1335.

Emery, N. J. (2005). *The evolution of social cognition.* In Alexander Easton and Nathan J. Emery The Cognitive Neuroscience of Social Behaviour (pp. 115-157). Hove and New York: Taylor and Francis Group.

Enticott, P. G., Hoy, K. E., Herring, S. E., Johnston, P. J., Daskalakis, Z. J., & Fitzgerald, P. B. (2008). Reduced motor facilitation during action observation in schizophrenia: A motor neuron deficit? *Schizophrenia Research, 102,* 116-121. doi:10.1016/j.schres.2008.04.001

Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature, 392,* 598–601.

Erikson, B. A., & Erikson, C. W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception and Psychophysics, 16(1),* 143-149.

Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods, 41,* 1149-1160

Friston, K.J., Bu¨chel, C., Fink, G.R., Morris, J., Rolls, E., Dolan, R.J., 1997. Psychophysiological and modulatory interactions in neuroimaging. *NeuroImage 6,* 218–229 doi:10.1006/nimg.1997.0291

Friston, K. J., Worsley, K. J., Frackowiak, R. S. J., Mazziotta, J. C., & Evans, A. C. (1994). Assessing the significance of focal activations using their spatial extent. *Human Brain Mapping, 1(3),* 210-220.

Frith, C. D., & Frith, U. (2012). Mechanisms of social cognition. *Annual Review of Psychology, 63,* 287–313. doi: 10.1146/annurev-psych-120710-100449

Frith, C. D. (2007). The social brain? *Philosophical Transactions of the Royal Society B: Biological Sciences, 362,* 671–78. doi:10.1098/rstb.2006.2003

Frith, C. (2009). Role of facial expressions in social interactions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364,* 3453–3458 doi:10.1098/rstb.2009.0142

Goldberg, L. R. (1999). A broad-bandwidth, public-domain, personality inventory measuring the lower-level facets of several five-factor models. In I. Mervielde, I. Deary, F. De Fruyt, & F. Ostendorf (Eds.). Personality psychology in Europe (Vol. 7, pp. 7–28). Tilburg, The Netherlands: Tilburg University Press.

Goldman, A. I., & Sripada, C. S. (2005). Simulationist models of face-based emotion recognition. *Cognition, 94(3),* 193-213. doi: 10.1016/j.cognition.2004.01.005

Grecucci, A., Koch, I., & Rumiati, R. I. (2011). The role of emotional context in facilitating imitative actions*. Acta Psychologica, 138(2),* 311e315. http://dx.doi.org/10.1016/j.actpsy.2011.07.005.

Grecucci, A., Brambilla, P., Siugzdaite, R., Londero, D., Fabbro, F., Rumiati, R. I. (2013). Emotional resonance deficits in autistic children. *Journal of Autism and Developmental Disorders, 43,* 616-628. doi: 10.1007/s10803-012-1603-z

Grill-Spector, K., Kourtzi, Z. & Kanwisher, N. (2001) The lateral occipital complex and its role in object recognition. *Vision Research, 41, (10-11)*, 1409-1422. doi:10.1016/S0042-6989(01)00073-6

Gur, R. C., Alsop, D., Glahn, D., Petty, R., Swanson, C. L., Maldjian, J. A., Turetsky, B. I., Detre, J. A., Gee, J., & Gur, R. E. (2000). An fMRI study of sex differences in regional activation to a verbal and a spatial task. *Brain and Language, 74(2),* 157-170. doi: 10.1006/brln.2000.2325

Halpern, D. F. (2012). *Sex Differences in Cognitive Abilities.* Hove and New York: Taylor and Francis Group.

Hamilton, A. F. de C. (2014). Cognitive underpinnings of social interaction. *The Quarterly Journal of Experimental Psychology, 68(3),* 417-432 doi: 10.1080/17470218.2014.973424

Hamilton, A. F. de C. (2013). Reflecting on the mirror neuron system in autism: A systematic review of current theories. *Developmental Cognitive Neuroscience, 3,* 91–105. doi: 10.1016/j.dcn.2012.09.008

Harms, M. B., Martin, A., & Wallace, G. L. (2010). Facial Emotion Recognition in Autism Spectrum Disorders: A Review of Behavioral and Neuroimaging Studies. *Neuropsychology Review, 20,* 290–322. doi: 10.1007/s11065-010-9138-6

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences, 4,* 223–233. doi:10.1016/S1364-6613(00)01482-0)

Hazeltine, E., Poldrack, R., & Gabrieli, J. D. E. (2007). Neural activation during response competition. *Journal of Cognitive Neuroscience, 12(2),* 118-129. doi:10.1162/089892900563984

Heyes, C., Bird, G., Johnson, H., & Haggard, P. (2005). Experience modulates automatic imitation. *Cognitive Brain Research, 22,* 233–240. doi:10.1016/j.cogbrainres.2004.09.009

Heyes, C. (2009). Evolution, development and intentional control of imitation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 364(1528),* 2293–2298. doi:10.1098/rstb. 2009.0049

Heyes, C. (2011). Automatic imitation. *Psychological Bulletin, 137(3),* 463-483. doi: 10.1037/a0022288

Hirschfeld, L. A. & Gelman, S. A. (1994). *Mapping the mind: Domain specificity in cognition and culture.* New York: Cambridge University Press.

Hogeveen, J., & Obhi, S. S. (2013). Automatic imitation is automatic, but less so for narcissists. *Experimental Brain Research, 224,* 613-621. doi: 10.1007/s00221-012-3339-6

Hogeveen, J., Obhi, S. S., Banissy, M. J., Santiesteban, I., Press, C., Catmur, C., & Bird, G. (2014). Task-dependent and distinct roles of the temporoparietal junction and inferior frontal cortex in the control of imitation. *Social Cognitive and Affective Neuroscience, 10(7),* 1003-1009. doi: 10.1093/scan/nsu148

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation*. Science, 286(5449),* 2526e2528.

Iacoboni, M. (2009). Imitation, Empathy, and Mirror Neurons. *Annual Review of Psychology, 60(1),* 653-670. doi: 10.1146/annurev.psych.60.110707.163604

Iacoboni, M., Woods, R. P., & Mazziotta, J. C. (1998). Bimodal (auditory and visual) left frontoparietal circuitry for sensorimotor integration and sensorimotor learning. *Brain, 121,* 2135-2143.

Jones, A. L., Kramer, R. S. S., & Ward, R. (2012). Signals of personality and health: the contributions of facial shape, skin texture, and viewing angle. *Journal of*

Experimental Psychology: Human Perception and Performance, 38(6), 1353-61. doi: 10.1037/a0027078.

Josephs, O., & Henson, R.N. (1999). Event-related functional magnetic resonance imaging: modelling, inference and optimization. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 354 (1387),* 1215–1228. doi: 10.1098/rstb.199.0475

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The Fusiform Face Area: A module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience, 17(11),* 4302–4311.

Kanwisher, N. (2010). Functional specificity in the human brain: A window into the functional architecture of the mind. *Proceedings of the National Academy of Sciences, 107(25),* 11163-11170. doi: 10.1073/pnas.1005062107

Klapper, A., Ramsey, R., Wigboldus, D., & Cross, E. S. (2014). The Control of Automatic Imitation Based on Bottom-Up and Top-Down Cues to Animacy: Insights from Brain and Behavior. *Journal of Cognitive Neuroscience, 26(11).* 2503-13. doin: 10.1162/jocn_a_00651.

Kraemer, H. C., & Blasey, C. M. (2004). Centring in regression analyses: a strategy to prevent errors in statistical inference. *International Journal of Methods in Psychiatric Research, 13(3),* 141-151.

Kramer, R. S. S., & Ward, R. (2010). Internal facial features are signals of personality and health. *The Quarterly Journal of Experimental Psychology, 63(11),* 2273-2287. doi:10.1080/17470211003770912

Lakens, D. (2013). Calculating and reporting effect sizes to facilitate cumulative science: A practical primer for t-tests and ANOVAs. *Frontiers in Psychology, 4,* 863. doi:10.3389/fpsyg.2013.00863

Lakin, J. L., & Chartrand, T. L. (2003). Using nonconscious behavioral mimicry to create affiliation and rapport. *Psychological Science, 14(4),* 334e339. http://dx.doi.org/10.1111/1467-9280.14481.

Larsen, H., Overbeek, G., Granic, I., & Engels, R. C. M. E. (2010). Imitation of alcohol consumption in same-sex and other-sex dyads. *Alcohol and Alcoholism, 45(6),* 557-562. doi: 10.1093/1lcalc/agq053

Leighton, J., Bird, G., Orisini, C., & Heyes, C. (2010). Social attitudes modulate automatic imitation. *Journal of Experimental Social Psychology, 46,* 905-910. doi:10.1016/j.jesp.2010.07.001

LePine, J. A., & van Dyne, L. (2001). Voice and cooperative behaviour as contrasting forms of contextual performance: Evidence of differential relationships with big five personality characteristics and cognitive ability. *Journal of Applied Psychology, 86(2),* 326-336. doi:10.1037//0021-9010.86.2.326

Leslie, K.R., Johnson-Frey, S.H., Grafton, S.T., 2004. Functional imaging of face and hand imitation: towards a motor theory of empathy. *NeuroImage 21,* 601 – 607 doi:10.1016/j.neuroimage.2003.09.038

Li, W., Zinbarg, R. E., Boehm, S. G., & Paller, K. A. (2008). Neural and behavioral evidence for affective priming from unconsciously perceived emotional facial expressions and the influence of trait anxiety. *Journal of Cognitive Neuroscience, 20,* 95–107. doi:10.1162/jocn.2008.20006

Lieberman, M. D., & Cunningham, W. A. (2009). Type I and Type II error concerns in fMRI research: Re-balancing the scale. *Social Cognitive and Affective Neuroscience, 4(4),* 423-428.

Lietz, C. A., Gerdes, K. E., Sun, F., Geiger, J. M., Wagaman, M. A., & Segal, E. A. (2011). The empathy assessment index (EAI): A confirmatory factor analysis of a multidimensional model of empathy. *Journal of the Society for Social Work and Research, 2(2),* 104-124. doi:10.5243/jsswr.2011.6

Lim, B.-C., & Ployhart, R. E. (2004). Transformational leadership: Relations to the five-factor model and team performance in typical and maximum contexts. *Journal of Applied Psychology, 89(4),* 610-621. doi: 10.1037/0021-9010.89.4.610

Liu, J., Harris, A., & Kanwisher, N. (2010). Perception of face parts and face configurations: An fMRI study. *Journal of Cognitive Neuroscience, 22,* 203–211.

Ma, N., Vandekerckhove, M., Van Overwalle, F., Seurinck, R., & Fias, W. (2011) Spontaneous and intentional trait inferences recruit a common mentalizing network to a different degree: Spontaneous inferences activate only its core areas, *Social Neuroscience, 6(2),* 123-138, doi: 10.1080/17470919.2010.485884

Malach, R., Reppas, J. B., Benson, R. B., Kwong, K. K., Jiang, H., Kennedy, W. A., Ledden, P. J., Brady, T. J., Rosen, B. R., Tootell, R. B. H. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy Sciences USA, 92,* 8135–8138.

Marsh, A. A., Ambady, N., & Kleck, R. E. (2005). The effects of fear and anger expressions on approach- and avoidance-related behaviors. *Emotion, 5(1),* 119-124. DOI: 10.1037/1528-3542.5.1.119

Maxwell, S. E., Kelley, K., & Rausch, J. R. (2008). Sample size planning for statistical power and accuracy in parameter estimation. *Annual Review of Psychology, 59,* 537-563. doi: 10.1146/annurev.psych.59.103006.093735

McNamee, R. (2005). Regression modelling and other methods to control confounding. *Occupational and Environmental Medicine, 62,* 500-506. doi: 10.1136/oem.2002.001115

Miller DI, Halpern DF (2014) The new science of cognitive sex differences. Trends Cogn Sci 18(1):37–45. doi:10.1016/j.tics.2013.10.011

Moody, E. J., McIntosh, D. N., Mann, L. J., & Weisser, K. R. (2007). More Than Mere Mimicry? The Influence of Emotion on Rapid Facial Reactions to Faces. *Emotion, 7(2),* 447–457. doi: 10.1037/1528-3542.7.2.447

Morf, C. C. & Rhodewalt, F. (2001). Unraveling the Paradoxes of Narcissism: A Dynamic Self-Regulatory Processing Model. *Psychological Inquiry, 12(4),* 177-196. doi: 10.1207/S15327965PLI1204_1

Nee, D. E., Wager, T. D., Jonides, J. (2007). Interference resolution: Insights from a meta-analysis of neuroimaging tasks. *Cognitive, Affective, & Behavioral Neuroscience, 7(1),* 1-17.

Nelson, M. T., Seal, M. L., Pantelis, C., & Phillips, L. J. (2013). Evidence of a dimensional relationship between schizotypy and schizophrenia: A systematic review. *Neuroscience and Biobehavioural Reviews, 37,* 317-327. doi:10.1016/j.neubiorev.2013.01.004

Niedenthal, P. M., Brauer, M., Halberstadt, J. B., & Innes-Ker, Å., H. (2001) When did her smile drop? Facial mimicry and the influences of emotional state on the detection of change in emotional expression. *Cognition and Emotion, 15(6),* 853-864. doi: 10.1080/02699930143000194

Norman, K. A., Polyn, S. M., Detre, G. J., & Haxby, J. V. (2006). Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends in Cognitive Sciences, 10 (9),*424–430. doi:10.1016/j.tics.2006.07.005Oberman, L. M., & Ramachandran, V.

S. (2007). The simulating social mind: the role of the mirror neuron system and simulation in the social and communicative deficits of autism spectrum disorders. *Psychological Bulletin, 133(2),* 310-327. doi: 10.1037/0033-2909.133.2.310

Oberman, L. M., Winkielman, P., & Ramachandran, V. S. (2007). Face to face: Blocking facial mimicry can selectively impair recognition of emotional expressions. *Social Neuroscience, 2(3-4),* 167-178. doi: 10.1080/17470910701391943

Obhi, S. S., Hogeveen, J., Giacomin, M., & Jordan, C. H. (2013). Automatic imitation is reduced in narcissists. *Journal of Experimental Psychology: Human Perception and Performance, 40(3),* 920-928. doi: 10.1037/a0034056

Ochsner, K. N., & Lieberman, M. D. (2001). The emergence of social cognitive neuroscience. *The American Psychologist, 56 (9),* 717–34

Open Science Collaboration. (2015). Estimating the reproducibility of psychological science. *Science, 349 (6251),* doi: 10.1126/science.aac4716

Park, S., Matthews, N., & Gibson, C. (2008). Imitation, Simulation, and Schizophrenia. *Schizophrenia Bulletin, 34(4),* 698-707. doi:10.1093/schbul/sbn048

Pashler, H., Coburn, N., Harris, C. R. (2012). Priming of Social Distance? Failure to Replicate Effects on Social and Food Judgments. *PLoS ONE, 7(8),* e42510. doi:10.1371/journal.pone.0042510

Peelen, M.V., & Downing, P.E. (2007). The neural basis of visual body perception. *Nature Reviews Neuroscience, 8,* 636–648. doi:10.1038/nrn2195

Penton-Voak, I. S., Pound, N., Little, A. C., & Perrett, D. I. (2006). Personality judgments from natural and composite facial images: More evidence for a "kernel of truth" in social perception. *Social Cognition, 24(5),* 607-640. doi: 10.1521/soco.2006.24.5.607

Philip, R. C. M., Dauvermanna, M. R., Whalleya, H. C., Baynhama, K., Lawriea, S. M., & Stanfield, A. C. (2012). A systematic review and meta-analysis of the fMRI investigation of autism spectrum disorders. *Neuroscience and Biobehavioral Reviews, 36,* 901–942. doi:10.1016/j.neubiorev.2011.10.008

Pitcher, D., Charles, L., Devlin, J. T., Walsh, V., & Duchaine, B. (2009). Triple dissociation of faces, bodies, and objects in extrastriate cortex. *Current Biology, 19,* 319–324.

Pitcher, D., Walsh, V., & Duchaine, B. (2011). The role of the occipital face area in the cortical face perception network. *Experimental Brain Research, 209,* 481– 493.

Poggi, I., DÉrrico, F., & Vincze, L. (2011). *68 Nods. But not of agreement,* Stauffenburg Verlag: Tubingen.

Praamstra, P., Kleine, B. U., & Schnitzler, A. (1999). Magnetic stimulation of the dorsal premotor cortex modulates the Simon effect*. NeuroReport, 10(17),* 3671-3674.

Press, C., Richardson, D., & Bird, G. (2010). Intact imitation of emotional facial actions in autism spectrum conditions. *Neuropsychologia, 48(11-3),* 3291-3297. doi: 10.1016/j.neuropsychologia.2010.07.012

Quadflieg, S., Flannigan, N., Waiter, G. D., Rossion, B., Wig, G. S., Turk, D. J., Macrae, C. N. (2011). Stereotype-based modulation of person perception. *Neuroimage. 57,* 549–557.

Rahman, Q., Wilson, G. D., & Abrahams, S. (2004). Sex, sexual orientation, and identification of positive and negative facial affect. *Brain and Cognition, 54,* 179–185. doi:10.1016/j.bandc.2004.01.002

Raine, A., & Benishay, D. (1995). The SPQ-B: A brief screening instrument for schizotypal personality disorder. *Journal of Personality Disorders, 9(4),* 346-355.

Rauchbauer, B., Majdandžić, J., Hummer, A., Windischberger, C., & Lamm, C. (2015). Distinct neural processes are engaged in the modulation of mimicry by social group-membership and emotional expressions*. Cortex, 70,* 49-67, doi:10.1016/j.cortex.2015.03.007

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Reviews Neuroscience, 27,* 169-192. doi: 10.1146/annurev.neuro.27.070203.144230

Rogers, S. J., Hepburn, S. L., Stackhouse, T., & Wehner, E. (2003). Imitation performance in toddlers with autism and those with other developmental disorders. *Journal of Child Psychology and Psychiatry, 44,* 763–781. doi:10.1111/1469-7610.00162

Rubia, K., Hyde, Z., Halari, R., Giampietro, V., & Smith, A. (2010). Effects of age and sex on developmental neural networks of visual-spatial attention allocation. *NeuroImage, 51,* 817-827. doi:10.1016/j.neuroimage.2010.02.058

Russell, T. A., Tchanturia, K., Rahman, Q., & Schmidt, U. (2007). Sex differences in theory of mind: A male advantage on Happé's "cartoon" task. *Cognition and Emotion, 21,* 1554–1564. doi: 10.1080/02699930601117096

Rychlowska, M., Cañadas, E., Wood, A., Krumhuber, E. G., Fischer, A., & Niedenthal, P. M. (2014). Blocking mimicry makes true and false smiles look the same. *PLoS ONE, 9(3),* e90876. doi: 10.1371/journal.pone.0090876

Said, C. P., Haxby, J. V., & Todorov, A. (2011). Brain systems for assessing the affective value of faces. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366,* 1660-1670. doi: 10.1098/rstb.2010.0351

Santiesteban, I., White, S., Cook, J., Gilbert, S.J., Heyes, C., and Bird, G. (2012a). Training social cognition: from imitation to Theory of Mind. *Cognition, 122,* 228–235. doi:10.1016/j.cognition.2011.11.004

Santiesteban, I., Bird, G., Tew, O., Cioffi, M. C., & Banissy, M. J. (2015). Mirror-touch synaesthesia: Difficulties inhibiting the other. *Cortex, 71,* 116-121, doi:10.1016/j.cortex.2015.06.019

Santiesteban, I., Banissy, M. J., Catmur, C., & Bird, G. (2012b). Enhancing Social Ability by Stimulating Right Temporoparietal Junction. *Current Biology, 22(23),* 2274-2277.

Sato, W., Fujimura, T., Kochiyama, T., & Suzuki, N. (2013). Relationships among facial mimicry, emotional experience, and emotion recognition. *PLoS ONE, 8(3),* e57889. doi:10.1371/journal.pone.0057889

Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people. The role of the temporo-parietal junction in "theory of mind." *NeuroImage, 19,* 1835–1842.

Schmitt, D. P., Realo, A., Voracek, M., & Allik, J. (2008). Why can't a man be more like a woman? Sex differences in big five personality traits across 55 cultures. *Journal of Personality and Social Psychology, 94(1),* 168-182. doi: 10.1037/0022-3514.94.1.168

Schulte-Ruther, M., Markowitsch, H.J., Shah, N.J., Fink, G.R., Piefke, M., (2008). Gender differences in brain networks supporting empathy. *NeuroImage 42 (1),* 393–403. doi:10.1016/j.neuroimage.2008.04.180

Scott, N. J., Kramer, R. S. S., Jones, A. L., & Ward, R. (2013). Facial cues to depressive symptoms and their associated personality attributions. *Psychiatry Research, 208(1),* 47-53. doi: 10.1016/j.psychres.2013.02.027

Shanks, D. R., Newell, B. R., Lee, E. H., Balakrishnan, D., Ekelund, L., Cenac, Z., Kavvadia, F., & Moore, C. (2013). Priming Intelligent Behavior: An Elusive Phenomenon. *PLoS ONE, 8(4),* e56515. doi:10.1371/journal.pone.0056515

Shaver, P. R., & Brennan, K. A. (1992). Attachment styles and the "big five" personality traits: Their connections with each other and with romantic relationship outcomes. *Personality and Social Psychology Bulletin, 18,* 536-545. doi: 10.1177/0146167292185003

Shutts, K., Banaji, M. R., & Spelke, E. S. (2010). Social categories guide young children's preferences for novel objects. *Developmental Science, 13(4),* 599-610. doi: 10.1111/j.1467-7687.2009.00913.x

Simmons, J. P., Nelson, L. D., & Simonsohn, U. (2011). False-positive psychology: Undisclosed flexibility in data collection and analysis allows presenting anything as significant. *Psychological Science, 22,* 1359–1366.

Sonnby-Borgström, M. (2002). Automatic mimicry reactions as related to differences in emotional empathy. *Scandinavian Journal of Psychology, 43,* 433-443.

Sonnby-Borgström, M., Jönsson, P., & Svensson, O. (2003). Emotional empathy as related to mimicry reactions at different levels of information processing. *Journal of Nonverbal Behavior, 27(1),* 3-23.

Sonnby-Borgström, M., Jönsson, P., & Svensson, O. (2008). Gender differences in facial imitation and verbally reported emotional contagion from spontaneous to emotionally regulated processing levels. *Scandinavian Journal of Psychology, 49,* 111–122. doi: 10.1111/j.1467-9450.2008.00626.x

Southgate, V., & Hamilton, A. F. de C. (2008). Unbroken mirrors: challenging a theory of Autism. *Trends in Cognitive Sciences, 12(6),* 225-229. doi: 10.1016/j.tics.2008.03.005

Sowden S., & Catmur C. (2015). The role of the right temporoparietal junction in the control of imitation. *Cerebral Cortex, 25(4),* 1107-1113. doi: 10.1093/cercor/bht306

Speck, O., Ernst, T., Braun, J., Koch, C., Miller, E., & Chang, L. (2000). Gender differences in the functional organization of the brain for working memory. *NeuroReport, 11(11),* 2581-2585.

Spengler, S., von Cramon, D.Y., & Brass, M., (2009). Control of shared representations relies on key processes involved in mental state attribution. *Human Brain Mapping, 30(11),* 3704–3718 doi: 10.1002/hbm.20800

Spengler, S., von Cramon, D. Y., & Brass, M. (2010). Resisting motor mimicry: Control of imitation involves processes central to social cognition in patients with frontal and temporo-parietal lesions. *Social Neuroscience, 5(4),* 401-416.

Spunt, R. P., & Adolphs, R. (2015). Folk Explanations of Behavior: A Specialized Use of a Domain-General Mechanism. *Psychological Science, 26(6),* 724–736. doi: 10.1177/0956797615569002

Stel, M., & Vonk, R. (2010). Mimicry in social interaction: Benefits for mimickers, mimickees, and their interaction. *British Journal of Psychology, 101,* 311–323. doi:10.1348/000712609X465424

Stins, J. F., Roelofs, K., Villan, J., Kooijman, K., Hagenaars, M. A., Beek, P. J. (2011). Walk to me when I smile, step back when I'm angry: Emotional faces modulate whole-body approach-avoidance behaviors. *Experimental Brain Research, 212,* 603-611. DOI 10.1007/s00221-011-2767-z

Stoet, G. (2010). Sex differences in the processing of flankers. *The Quarterly Journal of Experimental Psychology, 63(4),* 633-638 doi: 10.1080/17470210903464253

Stürmer, B., Aschersleben, G., & Prinz, W. (2000). Correspondence effects with manual gestures and postures: A study of imitation. *Journal of Experimental Psychology: Human Perception and Performance, 26,* 1746–1759. doi:10.1037/0096-1523.26.6.1746

Thakkar, K. N., Peterman, J. S., & Park, S. (2014). Altered brain activation during action imitation and observation in schizophrenia: A translational approach to investigating social dysfunction in schizophrenia. *American Journal of Psychiatry, 171(5),* 539-548.

Thayer, J. F., & Johnsen, B. H. (2000). Sex differences in judgement of facial affect: a multivariate analysis of recognition errors. *Scandinavian Journal of Psychology, 41 (3),* 243–246. DOI: 10.1111/1467-9450.00193

Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Prototyping and transforming facial textures for perception research. *IEEE Computer Graphics and Applications, 21(5),* 42-45. doi: 10.1109/38.946630

Todorov, A., Olivola, C. Y., Dotsch, R., & Mende-Siedlecki, P. (2015). Social attributions from faces: Determinants, consequences, accuracy, and functional significance. *Annual Review of Psychology, 66,* 519-545. doi: 10.1146/annurev-psych-113011-143831

Todorov, A., Said, C. P., Engell, A. D., & Oosterhof, N. N. (2008). Understanding evaluation of faces on social dimensions*. Trends in Cognitive Sciences, 12,* 455-460. doi:10.1016/j.tics.2008.10.001

Tomasello, M. (1996). Do apes ape? In C. M. Heyes & B. G. Galef (Eds.), Social learning in animals: The roots of culture (pp. 319–346). New York, NY: Academic Press. doi:10.1016/B978-012273965-1/50016-9

Tottenham, N., Tanaka, J., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., Marcus, D. J., Westerlund, A., Casey, B. J., & Nelson, C. (2009). The NimStim set of facial expressions: Judgments from untrained research participants*. Psychiatry Research, 168,* 242–249. doi: 10.1016/j.psychres.2008.05.006

van Baaren, R., Janssen, L., Chartrand, T. L., & Dijksterhuis, A. (2009). Where is the love? The social aspects of mimicry. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364(1528),* 2381-2389. doi:10.1098/rstb.2009.0057

Van der Elst, W., Van Boxtel, M. P. J., Van Breakelen, G. J. P., Jolles, J. (2006). The Stroop Color-Word Test: Influence of Age, Sex, and Education; and Normative Data for a Large Sample Across the Adult Age Range. *Assessment, 13(1),* 62-79, doi: 10.1177/1073191105283427

Vik, P. W. (2013). *Regression, ANOVA, and the general linear model: A statistics primer.* California: SAGE Publications Inc.

Wager, T. D. & Nichols, T. E. (2003). Optimization of experimental design in fMRI: a general framework using a genetic algorithm. *NeuroImage, 18(2),* 293-309. doi:10.1016/S1053-8119(02)00046-0

Wager, T. D., Sylvester, C.-Y. C., Lacey, S. C., Nee, D. E., Franklin, M., & Jonides, J. (2005). Common and unique components of response inhibition revealed by fMRI. *NeuroImage, 27,* 323-340. doi:10.1016/j.neuroimage.2005.01.054

Wai, M., & Tiliopoulos, N. (2012). The affective and cognitive empathic nature of the dark triad of personality. *Personality and Individual Differences, 52,* 794-799. doi:10.1016/j.paid.2012.01.008

Wang, Y., Hamilton, A. F. de C. (2012). Social top-down response modulation (STORM): a model of the control of mimicry in social interaction. *Frontiers in Human Neuroscience, 6(153),* 1-10. doi:10.3389/fnhum.2012.00153.

Wang, Y., & Hamilton, A. F. de C. (2013). Understanding the role of the 'self' in the social priming of mimicry. *PLoS ONE, 8(4),* e60249, 1-11. doi:10.1371/journal.pone.0060249

Wang, Y., & Hamilton, A. F. de C. (2014a). Anterior medial prefrontal cortex implements social priming of mimicry. *Social Cognitive and Affective Neuroscience, 10(4),* 486e493. doi:10.1093/scan/nsu076

Wang, Y., & Hamilton, A. F. de C. (2014b). Why does gaze enhance mimicry? Placing gaze-mimicry effects in relation to other gaze phenomena*. Quarterly Journal of Experimental Psychology, 67(4),* 747-762. doi:10.1080/17470218.2013.828316

Wang, Y., Newport, R., & Hamilton, A. F. de C. (2011a). Eye contact enhances mimicry of intransitive hand movements. *Biology letters, 7,* 7–10. doi: 10.1098/rsbl.2010.0279

Wang, Y., Ramsey, R., & Hamilton, A. F. de C. (2011b). The control of mimicry by eye contact is mediated by medial prefrontal cortex. *Journal of Neuroscience, 31(33),* 12001e12010. http://dx.doi.org/10.1523/Jneurosci.0845-11.2011.

Wei, P., Szameitat, A. J., Müller, H. J., Schubert, T., & Zhou, X. (2013). The neural correlates of perceptual load induced attentional selection: An fMRI study. *The Journal of Neuroscience, 250,* 372-380. doi: 10.1016/j.neuroscience.2013.07.025

Weigelt, S., Koldewyn, K., & Kanwisher, N. (2012). Face identity recognition in autism spectrum disorders: A review of behavioral studies. *Neuroscience and Biobehavioral Reviews, 36,* 1060–1084. doi:10.1016/j.neubiorev.2011.12.008

Williams, J. H., Whiten, A., & Singh, T. (2004). A systematic review of action imitation in autistic spectrum disorder. *Journal of Autism and Developmental Disorders, 34(3),* 285-299.

Williams, J. H., Whiten, A., Suddendorf, T., & Perrett, D. I. (2001). Imitation, mirror neurons and autism*. Neuroscience and Biobehaviour Review, 25,* 287–295. doi: 10.1016/S0149-7634(01)00014-8

Winston, J.S., Henson, R.N., Fine-Goulden, M.R., & Dolan, R.J. (2004). fMRI adaptation reveals dissociable neural representations of identity and expression in face perception. *Journal of Neurophysiology, 92(3),* 1830–1839. doi: 10.1152/jn.00155.2004

Yarkoni, T. (2014). *Neurobiological substrates of personality: A critical overview.* APA Handbook of Personality and Social Psychology.

Yarkoni, T., Barch, D. M., Gray, J. R., Conturo, T. E., & Braver, T. S. (2009). BOLD correlates of trial-by-trial reaction time variability in gray and white matter: a multi-study fMRI analysis. *PLoS ONE, 4(1),* e4527. doi: 10.1371/journl.pone.0004257

Yovel, G., & Kanwisher, N. (2004). Face perception: Domain specific, not process specific. *Neuron, 44(5),* 889–898.

Zaki, J., Hennigan, K., Weber, J., & Ochsner, K. N. (2010). Social cognitive conflict resolution: Contributions of domain general and domain specific neural systems. *Journal of Neuroscience, 30(25),* 8481–8488. doi:10.1523/JNEUROSCI.0382-10.2010

APPENDIX 1

Mean reaction time for each condition across Experiments 1-4 (Chapter 2)

	Congruent	Incongruent	Congruency Effect
Experiment 1			
RT	500.70 (78.42)	609.36 (96.18)	
Accuracy	98.47 (1.76)	91.05 (4.86)	
Low Agreeable	506.44 (84.65)	610.80 (98.52)	104.36 (56.28)
High Agreeable	495.83 (82.70)	612.82 (93.19)	116.99 (50.08)
Neutral	499.95 (77.18)	604.98 (105.25)	105.03 (52.49)
Experiment 2			
RT	514.36 (75.52)	588.52 (95.86)	
Accuracy	98.19 (1.90)	92.17 (6.44)	
Low Agreeable	506.27 (79.99)	596.12 (107.96)	89.84 (51.00)
High Agreeable	518.41 (90.27)	600.96 (112.65)	82.55 (49.66)
Experiment 1 & 2 combined			
Low Agreeable	506.33 (81.25)	601.60 (104.17)	95.27 (53.16)
High Agreeable	509.98 (87.70)	605.39 (105.38)	95.41 (52.28)
Experiment 3			
RT	489.79 (63.11)	573.57 (74.46)	
Accuracy	98.63 (1.84)	95.03 (3.14)	
Angry	482.14 (66.89)	575.65 (71.26)	93.51 (41.97)
Happy	495.30 (68.31)	580.86 (78.91)	85.55 (44.12)
Neutral	491.87 (60.73)	564.37 (78.90)	72.50 (42.10)
Experiment 4			
RT	492.22 (83.69)	600.48 (125.79)	
Accuracy	99.07 (1.00)	91.27 (6.89)	
Angry	489.13 (82.12)	591.32 (120.80)	102.18 (70.61)
Happy	483.69 (84.37)	606.03 (137.35)	122.35 (78.04)
Neutral	499.12 (98.45)	598.07 (128.56)	98.95 (79.20)
Salient Neutral	496.68 (83.04)	606.73 (128.65)	110.05 (68.60)

Appendix 1. Mean reaction time (RT) and standard deviation (in parentheses) for each condition across Experiments 1-4 in Chapter 2.

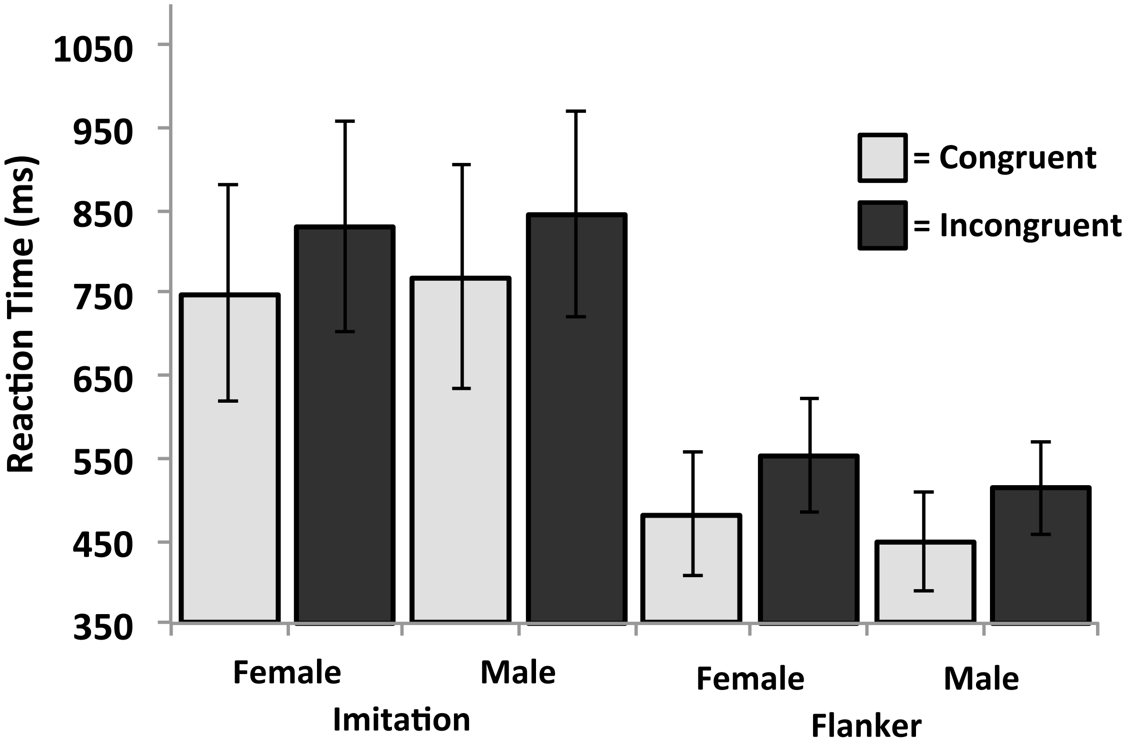
APPENDIX 2

Simple correlations between each predictor and the congruency effect for each multiple regression model (Chapter 3)

		Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
Base model predictors	**Mean RT**	r(230)=.50,p<.001	r(224)=.49,p<.001	r(57)=.73,p<.001	r(57)=.73,p<.001	r(220)=.50,p<.001	r(199)=.48,p<.001
	Sex	r(230)=.29,p<.001	r(224)=.28,p<.001	r(57)=.25,p=.032	r(57)=.25,p=.032	r(220)=.28,p<.001	r(199)=.26,p<.001
	Mean RT * Sex	r(230)=.19,p=.002	r(224)=.21,p=.001	r(57)=.24,p=.034	r(57)=.24,p=.034	r(220)=.19,p=.002	r(199)=.21,p=.002
Personality characteristic predictors	**Extraversion**		r(224)=.06,p=.172				
	Agreeableness		r(224)=.06,p=.201				
	Conscientiousness		r(224)=-.06,p=.195				
	Neuroticism		r(224)=.08,p=.126				
	Intellect/ Imagination		r(224)=.02,p=.396				
	Narcissism			r(57)=-.17,p=.109			
	Empathy				r(57)=.04,p=.382		
Subclinical predictors	**Autism Quotient**					r(220)=.06,p=.186	
	Schizotypy						r(199)=-.16,p=.014

Appendix 2. Model 1 includes the base model factors of mean RT, sex and the interaction between mean RT and sex. These base model factors all correlate with the congruency effect but are not part of our personality-based predictions. In general, these simple correlations are consistent with results from the multiple regression analyses. The only exception is that schizotypy shows a simple correlation with the congruency effect. However, when we control for base model factors in the regression analysis, schizotypy is not predictive of the congruency effect. This suggests that the simple correlation between schizotypy and the congruency effect is driven by one or more of the base model factors.

APPENDIX 3
RT data for Experiment 2 (fMRI scanning) (Chapter 4)



Appendix 3. RT data for Experiment 2 showing a main effect of task (F(1,22)=61.28, p<.001, η_p^2=.736), and a main effect of congruency (F(1,22)=146.09, p<.001, partial eta squared=.869). No other main effect or interaction was significant (all p's >.29). Error bars represent 95% confidence intervals.

APPENDIX 4

Interference effects for imitation and flanker task (Chapter 4)

Region	Cluster Size	P FWE Corr	t-value	Montreal Neurological Institute coordinates		
				x	y	z
A) Imitation interference: Incongruent>Congruent						
L Inferior Parietal Lobule	**1527**	**<0.001**	**8.52**	**-39**	**-40**	**43**
L Postcentral Gyrus			**6.43**	**-36**	**-37**	**70**
L Superior Frontal Gyrus			**6.29**	**-27**	**-7**	**70**
L Cerebellum (VIIII)	**2594**	**<0.001**	**5.83**	**-21**	**-55**	**-41**
R Cerebellum (VIIII)			**5.71**	**21**	**-58**	**-44**
R Cerebellum (Crus 1)			**5.12**	**45**	**-46**	**-32**
L Insula Lobe	62	0.618	4.57	-36	17	-2
L Insula Lobe			3.10	-30	26	1
L Posterior-medial frontal	44	0.844	4.56	0	-7	73
R Paracentral Lobule			3.07	6	-19	76
R Inferior Frontal Gyrus	103	0.232	4.35	42	23	10
R Inferior Frontal Gyrus			3.62	33	26	-5
R Insula Lobe			3.31	36	17	-8
L Posterior-medial frontal	**247**	**0.007**	**4.27**	**-3**	**-1**	**52**
L Posterior-medial frontal			**3.66**	**-6**	**11**	**52**
R Midcingulate Cortex			**3.65**	**9**	**14**	**43**
Thalamus	24	0.987	4.09	0	-25	7
R Pallidum	62	0.618	4.03	21	-7	-2
Thalamus			3.79	18	-7	10
L Inferior Occipital Gyrus	135	0.103	4.02	-48	-73	-17
L Inferior Occipital Gyrus			3.84	-42	-64	-5
L Middle Temporal Gyrus			3.46	-48	-64	1
R Middle Frontal Gyrus	51	0.760	3.89	45	29	31
R Inferior Frontal Gyrus			3.30	51	26	22
R Inferior Occipital Gyrus	14	0.999	3.72	36	-73	4
L Temporal Pole	20	0.995	3.57	-57	8	-5
L Rolandic Operculum			3.37	-60	8	4
Cerebellar Vermis (6)	76	0.454	3.56	0	-70	-17
Cerebellar Vermis (4/5)			3.42	3	-55	-11
L Cerebellum (IV-V)			3.29	-6	-58	-11
L Inferior Frontal Gyrus	12	1.000	3.44	-36	32	16
R Inferior Frontal Gyrus	22	0.992	3.40	48	38	-2
R Inferior Frontal Gyrus			3.15	42	35	7
L Middle Frontal Gyrus	29	0.968	3.24	-39	23	37
L Inferior Frontal Gyrus			3.14	-48	23	31
R Middle Occipital Gyrus	12	1.000	3.13	33	-70	28
B) Flanker interference: Incongruent>Congruent						
L Inferior Occipital Gyrus	**349**	**<0.001**	**6.95**	**-45**	**-79**	**-8**
L Inferior Occipital Gyrus			**5.44**	**-36**	**-85**	**-5**
L Middle Occipital Gyrus			**4.57**	**-30**	**-88**	**7**
R Inferior Occipital Gyrus	**553**	**<0.001**	**6.69**	**42**	**-85**	**-8**

R Middle Occipital Gyrus			**5.42**	**39**	**-85**	**10**
R Middle Occipital Gyrus			**5.15**	**54**	**-76**	**1**
R Precentral Gyrus	**174**	**0.030**	**5.42**	**42**	**5**	**49**
R Superior Frontal Gyrus			**4.04**	**27**	**2**	**52**
R Middle Frontal Gyrus			**4.02**	**24**	**-7**	**46**
R Superior Occipital Gyrus	**716**	**<0.001**	**5.12**	**30**	**-82**	**43**
R Superior Parietal Lobule			**4.87**	**21**	**-64**	**67**
R Cuneus			**4.51**	**21**	**-79**	**46**
L Precentral Gyrus	63	0.576	4.34	-27	-7	55
L Precentral Gyrus			3.37	-36	-4	58
L Superior Frontal Gyrus			3.36	-24	-4	46
L Inferior Parietal Lobule	58	0.644	4.28	-33	-37	40
L Inferior Parietal Lobule			3.43	-36	-43	55
L Inferior Parietal Lobule			3.08	-42	-34	34
L Superior Parietal Lobule	130	0.096	4.13	-21	-61	58
L Middle Occipital Gyrus			3.87	-27	-76	31
L Superior Parietal Lobule			3.63	-15	-70	52
R Precentral Gyrus	52	0.727	3.98	48	5	28
R Precentral Gyrus			3.65	39	2	28
L Precentral Gyrus	44	0.833	3.54	-51	-4	31
L Precentral Gyrus			3.35	-57	2	31
L Postcentral Gyrus			3.09	-57	-4	40
L Superior Frontal Gyrus	12	1.000	3.44	-21	5	61
R Middle Frontal Gyrus	13	1.000	3.34	42	23	43
R Posterior-medial Frontal	11	1.000	3.16	6	17	58

Appendix 4. Regions surviving a voxel-level threshold of p<.005 and 10 voxels are reported for automatic imitation interference **(A)** and for flanker task performance **(B)**. Subclusters at least 8 mm from the main peak are listed. Bold font indicates clusters that survive correction for multiple corrections using a family-wise error (FWE) correction (p < .05).

APPENDIX 5

Sex*Congruency interactions (Chapter 4)

				Montreal Neurological Institute coordinates		
Region	Cluster Size	P FWE Corr	t-value	x	y	z
A) Imitation sex difference: Female(Incongruent>Congruent) > Male(Incongruent>Congruent)						
L Postcentral Gyrus	**394**	**<0.001**	**4.89**	**-21**	**-37**	**70**
L Precentral Gyrus			**4.87**	**-30**	**-19**	**46**
L Postcentral Gyrus			**4.63**	**-24**	**-31**	**52**
L Cerebellum (VIII)	73	0.475	4.29	-24	-55	-38
L Cerebellum (VI)			4.17	-21	-55	-29
L Cerebellum (IV-V)			2.93	-9	-52	-20
R Cerebellum (X)	44	0.839	3.98	24	-40	-41
R Cerebellum (IX)			3.08	15	-46	-38
R Cerebellum (IV-V)			2.90	18	-37	-23
R Superior Frontal Gyrus	26	0.980	3.77	9	-13	55
Cerebellum (VI)	55	0.700	3.61	-9	-67	-29
Cerebellar Vermis (VII)			3.48	3	-70	-29
R Middle Frontal Gyrus	20	0.995	3.57	39	-1	55
R Superior Frontal Gyrus	27	0.976	3.47	24	47	37
R Superior Frontal Gyrus			3.02	15	38	34
B) Flanker sex difference: Female(Incongruent>Congruent) > Male(Incongruent>Congruent)						
No suprathreshold clusters emerge from this contrast						

Appendix 5. Regions surviving a voxel-level threshold of p<.005 and 10 voxels are reported for the automatic imitation sex*congruency interaction **(A)** and for the Flanker task sex*congruency interaction **(B)**. Subclusters at least 8 mm from the main peak are listed. Bold font indicates clusters that survive correction for multiple corrections using a family-wise error (FWE) correction (p < .05).